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SITUATIONAL CONDITIONED REFLEXES IN DOGS IN NORMAL AND PATHOLOGICAL STATES

by

P. S. Kupalov, O. N. Voyevodina et al.

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ABSTRACT : This monograph presents the results of many years of research on regularities in animal behavior by the conditioned-reflex method. A great deal of attention is paid to complex conditioned motor reflexes induced in response to auditory and visual stimuli, taking into account their spatial localization and the spatial position of the animal itself.

Use of various drugs, extirpation and transection at different cerebral levels, and X-irradiation enabled the authors to elucidate both the dynamics and structure of the forms of motor activity they studied. These data are of both theoretical and practical importance.

This monograph will be of interest to physiologists, neuropathologists, psychologists, psychiatrists, pharmacists, and radiobiologists. English translation: 282 pages.

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INTRODUCTION

Animal movements, which are effected by the skeletal muscles in diverse combinations and sequences, as well as animal behavior as a whole, are the result of the activity of the higher elements of the brain. This motor activity is accessible to direct observation and it would seem that the study of cerebral physiology should be in a favorable position with respect to other branches of physiology that deal with the functional trends of various deeply hidden internal organs. However, from its very outset, physiology has been concerned with studying the internal activity of the body, which is still one of the principal areas of physiological research. Manifest activity and its neural mechanisms came under physiological scrutiny substantially later. As I.P. Pavlov emphasized, this was due primarily to the tendency to approach the study of so-called voluntary motor activity and to interpret behavior from the standpoint of suggestive psychology.

Russian physiology, which was founded by I.M. Sechenov and I.P. Pavlov, immediately attacked these problems from a strictly materialistic viewpoint. We believe that, through its structure and neural functions, the brain analyzes and synthesizes external activity, governs the motor activity of the body, and is the highest organ of animal behavior. Hence, there is a direct need to study the purely physiological aspect of this activity and to determine the mechanisms of the most complicated neural processes, utilizing both the various specific indices of neural functioning and the external manifestations of complex normal behavior.

Motor reactions play an exceptionally large role in the adaptation of animals to their environment. In order to cope successfully with the struggle for existence, i.e., to survive, an animal must exhibit a definite motor activity, which is necessary, for example, in seeking food, procuring shelter, avoiding enemies, and propagating the species. This activity is executed in the form of the most diverse motor reactions.

The motor activity of many animals (monkeys, birds, etc.) had previously been studied, principally by zoopsychologists and naturalists, but they did not generally explain it from the standpoint of reflex theory, permitting anthropomorphic and idealistic interpretations.

Research on canine behavior by the conditioned-reflex method began in the nineteen-thirties. It included the work of K.S. Abuladze (1927), who described an original method and the results of its use to study conditioned motor reflexes in a free-movement setup. An enormous amount of data on this problem has now been amassed

(I. Beritov, 1932, 1934, 1947, 1961, etc.; I. Beritov, N. Beburishvili, and M. Tsereteli, 1934; I. Beritov and M. Tsereteli, 1934; I. Beritov, M. Tsereteli, and N. Akhmeteli, 1934; V.Ya. Kryazhev, 1932; S.A. Karitonov, 1932; M.P. Shtodin, 1947; A.Ye. Khil'chenko, 1950; R. Floru and M. Steresku-Volanskaya, 1957; E.Sh. Ayrapet'yants, 1959, 1961; A. Krayndler, Yu. Unger, and D. Volanskiy, 1959; N.A. Shustin, 1959; B.Kh. Gurevich, 1961; L.V. Lobanova and Ye.Ye. Nikulina, 1961; L.S. Gambaryan, 1962, and many others).

In the Soviet Union, the most systematic study of the motor activity of free-moving dogs has been made by Academician I.S. Beritov.

The work of Beritov and many other researchers is characterized by the fact that the animal is kept under conditions where its activity is strictly regulated by specially selected conditioned and unconditioned stimuli; during induction of a conditioned reflex, the experimenter often intervenes directly in the course of the experiment, forcing the animal to execute definite motor acts. Strict regulation of the animal's behavior naturally makes it possible to obtain more uniform experimental data and facilitates their generalization. When using this research technique, however, the motor activity characteristic of the animal's behavior under natural conditions is to a considerable extent artificially suppressed. For more extensive and thorough study of canine motor activity it was important to develop a method with which the animal would be in a situation that approximated natural circumstances. For this purpose it was necessary to isolate the experimenter from the animal, to give it complete freedom of movement, and to avoid interfering with its behavior in any way other than employing the usual laboratory factors as unconditioned (alimentary) and conditioned stimuli, but without any physical compulsion. It was also important that this new method not differ radically from the research techniques used in I.P. Pavlov's laboratory. Development of such a method was undertaken in 1942 by P.S. Kupalov.

One of the advantages of the new technique lies in the fact that it has made it possible to study complex motor activity whose primary and most important component is the type of active movement generally referred to as voluntary. Such movements include licking an electric bulb, tapping a paw with dynamic gradation, occupying a definite place in the experimental room, etc. The dog makes these movements independently, without any compulsion on the part of the experimenter, and, as numerous data have shown, they not only have known characteristics, but also impart a special character to the entire pattern of induced behavior. One of the features of active reaction and induced behavior is their dependence on the specific experimental situation.* In this connection, P.S. Kupalov referred to such conditioned motor reactions as "conditioned situational reflexes" and to the method by which they are induced as the "situational conditioned-reflex method."

The difference between the situational conditioned-reflex method and other motor methods (I.S. Beritashvili, 1934, 1947; L.G. Voronin, 1947, 1952; V.P. Protopopov, 1930, 1950; G.V. Skipin, 1951, and others) lies in the fact that the animal has its liberty: it can move as it wishes, go to any place in the room, etc. A definite behavior pattern is created by making experimental use of two specific factors - an unconditioned alimentary stimulus (meat or cereal) and the usual conditioned stimulus (e.g., the beat of a metronome, the light of a bulb, etc.). This is important, since when several unconditioned stimuli are employed, strict physiological analysis of the data becomes extremely difficult and often impossible, as is known from the body of prior work on the physiology of higher nervous activity. In animal training, for example, an unconditioned alimentary stimulus is always supplemented by a command, physical compulsion (forcibly keeping the animal in a certain place, putting it in some desired pose, etc.), a fright, etc. The trainer himself is also a complex and a highly effective agent.

The situational conditioned-reflex method excludes any training for any direct action on the animal on the part of the experimenter. As in the sancretory conditioned-reflex method, the latter does not come into direct contact with the animal during the experiment.

Finally, an important aspect of this method is the gradually increasing complexity of the behavior pattern, which makes it possible both to analyze and study each behavioral element and to observe how a complicated pattern is built up from simpler individual acts. This enables the researcher to draw positive conclusions regarding the nervous processes on which the observed motor activity is based.

The situational conditioned-reflex method has been widely used for many years in the Physiology Department imeni I.P. Pavlov of the Institute of Experimental Medicine, Academy of Medical Sciences USSR (IEM AMN SSSR)and is now being employed in other physiology laboratories, such as those Prof. Krayndler, Dr. Floru and others in Roumania.

The situational conditioned-reflex method has enabled the workers of the Physiology Department imeni I.P. Pavlov to collect a large amount of original experimental data.

The book here presented for the reader's attention is the first attempt of an overall generalization of this material.

Since the situational conditioned-reflex method and the different variants in which it is employed have never been given detailed consideration in print, they are paid special attention in this monograph. We also extensively discuss such topics as the features of the induction, reinforcement, alteration, and extinction of situational reflexes, the specific and general characteristics of voluntary and involuntary reactions, and the influence of various factors (drugs, X-rays, extirpation of the cerebral vortex, etc.) on canine.

The authors of this monograph have used both their own experimental data and those of P.S. Kupalov's coworkers (I.A. Alekseev, V.K. Fedorov, V.V. Yakovleva, and others), who have conducted investigations by the situational conditioned-reflex method.

We know that our first attempt at the overall generalization of data gathered over a long period of time is not free of deficiencies and we are therefore quite prepared to gratefully receive friendly criticism.

Manu-script Page No.	FOOTNOTE
2	The term "situation" derives from the Latin word "situs," which means "position" or "location." One of the modern meanings of this term is the aggregate of the circumstances or conditions that create a given relationship, setting, or state.

Chapter 1
FORMATION OF CONDITIONED SITUATIONAL REFLEXES

METHOD

The investigations described in this monograph were conducted with dogs in a large, specially equipped room 7.5 × 5 m in area. It contained two tables bearing standard mechanical feeders (Fig. 1 and 2) and various devices for applying conditioned stimuli. The feeders were not rigidly fastened to the tables, so that they could easily be placed on the floor if necessary. In a number of investigations we used an electric feeder, in which the pan-bearing disc was rotated by a Selsyn motor. Operation of this feeder was less noisy than that of the mechanical feeder.

The tables differed little from one another in appearance and had the following dimensions: table No. 1 - 250 cm long, 100 cm wide, and 75 cm high; table No. 2 - 215 cm long, 85 cm wide, and 75 cm high. In order to make it easier for the dog to jump onto the table, a bench was placed in front of table 1 and a movable stairstep in front of table 2 (Fig. 2).

Three rows of light bulbs in small frosted-glass globes were mounted on the ceiling, while jupiter lights were fastened along the wall. This made it possible to vary the illumination of both the entire room and individual areas over a wide range, which is especially important in taking still and motion pictures. The windows of the room were draped with heavy black cloth so as to exclude the action of such difficult-to-evaluate stimuli as variations in the natural illumination.

During the experiment the investigator stayed in a special closet abutting directly on one wall of the room, in which was a glass window (4, Fig. 1) 200 × 70 cm in size, through which the animal was observed. The window could be completely covered with an opaque shade and observations were then made through a small hole in the latter. The carpet had a floor 1 m higher than that of the room; it contained a control panel, a switchboard (for the illuminating devices), rubber bulbs (connected pneumatically to the mechanical feeders and the stimulus-application devices), electric metronomes, a tone generator (ZG-10), a kymograph, and a table and chair for the experimenter.

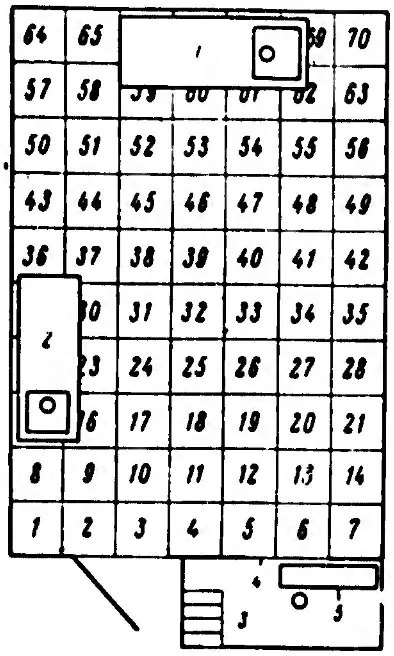

Fig. 1. Diagram of experimental room. 1) Table 1; 2) table 2; 3) experimenter's closet; 4) observation window; 5) experimenter's table.

The conditioned signals were various auditory and visual stimuli: a bell, a buzzer, a metronome, tones of different frequencies and loudnesses, a gurgling noise, light (continuous, flashing, and reflected), the sight of geometric figures (circles, squares, and crosses), etc. The devices for applying the conditioned stimuli were placed in a definite area of the room, but their location could be varied in accordance with the purpose of the investigation. The isolated action of each conditioned stimulus generally lasted 3-5 sec. The interval between the conditioned stimuli ranged from 30 sec to 1-2 min. We employed 8-15 conditioned stimuli in each experiment.

In inducing conditioned reflexes, the reinforcement was powdered meat biscuits moistened with milk or water (1:1), pieces of meat, or a mixture of the two. A single portion of the powdered biscuits was 15-20 g, while a single portion of meat was 10-20 g. A dish of water was always kept on the floor of the experimental room.

The animal was observed during the experiment and the results were recorded in a notebook. The position of the experimental dog at any moment and thus the path of his movement could be precisely determined as a result of the fact that the floor of the room was divided into 70 squares (Fig. 1). In the individual experiment the animal's movement was depicted in the form of a continuous line on a previously prepared diagram of the experimental room. When necessary, the kymograph was used to record the time for which the dog remained at individual points in the room, the latent period of its motor reactions, and its reaction rate. For this purpose, linoleum mats fitted with contact plates, which were connected in series with an electric timer and a DC current source, were placed beneath the rug in front of the feeders and at certain other points in the room.

We made extensive use of still and motion-picture photography to document the experiment.

The investigation generally began by inducing the dog to go from the door of the experimental room to one of the feeders. At the start of the experiment the path from the door to the feeder was strewn with pieces of meat. The dog entered the room, picked up the pieces of meat, and thus reached the feeder, the open pan of which also contained meat. A "meat trail" was laid 3-5 times during the experimental day. On following days the distance between the individual pieces of meat was increased each time, until finally the meat was placed only in the open feeder tray. Then the dog, on entering the room, went immediately from the door to the feeder and ate his first portion of food.

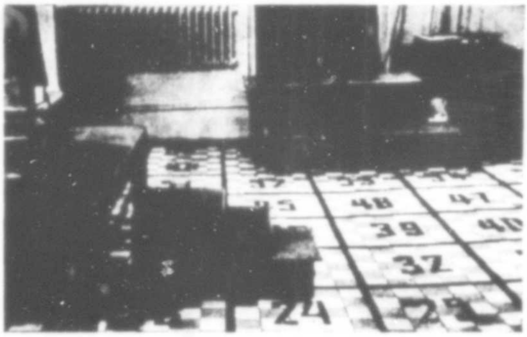

Fig. 2. Stairstep and bench arranged near tables bearing feeders.

Fixation of the reflex entailing movement from the door to the feeder was followed by induction of a conditioned reflex to the noise accompanying the shifting of the pan when the feeder was switched on. As soon as the animal ate the first portion of meat in the feeder a second was supplied, then a third, etc. After the noise of the feeder became a positive stimulus, the pan was shifted only when the animal was some distance from the feeder.

After fixation of the reflex to the sound of the feeder we began induction of a conditioned reflex to one of the usual artificial stimuli, such as the light of an electric bulb, the sound of a bell, etc. Each conditioned stimulus was first tested for indifference and then conjoined with the noise of the feeder and alimentary reinforcement.

Fixation of the conditioned reflex to some artificial stimulus was followed by induction of a reflex to occupation by the dog of a definite place in the experimental room. A mat was generally placed at the point in question. The conditioned stimulus was then applied only when the animal passed over the mat or stopped on it.

As soon as the reflex involving standing in a definite place was fixed we began to induce positive and negative reflexes to new stimuli.

Thus, on completing this part of the investigation, the first component of the animal's induced conditioned-reflex activity was always to go from the door to the feeder, the second was to stand on the mat, and the third was to go to the feeder table on the first distant (visual or auditory) conditioned stimulus. The animal stopped moving toward the feeder when the inhibitory conditioned stimulus was applied.

We have described above the system most frequently employed in our laboratory for formation of conditioned situational reflexes. In individual experiments the reflexes were induced in a somewhat different order.

Thus, the meat trail was sometimes laid only once, but the 2nd, 3rd, 4th, etc. portions of food were supplied as soon as the first portion was eaten from the feeder pan.

The conditioned reflex to a definite position in the room was occasionally developed immediately after formation of the conditioned reflex to the noise of the feeder.

In some investigations the conditioned reflex to the noise of the feeder was not developed separately; in these experiments the sound of the feeder was conjoined with one of the usual conditioned stimuli, such as the sound of a metronome, etc.

When necessary we induced a new system of reflexes involving reinforcement of conditioned stimuli from the feeder on the other table. The procedures for developing these reflexes were the same as those described above.

In a special series of experiments the formation of conditioned motor reflexes was based on fright.

As was mentioned above, the animal's behavior during each experiment was fully recorded, special attention being paid to the following indices of the conditioned-reflex reactions: the time for which the animal remained in a definite place in the experimental room (on a mat near a conditioned stimulus, etc.), the latent period of the motor reaction, the time required to reach the feeder, the time consumed in eating, and the time required for the animal to return to its original position. The dog's general behavior during the intervals between applications of the conditioned stimulus was also noted in detail. The experiment was generally conducted at the same time of day.

The experimental animals received one daily ration of food at a definite time, usually after the experiments were finished; they were all periodically weighed and kept under the observation of a veterinarian.

Our investigations were conducted more than 100 dogs.

FORMATION OF CONDITIONED SITUATIONAL REFLEXES TO AUDITORY AND VISUAL STIMULI

As was pointed out above, the formation of conditioned situational reflexes involved several stages; we will now consider each of them in more detail.

In the first experiment, when inducing the animal to move from the door to the feeder, all animals exhibit a distinct orientation reaction to the experimental setup as the result of their innate exploratory reflex. On entering the room, the dog begins to walk or run randomly about it, inspecting and sniffing the floor and the objects on it and occasionally jumping up onto the tables. Finding the pieces of meat arranged on the floor in a straight line from the door to the feeder (the meat trail), he eats them. In the first experiment the animal makes many additional random movements about the room near the trail before he has picked up all the pieces of meat.

The number of additional movements gradually becomes smaller and the dog finally goes from the door to the feeder without straying from the meat trail, something which the majority of animals accomplish on the first experimental day if the trail is laid several times. From the 2nd or 3rd experimental day onward the distance between the individual pieces of meat is increased each time and finally the meat is placed only in the open feeder pan.

The positive reaction to the sight of the feeder becomes stable in most animals after 3-5 days: when the dog enters the room he immediately goes from the door to the table bearing the feeder and eats the first portion of food. At this time a conditioned association is formed and stably fixed with both a definite location in the room and with the experimental setup as a whole. This is manifested in the fact that some animals will run from the vivarium where they are usually kept to the experimental room without an attendant.

The conditioned reflex to the noise of the feeder is formed in the following manner. The majority of animals react to the first noise made by the feeder when the pan is shifted with a simple orientation reaction and, when they see the meat in the new pan, first examine it and then quietly begin to eat it, but others carefully take the meat from the pan in their teeth, move away from the feeder, and only then eat; some animals exhibit a passive defense reaction, moving away from the feeder or jumping to the floor and trying to get as far as possible from the table, although after a time they again jump onto the table and eat the food. After 5-10 days all animals usually eat quietly from the other pans. Beginning with the 5th-11th day most animals, no matter where in the room at the time, immediately run to the table bearing the food-containing pan when they hear the sound of the feeder, i.e., the noise of the feeder acquires a signal value at this time.

In producing the conditoned reflex to the first artificial (visual or auditory) conditioned stimulus, each stimulus is first tested for indifference. Its first application generally evokes a pronounced orientation reaction: the dog usually turns his head toward the stimulus and looks at it, although he sometimes approaches it. In the latter case, if the stimulus is located on the floor, some animals will sniff it, paw it, or lick it. In rare cases, the animals runs to the feeder on the first application of the stimulus. The stimulus is regarded as indifferent if the dog does not go to the feeder table when it is applied. After being tested for indifference, the stimulus is conjoined with the noise of the feeder (to which a motor reflex involving going to the table has already been developed).

The dog at first runs to the feeder only when he hears its noise, but, after several applications of the conditioned stimulus in conjunction with the sound of the feeder and reinforcement with food, the animal goes to the feeder when the conditioned stimulus around is applied. The conditioned motor reflex is regarded as stable when the dog runs to the table bearing the feeder as soon as he perceives the conditioned stimulus. The rate of formation of the first conditioned motor reflex to distant stimuli differs from animal to animal (Table 1) and varies within wide limits, depending on the physical strength of the conditioned stimulus, the individual characteristics of the animal's nervous system, and a number of other

TABLE 1

Induction of Positive Motor Conditioned Reflexes Involving Going to One Table (from a A.T. Selivanova's Data)

1 Кличка животного	Скорость образования условного рефлекса на: 2			
	3 звонок I	4 коврик II	М-120 III	5 свет IV
6 Джек	14	35	9	2
7 Дозор	10	24	9	2
8 Тобик	8	23	5	1
9 Рекс	12	27	12	2
10 Рыжий	9	20	5	3
11 Жан	48	23	3	4
12 Тарзан	7	21	5	2
13 Джим	18	30	9	7
14 Пискля	28	81	8	5
15 Барон	15	48	5	2

Note: The Roman numerals indicate the sequence in which the conditioned reflexes were developed, while the Arabic numerals indicate the number of applications.

1) Dog's name; 2) rate of formation of conditioned reflex to; 3) bell; 4) mat; 5) light; 6) Dzhek; 7) Dozor; 8) Tobik; 9) Reks; 10) Ryzhiy; 11) Zhan; 12) Tarzan; 13) Dzhim; 14) Pisklya; 15) Baron.

TABLE 2

Average Rate of Formation of Conditioned Motor Reflexes to Different Stimuli (from M.M. Khananashvili's Data)

1 Условные раздражители	2 С какого сочетания рефлекс	
	3 появился	4 упрочился
5 Звонок (сильный)	2—10	5—15
6 Тон 600 *гц* (средней силы)	8—20	18—25
7 Свет 55 *вт*	20—30	35—60
8 Свет 150 *вт*	10—20	25—40
9 Движущаяся фигура (круг)	10—20	35—40

1) Conditioned stimuli; 2) with which application reflex; 3) appeared; 4) became stable; 5) bell (loud); 6) 600 HZ tone (moderately loud); 7) 55-watt bulb; 8) 150-watt bulb; 9) moving figure (circle).

factors, which we will consider in detail somewhat later. Here we need only note that the rate of formation of the first conditioned reflex generally ranges from 5-25 applications for auditory stimuli, from 25-60 applications for visual stimuli using light, and from 35-40 applications for visual stimuli using objects (Table 2).

During the intervals between the conditioned stimuli the animals move about the room, sometimes stopping on certain squares, but they generally remain near the table bearing the feeder or near the conditioned stimuli.

The conditioned reflex to the animal's position in the experimental room during the interval between applications of the conditioned stimuli is formed in the following manner. The conditioned stimulus is at first applied only when the animal accidentally passes over or stops on a definite square; after several applications of the conditioned stimulus when the animal is on this square, he begins to take up a position on it more and more frequently. The conditioned reflex to this location develops more rapidly if a mat is placed on this area of the floor.

As has already been noted over the first 1-1½ weeks following induction of the conditioned reflex, the dog having jumped from the table to the floor after finishing his food, makes many random movements about the room (Fig. 3), sometimes standing for a few seconds on the mat but then leaving it again, walking or running about, and often jumping on the table and approaching the feeder. The trip to the table between signals gradually becomes fewer and fewer and finally cease altogether. The time required for intersignal trips to the table to disappear differs in different animals (Fig. 4). When the positional reflex is stable, the animal goes to the mat immediately after he finishes eating, steps on it, and adopts a definite pose (standing, sitting, or lying), usually with his head and trunk facing the table on which the reinforcement is given for the location of the conditioned stimulus. A definite place in the room is thus made a positive conditioned agent and the animal actively an independently goes to it, assumes a definite (Fig. 5), and remains there until the next positive conditioned stimulus is applied.

Formation of the subsequent (2nd, 3rd, 4th, etc.) conditioned reflexes with reinforcement at the same table is carried out in the same manner as induction of the first conditioned reflex. These reflexes usually develop more rapidly than the first one (see Table 1).

The latent periods of conditioned reflexes to auditory stimuli are generally somewhat shorter than those of reflexes to visual stimuli, while the rate of motor reactions to auditory stimuli is higher than that of reactions to visual stimuli. As training progresses, however, the formation rate of the reflexes (see Table 1), their latent periods (Fig. 6), and the rate of the actual motor reactions may be uniform in response to conditioned stimuli of differing physical strength (P.S. Kupalov and V.P. Pravosudov, 1959; N.S. Popov, 1960, et al.). The latent periods of conditioned reflexes in which the animal has been trained for a long time are usually 0.1-1.0 sec; The time required to move from the mat to the feeder ranges from 2-5 sec, depending on the individual characteristics of the animal's higher nervous activity, the rate of his motor reactions, and the

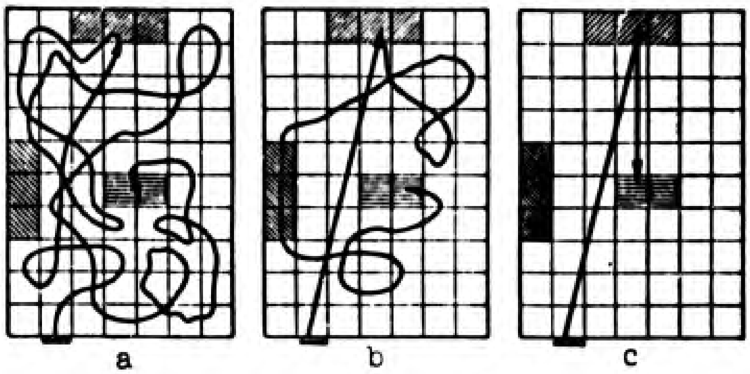

Fig. 3. Schematic diagram of movement of dog Sharik about experimental room from moment of entering to moment of reaching mat on different experimental days.
a) Experiment No. 3 reached mat after 4 min 19 sec; b) experiment No. 10, reached mat after 2 min 12 sec; c) experiment No. 32, reached mat after 45 sec. The oblique lines represent the tables and the horizontal lines the mat.

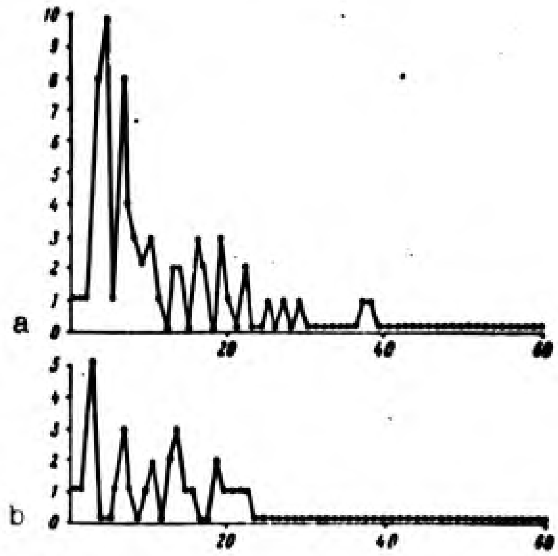

Fig. 4. Rate of disappearance of trips to feeder table between signals in dogs Dzhek (a) and Una (b). The number of experiments is shown along the abscissa and the number of trips during each experiment along the ordinate.

distance between the mat and the feeder. The eating time is 5-30 sec, depending on the amount and type of reinforcement and the animal's alimentary excitability.

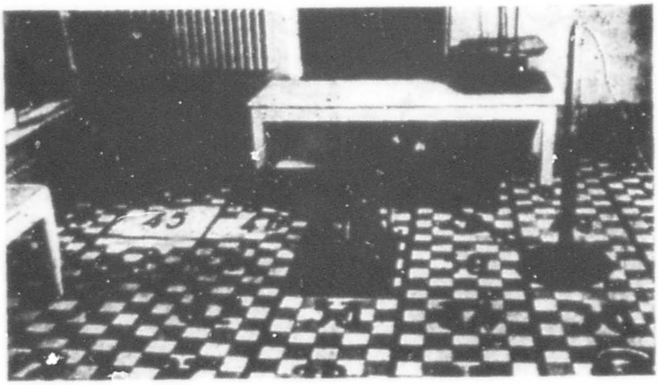

Fig. 5. Position and pose of dog Akkord in experimental room during intervals between applications of conditioned stimuli.

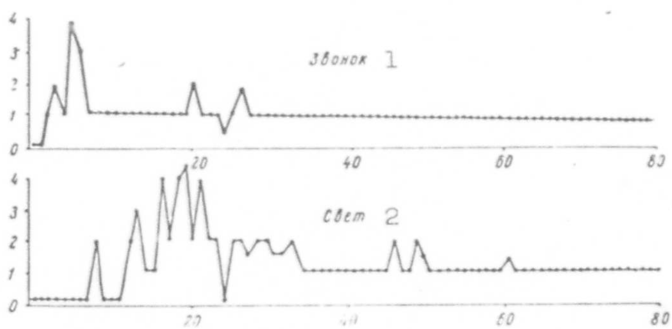

Fig. 6. Change in latent periods of conditioned motor reflexes in dog Una as reflexes became stable. The number of applications of the conditioned stimulus is shown along the abscissa and the latent period of the conditioned reflex in seconds is shown along the ordinate. 1) bell; 2) light.

The formation of conditioned reflexes involving going to both tables is a special case of stimulus differentiation, which we will consider in greater detail below. Here we need note only the following.

We developed differentiation of positive conditioned reflexes reinforced at different tables in two ways.

1st Variant. Conditioned reflexes reinforced at one table are induced first and only after they become stable are conditioned reflexes developed to new, differentiable stimuli reinforced at the other table.

The conditioned motor reflex involving going to feeder 2 is induced in the same manner as the first reflex, i.e., a meat trail is laid and a conditioned reflex is then developed to the noise of the feeder. The first conditioned motor reflex entailing going to the second feeder appears (after 4-10 applications of the conjoint stimuli) and is fixed more rapidly than the reflex using the first feeder. The induction period covers 3-8 experiments. When reflexes involving going to the second feeder have been developed, the conditioned stimuli used in forming the reflex entailing going to feeder 1 are temporarily no longer employed. When the conditioned reflexes using feeder 2 have become stable, application of the conditioned stimuli reinforced at feeder 1 is resumed.

When both feeders are used there is at first a disruption of their differentiation, i.e., the conditioned signals in response to which the animal previously went to feeder 1 now caused him to go to feeder 2 and vice versa. At the same time, the inhibition of inhibitory differentiated reflexes (if these have been induced) is observed over a period of several days and in some cases the animal does not stand precisely on the mat. The inhibitory differentiation is soon restored and the animal takes its precise position on the mat, while the disruption of feeder differentiation lasts longer.

2nd Variant. Stimulus differentiation is induced by simultaneous, i.e., parallel, formation of conditioned reflexes involving going to both tables (feeders).

Meat trails are first laid to both tables and reflexes are developed to the noise of the feeders. Induction of two conditioned reflexes to different distant (auditory or visual) stimuli reinforced at different tables is then begun on the same experimental day. When we compared the results of experiments in which differentiation of the stimuli associated with different feeders occurred during simultaneous induction of conditioned reflexes with those of experiments in which the reflexes were developed sequentially, i.e., in which the second reflex was induced after the first had become stable, it was found that the stimulus-differentiation reflexes were formed substantially in the latter case than in the former. It was also found that the animal's preliminary position in the room, his pose (the direction in which his head and trunk faced), and the location of the stimuli were significant for proper movement to the correct table after application of a conditioned stimulus (P.S. Kupalov, 1946; V.V. Yakovleva, 1947, 1949; L.K. Gordeladze, 1953; N.I. Kudryashova, 1955, 1958; M.M. Khananashvili, 1956; P.S. Kupalov and M.M. Khananashvili, 1958, 1960; V.I. Syrenskiy, 1961, 1962; et al).

MANIFESTATION OF THE "FORCE LAW"

The first works on the conditioned-reflex activity of animals called attention to the fact that such reflexes depend on the physical strength of the conditioned stimuli applied (G.P. Zeleniy, 1907, L.A. Orbeli, 1908; P.S. Kupalov and V.Kh. Gent, 1928; V.V. Rikman, 1928; L.O. Zevald, 1933; V.K. Fedorov, 1938; L.A. Andreyev, 1938; V.K. Krasusskiy, 1949, 1954; et al.). These investigations, which were conducted by the sancretory method, established that there is

Record of Experiment on 27/XI 1953, Dog Lis

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Время побежки от коврика до стола с кормушкой (сек)	6 Время еды (сек)	7 Время стояния на столе после еды (сек)	8 Время возвращения на коврик (сек)	9 Время стояния на коврике (сек)
114	M·120	10	4	3	20	0	10	15
115	M-120	10	2	3	15	0	15	15
116	M-120	10	2	3	20	0	10	15
117	M-120	10	2	3	15	0	3	15
118	M-120	10	2	3	25	0	2	15
119	M·120	10	2	3	20	0	3	15
120	M-120	10	2	4	20	0	5	15
121	M-120	10	2	4	15	0	3	15
122	M·120	10	2	5	20	0	3	15
123	M·120	10	2	5	25	0	3	15
124	M·120	10	2	3	20	0	3	—

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) time required for going from mat to feeder table (sec); 6) eating time (sec); 7) time for which animal remained at table after eating (sec); 8) time required for returning to mat (sec); 9) time for which animal remained on mat (sec).

a direct relationship between the magnitude of a conditioned alimentary reflex and the physical strength of the conditioned stimuli. This gave I.P. Pavlov grounds for formulating the "force law."

In 1952 V.M. Kasyanov and A.L. Fruktov investigated the influence of the force of the conditioned stimulus on the rate of motor acts in athletes. They established that the latent period of excitation and the time required to run a standard distance are shorter when the stimulus is physically strong than when it is weak.

P.S. Kupalov and V.P. Pravosudov (1959) set themselves the task of determining how the physical strength of the conditioned stimulus affects motor conditioned-reflex activity induced in animals by the situational conditioned-reflex method.

They first induced a conditioned reflex to the sound of the feeder in the dog Lis and trained him to remain on a mat placed on square 18. They then developed a conditioned reflex to a metronome with a frequency of 120 beats per minute and to a "soft noise." The conditioned stimuli were placed on a shelf on the wall to the right and in front of the mat (above squares 42 and 49). The physical strength of the 120 bpm metronome was 65 db, while that of the noise was 55 db. Each experiment involved from 10 to 12 applications of the conditioned stimulus accompanied by reinforcement at table No. 1. The distance between the mat and the feeder table was 4.5-5 m. When the conditioned reflex to the metronome had become stable, the latent period of the motor reaction was generally 2 sec, the time required to reach the feeder table was 3-5 sec, and the eating time was 15-20 sec. After eating, the dog immediately returned to the mat and remained on it until the metronome was switched on (see record of experiment on 27/XI 1953).

The conditioned reflex to the noise appeared on the 17th application of the stimulus. The latent period and the time required to reach the feeder table were at first longer under the action of the noise than under the action of the metronome. These intervals in the reaction to the noise gradually became shorter in subsequent experiments. Beginning with the 175th application of the noise, the conditioned reflexes to this stimulus and to the metronome were identical.

When these condtioned reflexes were fixed the motor activity of the dog Lis was made more complex in the following manner. A barrier (a taut net) was placed at a distance of 1.5-2 m from the mat; the dog had to jump over this barrier in going to the feeder table and returning to the mat. The barrier height was at first set at 40 cm. At this height it caused no changes in the dog's conditioned-reflex activity and the animal readily jumped over it.

In subsequent experiments the barrier height was raised by 5 cm after every 3rd or 4th experiment. As the barrier was made higher (raised from 45 cm to 60 cm) there was an increase in the time required to reach the feeder table and to return to the mat after eating (see the record of the experiment on 15/VI 1954).

Record of Experiment on 15/VI 1954. Barrier Raised to Height of 60 cm

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Время побежки от коврика до стола с кормушкой (сек)	6 Время еды (сек)	7 Время стояния на столе после еды (сек)	8 Время возвращения на коврик (сек)	9 Время стояния на коврике (сек)	10 Примечание
486	11 М-120	8	0,5	3	18	2	10	65	12 После еды ходит по комнате, мочится, пьет воду и только затем прыгает через барьер и бежит на коврик
466	Шум	8	0,5	4	20	2	28	67	
467	»	8	0,5	4	20	3	57	65	
487	М-120	7	0,5	3	20	1	7	60	
468	Шум	10	0,5	5	16	1	35	60	
488	М-120	8	0,5	4	15	1	90	60	
469	Шум	15	0,5	10	15	1	58	60	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) time required to go from mat to feeder table (sec); 6) eating time (sec); 7) time spent at table after eating (sec); 8) time required to return to mat (sec); 9) time for which animal remained on mat (sec); 10) note; 11) noise; 12) after eating, the dog walked about the room, urinated, drank water, and only then jumped over the barrier and returned to the mat.

The following phenomenon was observed in this case. While the dog had previously jumped down from the table immediately after eating and returned to the mat, readily leaping the barrier, now he often remained in front of the barrier, walked about the room, urinated, drank water, jumped back on the table, and faced the barrier; only after 5-10 min did he again jump down from the table and finally cross the barrier. In other words, after unsuccessful attempts to leap the barrier, the dog developed his own general motor stereotype for this purpose.

When the barrier height was first raised to 65 cm at the end of the experimental day, the dog approached the barrier in response to the condtioned stimulus (noise) but could not cross it; on the other hand, he readily jumped over it in response to a stronger auditory stimulus (the metronome). The dog's behavior was simultaneously somewhat altered: he became restless and began to pant. Further research was conducted on this dog after a 2-month interval; the experiments were resumed with a barrier height of 50 cm. The dog readily crossed the barrier both under the action of the conditioned stimuli and after eating. When the barrier height was raised to 65 cm the motor reaction again began to exhibit a dependence on the strength of the conditioned stimuli, i.e., the dog continued to jump over the barrier in response to a strong stimulus (the metronome), but he could not leap it in response to a weaker stimulus (the noise).

However, after 4 days of work with the barrier at a height of 65 cm, the animal began to cross it in response to the noise as well, i.e., as training progressed the dependence of the conditioned motor reactions on the physical strength of the stimulus disappeared.

When the height of the barrier was further raised to 85 cm we observed the following phenomenom: while at the beginning of the experiment, even before the conditioned auditory stimuli were applied, the dog usually leapt the barrier at once and went to the feeder, now he entered the room and began to run along the barrier, often whimpering and urinating and only then jumped over it. When the height of the barrier to 90 cm, the dog stopped crossing it at the very beginning of the experiment, jumping over only under the action of the conditioned auditory stimuli. He was unable to leap the barrier at this height after eating, i.e., in returning to the mat. Symptoms of disruption of higher nervous activity appeared at the same time: the dog became very excited and whimpered. In order to keep these disruptions from becoming more severe in subsequent experiments one edge of the net was raised and the dog was able to return to his initial position after eating without jumping the barrier.

Our results thus indicate "force law" for conditioned-reflex activity also extends to conditions where the animal can move freely. For example, the significance of the physical strength of the conditioned stimuli is clearly manifested when the barrier is raised to a height at which the dog freely crosses it under the action of a stronger conditioned auditory stimulus (the metronome) but cannot do so under the action of a weaker conditioned stimulus (the noise) for when the animal readily crosses the barrier under the action of conditioned stimuli but cannot do so when they are not applied (at the beginning of the experiment), etc.

This same dog was used to investigate the influence of variations in alimentary excitability on the manifestation of the "force law." The animal's alimentary excitability was varied by feeding it before the experiment began or by replacing the meat-sugar powder in the feeders with pure meat. In those cases where his alimentary excitability was varied by feeding him beforehand, two experiments were conducted each day, in the morning and the evening. The evening experiment was carried out immediately after the animal received half his daily portion of food. By way of example, let us consider one such investigation on the dog Lis (13/IX 1954). The barrier height was 67.5 cm. In the morning experiment (11:50 AM) the dog freely crossed the barrier in response to the conditioned stimuli and quickly returned to the mat after eating. The second experiment was carried out at 3:50 PM and the dog was preliminarily fed. At the beginning of the experiment there was an increase in the time required for the dog to go the feeder in response to a weak conditioned stimulus (the noise), while later he was completely unable to jump the barrier when this stimulus was applied. At the same time, he freely crossed the barrier in response to a strong auditory stimulus (the metronome; see the record of the experiment on 13/IX 1954).

3:50 PM. Record of Experiment on 13/IX 1954.
Barrier Height 67.5 cm.

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Время побежки от коврика до стола с кормушкой (сек)	6 Время еды (сек)	7 Время стояния на столе после еды (сек)	8 Время возвращения на коврик (сек)	9 Время стояния на коврике (сек)
	10							
547	М-120	8	0,5	4	18	2	15	88
547	Шум	10	0,5	5	20	4	30	90
548	»	12	5	3	28	2	7	87
548	М-120	10	11 1	4	20	2	5	87
549	Шум	15	Прислушивается, остается сидеть на коврике					
550	»	15	12 Встала, подошла к барьеру, затем снова возвратилась на коврик					
549	М-120	8	0.5	4	13 Преодолевает барьер, прыгает на стол с кормушкой, однако от еды отказывается. На этом опыт был прекращен			

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) time required to go from mat to feeder table (sec); 6) eating time (sec); 7) time spent at table after eating (sec); 8) time required to return to mat (sec); 9) time for which animal remained on mat (sec); 10) noise; 11) listened, remained seated on mat; 12) stood up, went to barrier, then returned to mat; 13) leapt barrier, jumped on feeder table, but refused to eat. Experiment discontinued.

Record of Experiment on 14/X 1954. Barrier Height 95 cm

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Время побежки от коврика до стола с кормушкой (сек)	6 Время еды (сек)	7 Время стояния на столе после еды (сек)	8 Время возвращения на коврик (сек)	9 Время стояния на коврике (сек)	10 Примечание
642	М-120	8	0,5	3	15	15	12	93	Подкрепление мясом 13
654	11 Шум	9	0,5	4	14	4	8	92	
655	»	8	0,5	3	15	2	8	92	
643	М-120	8	0,5	3	13	2	8	94	
656	Шум	8	0,5	3	12	8	12	90	
644	М-120	8	0,5	3	14	2	12 9	91	
657	Шум	9	0,5	4	10	—	Опыт закончен		

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) time required to go from mat to feeder table (sec); 6) eating time (sec); 7) time spent at table after eating (sec); 8) time required to return to mat (sec); 9) time for which animal remained on mat (sec); 10) note; 11) noise; 12) experiment terminated; 13) reinforcement with meat.

Record of Experiment on 15/X 1954. Barrier Height 95 cm

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного рефлекса (сек)	4 Латентный период условного раздражителя (сек)	5 Время побежки от коврика до стола с кормушкой (сек)	6 Время еды (сек)	7 Время стояния на столе после еды (сек)	8 Время возвращения на коврике (сек)	9 Время стояния на коврике (сек)	10 Примечание
645	М-120	8	0,5	4	18	4	8	91	15 Подкрепление мясо сухарным порошком, задевает барьер
658	11 Шум	15	12 Ориентировочная реакция, идет к сетке, затем возвращается на коврик						
659	»	15	13 То же самое						
646	М-120	15	14 Бежит к барьеру, но перед самым барьером останавливается, ходит вдоль барьера, пытается проникнуть под сетку, поскуливает. Ввиду того, что собака начала беспокоиться, скулить, появилась одышка, опыт был прекращен						

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) time required to go from mat to feeder table (sec); 6) eating time (sec); 7) time spent at table after eating (sec); 8) time required to return to mat (sec); 9) time for which animal remained on mat (sec); 10) note; 11) noise; 12) orientation reaction, dog going to net and then returning to mat; 13) the same; 14) ran to barrier, but halted in front of it, ran

along it, tried to crawl under it, and whimpered. In view of the fact that the dog became restless, whimpered, and began to pant the experiment was discontinued; 15) reinforcement with meat-sugar powder, grazed net.

This relationship was even more marked in experiments in which the nature of the unconditioned reinforcement was varied. When we shifted to reinforcement with meat the dog freely crossed the barrier at heights of 90 and 95 cm in response to the conditioned stimuli and quickly returned to the mat through a passage made in the net (see the record of the experiment on 14/X 1954).

It can be seen from the experiment of 14/X 1954 that the dog leapt a barrier 95 cm high in both response to both strong and weak conditioned stimuli when the reinforcement was with meat.

On the following day the meat reinforcement was replaced by meat-sugar powder, which immediately affected the animal's conditioned-reflex activity. The dog cleared a barrier 95 cm high at the beginning of the experiment and in response to the first application of the metronome, but he was unable to jump it in response to two subsequent applications of the noise and a second application of the metronome (see the record of the experiment on 15/X 1954).

It follows from these experiments that both an increase and a decrease in alimentary excitability alter the animal's conditioned-reflex motor activity: in one case (when alimentary excitability decreases) the dependence of the motor reaction on the physical strength of the conditioned stimuli becomes more pronounced, while in the other case (when alimentary excitability increases) this dependence disappears. The dependence of the motor reaction on the physical strength of the conditioned stimuli was also quite manifest when the conditioned signals were applied against a background of extraneous stimuli (random noise, tones, etc.). Such stimuli generally inhibited the motor reaction to the weak conditioned stimulus (noise) and did not affect that to the strong stimulus (M-120).

Under the experimental conditions in question, the animal's conditioned-reflex motor activity thus depends on the functional state of his cerebral cortex, which is to a substantial extent governed by the strength of both the conditioned and unconditioned stimuli.

M.M. Khananashvili experimentally investigated the manifestation of the "force law" in visual and auditory stimuli in the following manner. He first developed stable conditioned reflexes in the dog Dzhek to an 800 hz tone and to the light of 40, 96, and 150 watt bulbs. All the bulbs were in a rack that was placed on the 47th square. When these stimuli were applied the dog ran from the mat to a stand near table 1, jumped up on it, and then leapt onto the table and went to the feeder to eat. When these reflexes had been fixed it was found that, in the overwhelming majority of cases, the trip to the feeder had the same latent period and was effected at the same rate whether the 40, 96, or 150 watt bulb was lit (see the record of the experiment on 13/XI 1956).

Record of Experiment on 13/XI 1956. Dog Dzhek

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Реакция на условное раздражение
1,5	58	Свет 96 вт	5	1	Бежит на стол 1
1,5	50	» 150 »	5	1	То же
2,0	60	» 40 »	5	1	» »
2,0	51	» 150 »	5	1	» »
2,0	41	Тон 800 гц	5	1	» »
1,5	42	» 800 »	5	1	» »

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) light; 8) watts; 9) tone; 10) hz; 11) ran to table 1; 12) the same.

Note: Stand near table 1.

Record of Experiment on 25/XI 1956. Dog Dzhek

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Реакция на условное раздражение
2,0	69	Свет 150 вт	5	1	Бежит на стол 1
2,0	81	» 40 »	10	6	То же
2,5	70	» 150 »	5	2	» »
1,5	82	» 40 »	10	9	» »
1,5	63	Тон 800 гц	5	1	» »

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) light; 8) watts; 9) tone; 10) hz; 11) ran to table 1; 12) the same.

Note: Stand placed at distance of 100 cm from table 1.

The experimental conditions were then modified: the stand was moved to a distance of 1 m from the table, i.e., the dog now had to carry out a more complex motor activity – jumping from the stand to the table. This complication of the task caused an increase in the latent period of the conditioned reflexes and in the time required to reach the feeder in response to weak visual stimuli (see the record of the experiment 25/XI 1956). When the stand was moved to 120 cm from the table the dog was able to make the jump only in response to a strong visual stimulus (the light of the 150 watt bulb), while in response to a weak stimulus (the light of the 40 watt bulb) he merely went to the stand, climbed up on it, and then returned to the mat.

Similar results were subsequently obtained with the dog Dzhek in response to auditory stimuli of varying physical strengths.

DIFFERENTIATION OF STIMULI

From the very outset, our laboratory has employed the situational conditioned-reflex method to study the differentiation, or analysis, of conditioned stimuli and we have now amassed a wealth of data that enable us to establish regularities in stimulus discrimination under conditions of free motor activity. We investigated different types of conditioned-stimulus differentiation, based both on discrimination of positive stimuli reinforced at different tables and on opposition of positive (reinforced) and negative (unreinforced) stimuli.

Differentiation of positive stumuli located in different areas of experimental room and reinforced at different tables

Differentiation of visual (light) stimuli located in different areas of the room and reinforced at different tables was developed in the dog Blek, Sharik, and Ruslan (experiments conducted by M.M. Khananashvili).

Positive conditioned reflexes involving going to table 1 were initially developed in the dog Blek in response to a bell, a circle, and the light of a 55 watt bulb. The bulb was mounted on a rack placed on square 47. The dog remained on a mat (square 26) during the intervals between applications of the stimuli. After these reflexes had become stable induction of a conditioned reflex to the light of a 200 watt bulb on the left-hand shelf (above square 36) was begun; this stimulus was reinforced at table 2. Differentiation of these two light stimuli located in different areas of the room and reinforced at different tables was developed in the following manner. Only the left-hand stimulus, reinforced at table 2, was applied during the first six experimental days; at the same time, all the conditioned stimuli reinforced at table 1 were discontinued. The conditioned reflex to the left-hand stimulus appeared on its 37th application and became stable on its 54th application. Application of all the conditioned stimuli reinforced at table 1 was then resumed. The first trial showed that the dog had developed clear differentiation of the aforementioned stimuli, as was seen from the fact that he always went to table 1 when the 55 watt bulb was lit and to table 2 when the 200 watt bulb was lit. Conditioned reflexes to the light of a 55 watt bulb (on square 47) and a circle reinforced at

Record of Experiment on 28/V 1957. Dog Ruslan

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Реакция на условное раздражение
1	109	7 Круг	4	1	10 Бежит на стол 1, ест, возвращается на коврик
1	110	»	4	1	То же 11
1	46	8 Крест	20	—	Продолжает стоять на коврике 12
1	111	Круг	4	1	Бежит на стол 1, ест, возвращается на коврик
1	47	Крест	20	—	Продолжает стоять на коврике
1	112	Круг	4	1	Бежит на стол 1, ест, возвращается на коврик
1	113	»	4	1	То же
1	48	Крест	20	—	Продолжает стоять на коврике
1	114	Круг	4	1	Бежит на стол 1, ест, возвращается на коврик
1	19	9 Свет 55 вт	5	1	То же

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) circle; 8) cross; 9) 55 watt light; 10) ran to table 1, ate, returned to mat; 11) the same; 12) remained on mat.

Record of Experiment on 11/XI 1957. Dog Ruslan

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Реакция на условное раздражение
1	6	8 Свет 200 вт	10	—	9 Бежит к столу 2 лишь на стук кормушки
1	7	» 200 »	5	1	Бежит к столу 2, ест и возвращается на коврик 10
7 40 сек	8	» 200 »	5	1	То же 11
1	9	» 200 »	6	2	» »
1	10	» 200 »	5	1	» »
1	11	» 200 »	6	2	» »

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) sec; 8) 200 watt light; 9) ran to table 2 only in response

to sound of feeder; 10) ran to table 2, ate, and returned to mat; 11) the same.

table 1, were first induced in the dog Ruslan; an inhibitory differentiation was then formed to a cross (see the record of the experiment on 28/V 1957).

After the reflexes involving going to feeder 1 were fixed, induction of conditioned reflexes involving going to table 2 was begun. For this purpose all the conditioned stimuli reinforced at table 1 were discontinued for several days and a meat trail was laid to table 2.

Under these conditions the animal still often jumped onto table 1 at the beginning of the experiment and during the intervals between applications of the conditioned stimulus (the sound of feeder 2), but clear movement toward table 2 was observed on the fourth application of the sound of feeder 2 and the reflex became stable after the 15th application. Induction of a conditioned reflex to the light of a 200 watt bulb (square 36) was begun after the conditioned reflex to the noise of feeder 2 was fixed. This reflex appeared after the 78th application of the stimulus (see the record of the experiment on 11/XI 1957).

After the reflex involving going to table 2 in response to the 200 watt bulb became stable, use of the previously induced conditioned reflexes involving going to table 1 was resumed. The first experiment with the conditioned stimuli reinforced at the first and second tables showed that the dog could distinguish the reinforcement sites of the two stimuli (see the experiment on 12/XI 1957). However, in this first instance there were certain changes in the animal's conditioned-reflex activity: thus, for example, the latent periods of the conditioned reflexes increased and the reflex to the light of the 55 watt bulb was sometimes unstable. These changes were observed during the first three experimental days, after conditioned-reflex activity was fully restored.

V.I. Syrenskiy conducted experiments to investigate the differentiation of positive auditory stimuli located at different places in the experimental room and reinforced at different tables.

In the dog Una a conditioned reflex was first developed to a 60 bpm metronome reinforced at table 1 and then to a 120 bpm metronome reinforced at table 2. The conditioned stimuli were not applied stereotypically. The conditioned reflex to the 60 bpm metronome appeared after the 30th application, while that to the 120 bpm metronome appeared after the 20th application.

The data cited thus show that an animal carries out positive differentiation of spatially separated conditioned stimuli (visual and auditory) reinforced at different tables with comparative ease.

Differentiation of positive stimuli located at the same place in the experimental room but reinforced at different tables

M.M. Khananashvili and V.I. Syrenskiy investigated the differentiation of positive stimuli located at the same place in the experimental room but reinforced at different tables.

In experiments on the dog Sharik conditioned visual stimuli (various figures) were projected on the same screen, i.e., were not spatially separated. After induction of a conditioned reflex to a square reinforced at table 1, development of a conditioned reflex reinforced at table 2 was begun (M.M. Khananashvili's experiments). The conditioned reflex to the square was disrupted after one application of the circle followed by reinforcement at table 2: the animal stopped going to table 1. This reflex was restored after repeated reinforcement of the square at table 1, but it became unstable and its latent period increased (see the record of the experiment on 21/I 1955). Sharik was unable to develop stable differentiation of the circle from the square even after 200 reinforcements of the former at table 2 and 100 reinforcements of the latter at table 1 (see the record of the experiment on 7/IV 1955).

The difficulty Sharik had in differentiating figures located in the same place but reinforced at different tables did not result from difficulty in differentiating the shape of objects. This was demonstrated by experiments on the dog Ryzhik, in which a circle was reinforced by feeding and a square was not reinforced, i.e., inhibitory differentiation to the square was formed. In this case stable differentiation of the circle from the square occurred after the 300th application. Similar results were also obtained with other animals.

All of this enables us to assume that the difficulty encountered by Sharik in differentiating different figures resulted principally from the spatial location of the conditioned visual stimuli.

Investigations conducted by V.I. Syrenskiy (1962) on 8 dogs established that differentiation of auditory or visual stimuli applied at the same place but reinforced at different tables occurs slowly and with great difficulty. The differentiation remained unstable in 6 of 8 animals after 100 applications of the stimuli to be differentiated. The error rate was 50-70%. After 2-3 applications of the stimuli to be differentiated, the animals often began to whine and bark, went to the door, and scratched at it, so that in a number of instances the experiment had to be halted.

The difficulty encountered by the experimental animals in differentiating metronome frequencies of 60 and 120 beats per minute was due both to the spational rotation of the conditioned stimuli and to the fact that, at these frequencies, the conditioned motor reaction could be executed before the stimuli could be distinguished (V.I. Syrenskiy, 1961), i.e., the latent period of the conditioned reflex was shorter than the interval between the beats of the metronome.

It should be emphasized that during the initial period of development of differentiation of auditory stimuli under the afore-

Record of Experiment on 12/XI 1957. Dog Ruslan

Интервалы между действием условных раздражителей (мин) 1	Число применений условного раздражителя 2	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	Латентный период условного рефлекса (сек) 5	6 Реакция на условное раздражение
		7 8			11
1	12	Свет 200 вт	6	2	Бежит к столу 2
1	13	» 200 »	6	2	То же 12
1	14	» 200 »	5	1	» »
1	21	» 55 »	10	—	Бежит к столу 1 лишь на стук кормушки 13
1	22	» 55 »	6	3	Бежит к столу 1 14
1	21	» 55 »	4	1	То же
1	53	» 200 »	6	2	Бежит к столу 2
1	24	» 55 »	5	2	Бежит к столу 1
1	126	9 Круг	4	1	То же
1	56	10 Крест	20	—	Стоит на коврике 15
1	127	Круг	4	1	Бежит к столу 1
1	16	Свет 200 вт	6	2	Бежит к столу 2
1	25	» 55 »	4	1	Бежит к столу 1
1	17	» 200 »	6	2	Бежит к столу 2
1	26	» 55 »	6	3	Бежит к столу 1

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) light; 8) watts; 9) circle; 10) cross; 11) went to table 2; 12) the same; 13) went to table 1 only in response to sound of feeder; 14) went to table 1; 15) remained on mat.

mentioned experimental conditions one important factor governing whether the animal reacted by going to one table or the other was its pose (the direction in which its head and torso pointed) during the intervals between applications of the conditioned stimuli (V.I. Syrenskiy, 1962).

That the difficulty of differentiating positive stimuli applied at the same place lies in the spatial location of the stimuli is also demonstrated by experiments in which V.I. Syrenskiy and M.M. Khananashvili moved the conditioned (dynamics) stimuli closer together.

In V.I. Syrenskiy's experiments the dynamic stimuli were first placed 4.5 m apart. After formation of stable conditioned reflexes to a 120 bpm metronome reinforced at table 1 and a 60 bpm metronome reinforced at table 2, the distance between the dynamic stimuli was reduced by 1 m in each succeeding experiment. Positive differentiation of the tables was disrupted when the stimuli were 1.5 m apart, but conditioned-reflex activity was restored after 4 experiments. The experiments were continued for a further two weeks, gradually bringing the stimuli closer together. When they were placed on the same square (44) the dog was unable to consistently differentiate the frequencies of the 60 and 120 bpm metronomes over the course of 7 experiments.

Record of Experiment on 21/I 1955. Dog Sharik

Интервалы между действием условных раздражителей (мин) 1	Число применений условного раздражителя 2	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Реакция на условное раздражение
1	59	7 Квадрат	3	2	9 Бежит к столу 1
1	60	»	3	2	» » » 1
1	1	8 Круг	8	—	Стоит на месте 10
1	2	»	5	—	На стук кормушки 2 бежит к ней, ест 11
1	61	Квадрат	15	—	На стук кормушки 1 бежит к ней, ест 12
1	62	»	15	—	То же 13
1	63	»	7	6	Бежит к кормушке 1, ест 14
1	3	Круг	5	—	На стук кормушки 2 бежит к ней, ест

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) square; 8) circle; 9) went to table 1; 10) remained in initial position; 11) in response to sound of feeder 2 went to it and ate; 12) in response to sound of feeder 1 went to it and ate; 13) the same; 14) went to feeder 1 and ate.

Record of Experiment on 7/IV 1955. Dog Sharik

Интервалы между действием условных раздражителей (мин) 1	Число применений условного раздражителя 2	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	Латентный период условного рефлекса (сек) 5	6 Реакция на условное раздражение
1	198	7 Круг	4	2	9 Бежит к столу 2
1	199	»	4	2	То же 10
1	200	»	8	—	Стоит на месте 11
1	201	»	5	—	То же
1	103	8 Квадрат	15	—	Смотрит то на стол 1, то на стол 2, но продолжает стоять на месте 12
1	202	Круг	10	—	То же
1	203	»	5	—	» »
1	204	»	5	4	Идет к столу 2 13

1) Intervals between applications of conditioned stimuli (min);

2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) reaction to conditioned stimulus; 7) circle; 8) square; 9) went to table 2; 10) the same; 11) remained in initial position; 12) looked sometimes at table 1 and sometimes at table 2, but remained in initial position; 13) went to table 2.

M.M. Khananashvili studied the mechanism of the differentiation of two identical but spatially separated auditory stimuli with reinforcement of the positive stimulus at feeder 1. In these experiments, which were conducted with three dogs, identical dynamic stimuli were hung from a wire along one wall of the experimental room, one to the left of the dog and the other to the right. Both stimuli were at the same distance from the dog's head. A positive conditioned reflex was developed to the sounding of a 600 hz tone on the dog's right and inhibitory differentiation was developed to the sounding of the same tone on his left. After this discrimination was induced, the limit of spatial differentiation of the auditory stimuli was studied by moving them closer together.

The animal remained on square 25 during the interval between the stimuli, usually with his head turned toward the table bearing feeder 1. The plane passing through the anteroposterior axis of the dog's head and intersecting the location of the feeder where food was supplied was perpendicular to the wall on which the dynamic stimuli were hung. These experiments showed that differentiation of the tones occurred rapidly when the stimuli were separated by the greatest distance (450 cm). The rate at which differentiation was formed depended to a substantial extent on the preliminary fixation of the positive reflex. For example, let us consider the experiment with the dog Lama. A positive reflex was developed to the sounding of a 600 hz tone on the right. After repeated application of this stimulus (168 times), induction of differentiation to the 600 hz tone on the left was begun. On the first application of the "left-hand" tone there was a strong orientation reaction toward the stimulus, but the dog remained in its initial position. One the second application of this tone there was an orientation reaction and the dog also went to the feeder (after 4 sec). The orientation reaction persisted on the 3rd application and the dog moved toward the feeder after 2 sec, but he stopped halfway and returned to his usual position. On the 4th application of the tone the dog remained in place, turning his head first slightly toward the stimulus and then away from it. He again went to the feeder on the 5th, 6th, and 8th applications of the left-hand tone but ceased to do so from the 9th application onward, although he took several steps toward the feeder in some instances; these abortive movements also ceased after the 15th application, i.e., complete differentiation of the left-hand 600 hz tone from the right-hand 600 hz tone appeared (experiment on 20/VI 1961).

After this differentiation had become stable, the two dynamic stimuli were moved toward the center, i.e., toward the feeder.

When the distance between the stimuli to 350 cm the reaction to the right-hand tone remained unchanged (the dog immediately went to the feeder), while a clear orientation reaction (turning of the head) developed in response to the left-hand tone; on the first two applications of the latter tone the dog remained in place, while on the third application he went to the feeder. Differentiation became clear after the 4th application.

When the distance between the stimuli was reduced to 250 cm the reaction to the right-hand tone still remained unchanged, but the dog sometimes took several steps toward the feeder in response to the left-hand tone, although he then stopped or immediately returned to his initial position; after eating, he often stood on squares adjacent to the mat rather than on the mat itself and sometimes exhibited unusual motor activity or whined. Differentiation became clear after the 5th application.

The distance between the stimuli was reduced to 150 cm after restoration of normal activity. This resulted in a disruption of the spatial differentiation of the tones and development of changes in the animal's behavior. After several applications of the left-hand tone the dog became restless, wandered from the mat onto adjacent squares, crossed his paws, and whined. These changes were most pronounced during the first three days and then became less marked. Complete differentiation of the tones developed after the 17th application of the left-hand tone.

The same disruptions of higher nervous activity were observed when the distance between the stimuli was reduced first to 50 cm, then to 25 cm, and finally to 10 cm as when it was reduced to 150 cm. However, these changes also gradually disappeared and normal conditioned-reflex activity was restored. The shorter the distance between the sound sources, the greater was the number of applications required for this to occur. Thus, complete differentiation of the left-hand tone from the right-hand tone was observed only after 60 unreinforced applications of the former when the stimuli were separated by 25 cm.

Induction of differentiation followed roughly the same plan in the dog Abrek and Ryzhik. The disturbances produced in Abrek by gradual approximation of the stimuli were indistinct and were observed only during the first 1-2 days. Severe disruptions of higher nervous activity were observed in Ryzhik when the distance between the stimuli was reduced to 25 cm: he stopped going to the feeder in response to positive stimuli, raced about the room, went to the door, scratched at it, and whined.

It was thus found that the limit of spatial differentiation of auditory stimuli (pure tones) by the dogs in our experiments was 10-25 cm.

M.M. Khananashvili's investigations also showed that differentiation of stimuli in close proximity can be employed as a convenient procedure for inducing experimental neuroses under free-movement conditions.

Record of Experiment on 20/VI 1961. Dog Lama

1 Интервалы между действием условных раздражителей (сек)	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Время побежки к кормушке (сек)	6 Реакция на условный раздражитель
40	7 Тон 600 гц (справа)	5	1	3	11 Бежит к кормушке, ест
40	8 Тон 600 гц (слева)	20	—	—	Стоит на коврике 12
50	9 То же	20	—	—	То же 13
40	10 Круг	5	1	3	Бежит к кормушке, ест
30	Тон 600 гц (справа)	5	1	3	То же
40	То же	5	1	3	» »
50	Тон 600 гц (слева)	20	—	—	Стоит на коврике
10	Тон 600 гц (справа)	5	1	3	Бежит к кормушке, ест

1) Intervals between applications of conditioned stimuli (sec); 2) Conditioned stimulus; 3) Action time of conditioned stimulus 4) Latent period of conditioned reflex (sec); 5) time required to go to feeder (sec); 6) reaction to conditioned stimulus; 7) 600 hz tone (right); 8) 600 hz tone (left); 9) the same; 10) circle; 11) went to feeder, ate; 12) remained on mat; 13) the same.

These investigation thus demonstrated that differentiation of conditioned visual or auditory stimuli, which is based on concentration of the excitation process, is hindered when the conditioned stimuli are located at the same point in the experimental room and facilitated when they are located at different points. Differentiation becomes easier as the distance between the stimuli to be differentiated increases. Both the spatial arrangement of the conditioned stimuli and their qualitative characteristics have a great influence on the differentiation rate.

Formation of inhibitory differentiation

As is well known, formation of inhibitory differentiation, i.e., differentiation in which one of two stimuli is always reinforced by an unconditioned stimulus and the other is not reinforced, is widely used to characterize the analytic and synthetic activity of the cortical analyzers. We induced inhibitory differentiation to various stimuli (visual, auditory, and spatial) for this purpose. The results obtained showed that induction of inhibitory differentiation by the situational conditioned-reflex method (P.S. Kupalov, 1946, 1950; A. Yemchenko, 1956; et al.) obeys the same general stimulus-differentiation laws established by the sancretory, electrocutaneous-defensive, and other conditioned-reflex methods; these laws are widely known from numerous higher investigations conducted by the Pavlovian laboratory (N.I. Leporskiy, 1911; et al.).

Our research also established certain characteristics of the development of inhibitory differentiation under conditions of free motor activity.

As an example of the development of inhibitory differentiation by the situational conditioned-reflex method, let us discuss the experiment by P.S. Kupalov and M.M. Khananashvili on two dogs in 1958.

After induction of a conditioned spatial reflex (to square 32) and positive conditioned reflexes to a metronome and a 55 watt bulb, a conditioned reflex was developed to a circle in the dog Rike, who was a very lively, easily excited young female. On the 4th application of the circle the dog went to the feeder table and sprang up onto it. After the conditioned reflex to the circle became stable, induction of differentiation to a cross was begun. The first appearance of the cross produced the same activity as the circle. On the 17th application of the cross the dog went to the screen and then to the table, but did not jump up onto it and returned to the mat after several seconds.

The dog did not leave the mat on the 19th and 20th applications of the cross, but another type of activity appeared at this time. The animal began to lick her coat and scratch when the cross was shown. On subsequent days she jumped up onto the table less and less frequently, remaining on the mat or taking 2-3 steps toward the table, immediately stopping, and returning to the mat. On the 45th application of the cross the dog merely lay on the mat instead of starting toward the table. This reaction to the cross was subsequently observed on numerous occasions.

Stable differentiation was formed on the 74th application of the cross: the dog had entirely ceased jumping up onto the table in response to the cross, but she instantly ran to the table and sprang up onto it in response to the circle.

Display of the cross did not, however, become an indifferent stimulus to the animal. During induction of differentiation it was found that the cross caused definite motor activity involving unusual, previously unobserved scratching and licking of the coat, with the dog sometimes lying on the floor. After differentiation became stable, display of the cross began to cause other forms of motor reactions. Thus, on the 82nd application of the cross, we observed severe negative activity directed at getting as far as possible from the cross and leaving the experimental room (see the record of the experiment on 17/X 1955).

The dog often subsequently ran from the mat to other squares and to the door when the cross appeared. This negative motor reaction was frequently accompanied by whining, severe panting, and increased thirst.

When a new conditioned reflex involving going to table 2 in response to a 200 watt bulb was developed and fixed in Rike during the course of the experiments, she repeatedly jumped up onto tabld 2 and licked the empty fe der pan when the cross was displayed, i.e., she exhibited a clear alimentary reaction entailing going to table 2 (see the record of the experiment on 26/X 1955).

A count of the various motor reactions shows that on the 26 applications of the cross following developments of stable differentiation to this figure, i.e., when the dog no longer jumped up on table 1 in response to the cross, she went from the mat to other squares or to the door 9 times, went to her water dish and began to drink 5 times, jumped up on table 2 and began to lick the empty pan once, and went to the screen and began to vigorously sniff the cross once. In the remaining instances she took two or three steps toward the table, immediately returned to the mat, and lay down on it, scratching or beginning to vigorously sniff the floor.

After induction of a conditioned spatial reflex to square 32 and positive conditioned reflexes to a light (55 watt bulb), a bell, and a circle with alimentary reinforcement at table 1, development of differentiation to a cross was begun in a second dog, Blek, a young male with high alimentary excitability.

The cross at first evoked the same reaction as the circle: the dog jumped up onto the table and approached the feeder, although he did not receive food. On the 5th application of the cross he went to the table but did not jump up on it, returning to the mat after the cross disappeared. The positive reaction involving going to the table entirely ceased after the 11th application and the dog generally remained on the mat. He generally remained in his initial position (on square 32) during the intervals between the stimuli, but he sometimes went to square 39, i.e., closer to the feeder table, and stood there until the conditioned stimulus was applied. It was found that the dog remained on the mat when the differential stimulus (the cross) was displayed, i.e., the conditioned spatial reflex had become more precise (see the recordsof the experiments 11/II and 27 III 1957).

When a conditioned reflex involving going to table 2 in response to a new conditioned stimulus (a 200 watt bulb) was induced in this dog during the course of the experiments, it was often found that when the cross appeared he turned from the screen toward table 2, went to it, jumped up onto it, and licked the empty pan (see the record of the experiment on 27/III 1957). It can be assumed that, once a new focus of increased excitability had been created in the cortex, application of the differential stimulus caused excitation of this focus.

Other reactions were also observed when the differential stimulus was applied; thus, for example, when the cross was displayed the animal often immediately turned its head, sometimes began to vigorously sniff the floor and the mat, went to other squares, etc. Analysis of the movements made by the dog Blek in response to the inhibitory stimulus shows that on the 50 applications of the cross after fixation of differentiation he shifted from his usual position on the mat in 6 cases, went to table 2, jumped up onto it, and licked the empty pan in 9 cases, went to the rack bearing the lamp and licked it in 5 cases, turned his head sharply away from the screen showing the cross in 10 cases, went to different areas of the room and vigorously sniffed the floor in 12 cases, lay on the mat in 1 case, and sat quietly in 2 cases.

Numerous investigations have established that differentiation of conditioned stimuli is based on development of inhibition to the unreinforced stimulus. This interpretation of differentiation holds regardless of the nature and localization of the inhibition. The gradual development of differentiation, which is manifested in the experiments described above in the gradual attenuation and disappearance of the positive reaction directed at reaching the feeder table, can be attributed to the gradual development of inhibition to the differential stimulus. When the inhibition reaches a definite strength there is no positive reaction at all to the differential stimulus; in some cases the dog responds to the inhibitory stimulus by lying down on the mat, resting his head on his paws, and remaining completely motionless. The inhibition obviously originates in the cortical areas that perceive the inhibitory stimulus and irradiate to the systems that keep the dog sitting on the mat.

The differential stimulus often caused motor reactions of varying complexity: shaking, scratching, going from the normal position to the door, running to table 2 and licking the empty feeder tray, going to the water dish and drinking, going to the bulb near the screen for objective stimuli and licking it, etc.

Use of the situational conditioned-reflex method thus enabled us to obtain new data on the motor reactions evoked by inhibitory stimuli.

What is the nervous mechanism of these motor reactions? We believe that they arise as a result of positive induction from the areas of the cerebral cortex that participate in effecting the positive conditioned reflex and are the first to be inhibited under the action of the differential stimulus.

On the basis of numerous investigations, I.P. Pavlov noted that: "if a conditioned stimulus that evokes a corresponding conditioned reaction continues for sometime (minutes) without being further conjoined with an unconditioned stimulus, the cortical cell for this stimulus invariably passes into the inhibited state." It is precisely this process that occurred in our experiments with differential stimuli. In certain cases the passage of given cortical elements into the inhibited state as a result of non-reinforcement causes positive induction in other cellular elements. Positive cortical induction was first clearly detected in the experiments of D.S. Fursikov (1923) and subsequently noted by many authors (Ye.M. Kreps, 1924; P.S. Kupalov, 1926; N.A. Podkopayev, 1926; V.V. Siryatskiy, 1926; N.V. Zimkin, 1929; G.P. Konradi, 1932; et al.).

There arises the question of why the motor reaction to the inhibitory stimulus, which we have explained as positive induction, varies in character, involving running to the door, jumping up onto table 2 and licking the feeder tray, etc. This is obviously a result of the functional state of the entire cerebral cortex.

After induction of a system of positive and negative conditioned reflexes, a definite functional structure is set up in the cortex and links the cortical points for all the reflexes developed under the conditions in question. It can consequently be assumed that inhibitions developing at one point in this functional structure has an inductive influence on its other points. Actually, after beginning induction of a new conditioned reflex (going to table 2), we often observed that the dog jumped onto table 2 in response to the differential stimulus. It is obvious that in these cases the positive induction extended to thos cortical cellular elements whose excitability was enhanced by development of the new reflex involving going to table 2. This may explain the dog's moving to its normal position (the mat) and the licking of the bulb in response to the inhibitory stimulus if the latter was applied when the animal was in an "unusual" position.

The differential stimulus obviously causes inhibition principally in the cortical centers of the positive reflex and, through negative induction, generates concomitant excitation in the group of centers associated with the opposite type of activity. The general restlessness and whining we observed in certain animals in such cases are an external manifestation of the struggle between the inhibitory process induced by the differential stimulus and the concomitant excitation; this poses a difficult problem for some animals.

Differentiation of conditioned stimuli thus occurs gradually when the animal can move freely about the experimental room. The number of positive motor reactions to the unreinforced stimulus decreases as the number of complications increases. Complete differentiation of the conditioned stimuli is manifested in the action of a positive reaction (the animal does not go to the feeder table). However, the unreinforced stimulus does not become indifferent after differentiation develops, but often causes various motor reactions. The character of these movements is governed by the functional state of the cerebral cortex at the instant when the inhibitory stimulus is applied. The nervous mechanism of the motor reactions to the inhibitory stimulus can be regarded as the result of positive induction from those areas of the cerebral cortex that are inhibited by the differential stimulus.

The work of P.K. Anokhin (1956) and his colleague established that development of inhibitory conditioned reflexes in inevitably accompanied by a biologically negative reaction in the form of a "difficult state." It is manifested in the dog's yapping, whining, growling, tearing away from his leash, and so forth under the action of the unreinforced stimulus; there are also functional changes in his respiratory and cardiovascular systems. P.K. Anokhin (1932) believes that the unreinforced stimulus itself becomes the signal for this "difficult state." He considers the inhibition of the positive reflex to result from suppression of the alimentary reflex by the negative reaction that develops in response to the unreinforced stimulus. Various motor reactions to inhibitory stimuli have also been observed in work conducted by the motor-defensive method (I.S. Beritov, 1932; E.A. Asratyan, 1941; et al.).

Records of Experiments on 17/X and 26/X 1955. Dog Rike

1 Интервалы между действием условных раздражителей (*мин*)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (*сек*)	5 Латентный период условного рефлекса	6 Поведение собаки при действии условного раздражителя
		7 17/X 1955 г.			
2	193	8 Круг	5	1	Подбегает к столу 1, прыгает на него 10
2	82	9 Крест	20	—	Делает шаг к столу 1, но останавливается, резко поворачивается на 180° и бежит назад к двери. Через 40 *сек* возвращается на коврик 11
2	194	8 Круг	5	1	Подбегает к столу 1, прыгает на него
3	195	»	5	1	То же 12
4	196	»	5	1	» »
1	83	»	20	—	Стоит на коврике, смотрит на крест 15 *сек*, затем убегает с коврика на боковые квадраты, поскуливает 13
4	197	»	5	1	Подбегает к столу 1, прыгает на него
		14 26/X 1955 г.			
2	220	Круг	5	1	Подбегает к столу 1, прыгает на него
2	221	»	5	1	То же
2	91	Крест	20	—	Смотрит на крест 3 *сек*, резко поворачивается к столу 2, прыгает на него, лижет пустую чашку 16
2	222	Круг	5	1	Подбегает к столу 1, прыгает на него
1,5	44	Метроном 15	5	1	Смотрит на источник звука, подбегает к столу 1, прыгает на него 17
1,5	92	Крест	20	—	Стоит на коврике 5 *сек*, затем идет к чашке с водой, пьет воду 18
1	223	Круг	5	1	Подбегает к столу 1, прыгает на него

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex; 6) dog's behavior under action of conditioned stimulus; 7) 17/X 1955; 8) circle; 9) cross; 10) went to table 1, jumped up on it; 11) took a step toward table 1 but stopped, turned by 180°, and went back toward door. Returned to mat after 40 sec; 12) the same; 13) stood on mat, looked at cross for 15 sec, then went from mat to nearby squares and whined; 14) 26/X 1955; 15) metronome; 16) looked at cross for 3 sec, turned abruptly toward table 2, jumped up onto it and licked empty tray; 17) looked at sound source, went to table 1, and jumped up onto it; 18) stood on mat for 5 sec, then went to water dish and drank.

Experiments on 11/II and 27/III 1957. Dog Blek.

1 Интервалы между действием условных раздражителей (*сек*)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (*сек*)	5 Латентный период условного рефлекса (*сек*)	6 Поведение собаки при действии условного раздражителя
			7 11/II 1957 г.		
1	86	8 Круг.	5	1	Подбегает к столу 1 и прыгает на него 10
1	87	»	5	1	То же; после еды опускается на пол и становится на квадрат 33 11
1,5	14	9 Крест	20	—	Смотрит на крест 15 *сек*, затем становится на коврик 12
1	88	8 Круг	5	2	Подбегает к столу и прыгает на него; после еды спускается на пол и становится на квадрат 33 13
1	15	9 Крест	20	—	Смотрит на крест 2 *сек*, затем быстро поворачивается на 180° и становится на коврик 14
1 *мин* 40 *сек*	89	8 Круг	5	1	Подбе ает к столу и прыгает на него 15
			16 27/III 1957 г.		
40	120	17 Свет 200 18 *вт*	5	1	Подбегает к столу 2 и пры ает на него 19
40	100	» 55 »	5	1	Подбе ает к столу 1 и пры ает на него
40	154	Круг	5	1	То же
40	42	Крест	20	—	Сразу поворачивает голову к столу 2, подходит к нему, прыгает на него, смотрит в пустую чашку. 20
1	155	Круг	5	1	Подбегает к столу 1, пры ает на него
40	121	Свет 200 *вт*	5	1	Подбегает к столу 2 и пры ает на не о
40	156	Круг	5	1	Подбегает к столу 1 и прыгает на него
40	43	Крест	20	—	Сразу отворачивает голову от креста, подходит к столу 2 и возвращается на коврик 21
1	157	Круг	5	1	Подбегает к столу 1 и прыгает на него
40	122	Свет 200 *вт*	5	2	Подбегает к столу 2 и прыгает на него

1) Intervals between applications of conditioned stimuli (sec); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) 11/II 1957; 8) circle; 9) cross; 10) went to table 1 and jumped up onto it; 11) the same, jumped down to floor after eating and stood on square 33; 12) looked at cross for 15 sec and remained on mat; 13) went to table, jumped up on it, jumped down to floor after eating, and stood on square 33; 14) looked at cross for 2 sec, quickly turned by 180°, and remained on mat; 15) went to table and jumped up onto it; 16) 27/III 1957; 17) light; 18) watts; 19) went to table 2 and jumped up onto it; 20) immediately turned his head toward table 2, went to it, jumped up onto it, and inspected empty tray; 21) immediately turned his head away from the cross, went to table 2, and returned to mat.

Moving from the mat (standing on which is a positive conditioned stimulus) to the door and the concomitant whining and the panting can be regarded as a reaction completely opposite to that evoked by the positive stimulus, i.e., as a negative reaction. It was pointed out above that P.K. Anokhin considers the negative reaction to the inhibitory stimulus to be the result of the "difficult" state that arises as a result of nonreinforcement of the conditioned alimentary excitation produced; the unreinforced stimulus subsequently becomes the signal for this difficult state and evokes a "biologically negative reaction" rather than an alimentary reaction. Having thus formulated the problem, it can be assumed that the inhibitory stimulus must always evoke a "biologically negative reaction." It is possible that such a reaction to the inhibitory stimulus acquires a conditioned reflex character in some cases. However, as free-movement experiments have shown, it is not a dominant reaction; there may also be other, in no way "biologically negative" reactions. Thus, if the inhibitory stimulus is applied when the animal is on an "unusual" square, he sometimes returns to his normal position. This response to the inhibitory stimulus must be regarded as biologically positive.

V.I. Syrenskiy's work with conditioned auditory stimuli (1962) showed that when differentiation is formed to qualitatively different auditory stimuli (positive and inhibitory) located at different points in the experimental room, the character of the motor reaction is governed by two factors: the location of the stimuli (the spatial factor) and their specific characteristics (strength, pitch, frequency, etc.). Each of these components acquires conditioned-reflex significance during the induction of conditioned reflexes. When conditioned stimuli that differ in their specific properties are located at different points in the room the animal's behavior depends on both components; when the stimuli are located at the same point their spatial components become identical and the animal's behavior is alternately governed solely by their specific characteristics.

DIFFERENTIATION OF DIFFERENT SPATIAL AREAS

Use of the situational conditioned-reflex method made it possible to establish the importance of the spatial factor in the complex reflex motor activity of animals. Thus, it was demonstrated that the area of the experimental room in which the animal is located when the positive conditioned stimuli are applied acquires the properties of a positive conditioned agent and, together with the other stimuli, becomes one of the factors governing its conditioned motor activity. If remaining in a definite area of the experimental room is conjoined with application of an inhibitory conditioned stimulus or if the positive conditioned reflex is extinguished while the animal is in this area, it acquires a negative, inhibitory value (P.S. Kupalov, 1946, 1949, 1959; V.V. Yakovleva, 1949; O.N. Voyevodina and P.S. Kupalov, 1954; L.K. Gordeladze, 1953).

Experimental data indicating the significance of the spatial factor in conditioned motor activity were also btained in the investigations of V.M. Kasyanov (1949), I.M. Apter (1952), I.S. Beritashvili (1953, 1957, 1959), E.Sh. Ayrapet'yants (1959), and others.

A further study of the spatial factor or, more precisely, of the mechanism by which different spatial areas are differentiated, was made in the investigations of P.S. Kupalov and M.M. Khananashvili (1960).

These experiments were conducted on the dogs Buyan and Pal'ma. A metronome placed on the floor to the animal's right was used as the conditioned auditory stimulus and a 55 watt bulb on a rack placed in front of the feeder (square 61) was used as the visual stimulus. Reinforcement was given from the feeder on table 2.

At first, during induction of the conditioned reflex to the sound of the metronome, Buyan's behavior in the experimental room had an aimless character; during the intervals between the conditioned stimuli he rapidly walked or ran about the room without staying in one area for very long. The conditioned stimulus (metronome) was then applied several times only when the animal was accidentally passing over square 28. After several conjunctions of the metronome with the dog's being on this square, it was found that he more and more frequently took up a position on square 28 during the intervals between the conditioned stimuli. When the metronome was subsequently applied the dog went to the feeder, ate the reinforcement, and immediately returned to square 28, where he remained until the next application of the metronome. A definite segment of the floor (square 28) thus became the spatial area where the animal preferred to stay during the intervals between the conditioned stimuli.

However, in a number of cases the animal did not immediately return to square 28 after receiving the reinforcement, but walked over various squares for 30-60 sec and only then went to the proper square. On one experimental day the metronome was applied when the animal did not return directly to square 28 after eating his portion of powdered meat biscuit, but began to wander from square to square. The metronome was switched on when the dog passed over square 52. He immediately halted and turned his head toward the metronome, i.e., a clear orientation reaction was observed. Despite continued sounding of the metronome, a conditioned reflex involving going to the feeder table did not appear in this case (see the experiments 6/VI 1955).

The metronome was subsequently applied without alimentary reinforcement each time that the dog passed over square 52. As before, the metronome was reinforced with food when the dog took up a position on square 28. Attentuation of the orientation reaction was observed on the second application of the metronome when the dog was on square 52. The dog then started going to the feeder in response to the sound of the metronome when he was on square 52, although no reinforcement was given.

The metronome was subsequently switched on 1 or 2 times during the experimental day when the dog happened to be on square 52. After the 13th application of the metronome with the dog on square 52,there was an increase in the latent period of this reaction and it was on the 18th application that the dog was first observed not to go to the feeder at all, remaining on square 52 for 3 sec; he looked alternately at the feeder and the metronome and then slowly went to square 28 over squares 53, 54, 55, 49, and 35 (experiment on 2/VII 1955). Complete differentiation of square 52 from square 28 developed with

Record of Experiment on 6/VI 1955. Dog Buyan

1 Интервалы между действием условных раздражителей (*мин*)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (*сек*)	5 Латентный период условного рефлекса (*сек*)	6 Поведение собаки при действии условного раздражителя
2	29	7 Метроном	5	1	Подбегает к кормушке. После еды становится на квадрат 28 8
2	30	»	5	1	Подбегает к кормушке. После еды медленно ходит по разным участкам комнаты 9
1	(1)	»	20	—	Ориентировочная реакция — смотрит на источник звука, по сторонам. Через 1 *мин* стоит на квадрате 28 10
2	31	»	5	1	Подбегает к кормушке. После еды ходит по разным участкам комнаты 11
1	(2)	»	10	3	Слабая ориентировочная реакция, подбегает к кормушке. Подкорм не ест. Стоит у кормушки 10 *сек* и направляется к квадрату 28 12
2	32	»	5	1	Подбегает к кормушке. После еды идет к квадрату 28 13

Note: The number of applications of the metronome when the dog was on square 52 is shown in parentheses.

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) metronome; 8) went to feeder. Stood on square 28 after eating; 9) went to feeder. Slowly walked through different areas of room after eating; 10) Orientation reaction – looked at sound source and then to all sides. Stood on square 28 after 1 min; 11) went to feeder. Walked through different areas of room after eating; 12) weak orientation reaction, went to feeder.Did not eat reinforcement. Remained at feeder for 10 sec and went to square 28; 13) went to feeder. Went to square 28 after eating.

the 22nd application of the metronome. This differentiation was manifested in the fact that under the action of the same conditioned auditory stimulus, the dog went to the feeder if he was on square 28 but did not do so if he was on square 52.

Differentiation of a new location with respect to square 28 was then begun. The metronome was applied without reinforcement as soon as the dog passed over square 62. On the first application of the metronome he immediately went to the feeder, but did not receive food and returned to square 28. This reaction was also observed on subsequent days when the metronome was switched on with the dog on square 62. An increase in the latent period of the trip to the feeder was observed on the 10th application of the metronome with the dog on square 62. The conditioned reflex involving going to the feeder was completely absent from the 11th application onward. At the same time, the dog immediately went to the feeder in response to the sound of the metronome when he was on square 28.

The dog's next task consisted in differentiating still another area of the room, square 24 from square 28. He stopped going to the feeder on the 10th application of the metronome when he was on square 24. The positive conditioned reflex to the sound of the metronome when the dog was on square 28 remained unchanged.

During the development of differentiation of different areas of the room it was found that application of the metronome when the dog was in the "negative" areas caused it to move to the "positive" area (square 28), i.e., if the dog was on square 52, 62, or 24 he went to square 28 when the metronome was switched on; this reaction was at first inconsistent and occurred slowly, but as differentiation became fixed the dog quickly left the negative area and went to square 28.

Still another phenomenom was observed after induction and fixation of differentiation of different areas of the experimental room: as soon as the dog found himself on a "negative" square he left it before the metronome was switched on and went to square 28, i.e., being situated in a "negative" area caused the dog to shift to the "positive" area.

Thus, if a conditioned auditory stimulus is reinforced by an unconditioned alimentary stimulus when the animal is in a definite position in the experimental room and not reinforced when he is in any other position, differentiation of these areas can be developed in him. The first stage of this differentiation consists of an orientation reaction to application of the conditioned auditory stimulus when the dog is not in his normal position in the experimental room. After repeated application of the auditory stimulus when the dog is in an unusual location, the orientation reaction becomes weaker and the second stage of differentiation begins; during this phase the animal goes to the feeder both from his normal position and from unusual positions.

The second stage of differentiation is characterized by generalization of the conditioned spatial reflex, so that the new location acquires biological alimentary significance. The third stage of differentiation begins after several further applications of the metronome without reinforcement when the animal is in an unusual position; in this phase the same auditory stimulus has a positive alimentary value or a negative value, depending on the animal's location.

This differentiation is based on the internal inhibition that develops in response to the complex stimulus, which incorporates auditory and spatial components; however, the spatial factor is of decisive importance in this case.

Record of Experiment on 2/VII 1955. Dog Buyan

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Поведение собаки при действии условного раздражителя
3	125	7 Метроном	5	1	Подбегает к кормушке. После еды становится на квадрат 28 9
3	126	»	5	1	То же 10
2,5	65	8 Свет	5	1	Подбегает к кормушке. После еды ходит по разным участкам комнаты 11
1,5	(18)	Метроном	10	—	Смотрит на кормушку,* на метроном, через 3 сек направляется к квадрату 28 по квадратам: 53—54—55—49—35 12
1	127	»	5	1	Подбегает к кормушке. После еды становится на квадрат 28
1	128	»	5	1	То же

Note: The number of applications of the metronome with the dog on square 52 is shown in

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) metronome; 8) light; 9) went to feeder. Went to square 28 after eating; 10) the same; 11) went to feeder. Wandered through different areas of room after eating; 12) looked alternately at feeder and metronome, went to square 28 after 3 sec over squares 53, 54, 55, 49, and 35.

The induction of differentiation of spatial factors has a great deal in common with the development of differentiation to other stimuli, as studied in I.P. Pavlov's laboratory (1927).

After induction of differentiation of different areas, application of the conditioned auditory stimulus when the animal is in a "unusual" position causes him to leave this area of the room. P.S. Kupalov (1949) observed a similiar phenomenon in inducing differentiation of two different auditory stimuli; when the differential stimulus was applied the dog quickly left the position he was occupying and moved to another area of the room. The same reaction was observed during differentiation of conditioned visual stimuli (P.S. Kupalov and M.M. Khananashvili, 1958).

In interpreting the nervous mechanism of this process, attention is merited by the fact that the dog quite often goes from the "negative" area of the room to the "positive" area, which has positive alimentary significance. This phenomenon, which has also been observed by other authors (V.V. Yakovleva, 1949; L.K. Gordeladze, 1953), indicates that there are definite inductive relationships among the conditioned spatial reflexes induced under these experimental conditions.

Record of Experiments on 2/I 1956. Dog Al'ma

1 Интервалы между действием условных раздражителей (*мин*)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (*сек*)	5 Латентный период условного рефлекса (*сек*)	6 Поведение собаки при действии условного раздражителя
1	244	7 Свет	5	0,5	Бежит к кормушке, ест, затем становится на 47-й квадрат 9
1	245	»	5	0,5	10 То же
1	246	8 »	5	0,5	» »
2	28	Метроном	5	0,5	» »
0,2	29	»	5	0,5	» »
1	30	»	5	0,5	» »
1	247	7 Свет	5	0,5	» »

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) light; 8) metronome; 9) ran to feeder, ate, then went to square 47; 10) the same.

Induction of positive and negative conditioned reflexes thus transforms the experimental room into a segment of space with "positive" and "negative" areas, which, in conjunction with other stimuli, governed the animal's behavior.

EXTINCTION OF CONDITIONED REFLEXES

The extinction of conditioned reflexes was a subject of thorough study in I.P. Pavlov's laboratory almost from the outset of research on higher nervous activity. The nervous mechanism of this phenomenon, the laws it obeys, and the processes by which conditioned reflexes are restored have been studied by many authors (V.P. Babkin, 1904; I.Ya. Perel'tsveyg, 1907; P.P. Pimenov, 1907; I.F. Tolochinov, 1912; E.L. Gorn, 1912; et al.).

As is well known, extinction is the process by which any conditioned stimulus repeated several times without being reinforced by an unconditioned stimulus gradually loses its conditioned action.

Our experiments with different types of extinction of conditioned motor reflexes were alternated over a period of several weeks or sometimes months with ordinary experiments, in which we tested all the previously induced conditioned reflexes, including the one investigation.

Extinction of conditioned reflexes to visual and auditory stimuli by elimination of reinforcement

We first developed positive conditioned reflexes to a mat on square 47, a 55 watt bulb, and a 120 bpm metronome in the dog Al'ma and then extinguished the conditioned reflex to the light (M.M. Khanashvili's experiments). When extinction began, the conditioned stimulus (light) had been applied 247 times and the metronome 30 times (experiment of 2/I 1956).

The conditioned reflexes were stable and their latent period did not exceed 1 sec. The reflex to be extinguished was evoked without reinforcement until the dog no longer moved toward the table.

Partial extinction of the conditioned reflex to the light occurred on the first experimental day (record of experiment on 3/I 1956). On the fifth application of the light the dog went to the table but did not jump up onto it, while on the 9th application she remained seated in her usual place, on square 47. Applying the metronome infrequently, at different intervals after the extinguished conditioned reflex to the light, it could be seen that nonreinforcement of the conditioned visual stimulus did not affect the conditioned reflex developed to the metronome, i.e., extinction of the reflex to the weak visual stimulus did not have an inhibitory effect on the conditioned reflex induced to the stronger auditory stimulus, although the dog's behavior during the intervals between applications of the conditioned stimuli was altered: after she finished eating she stayed on the table for several minutes, sometimes lying down on it, and after jumping from the table to the floor she ran about the room, went to the door, or jumped up on the second table, but she did not stay on square 47. Nonreinforcement of the conditioned stimulus (light) when the dog was on square 47 obviously caused a negative reaction to square 47 and possibly to the entire area in front of the feeder table. This may also explain why the dog remained on the table for so long after eating.

After we again started to reinforce the light the dog stopped staying on the table and generally remained on square 47 between applications of the conditioned stimuli. Shortly after restoration of the conditioned reflex to the light, the dog's behavior became the same as before extinction was begun.

The investigations conducted on Al'ma thus showed that extinction of the conditioned reflex to the light did not affect the conditioned reflex formed to the metronome but clearly altered the spatial reflex governing the dog's position in the experimental room during the intervals between applications of the conditioned stimuli.

Record of Experiment on 3/I 1956. Dog Al'ma

1 Интервалы между действием условных раздражителей (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Поведение собаки при действии условного раздражителя
1,5	31	7 Метроном	5	0,5	Бежит к кормушке 9
1,5	I	Свет 8	20	0,5	» » »
1	II	»	20	0,5	» » »
2	III	»	20	0,5	» » »
2	IV	»	20	0,5	» » »
1,5	V	»	20	—	10 Подошла к столу и остановилась
1	32	Метроном	5	0,5	Бежит к кормушке
1,5	VI	Свет	20	0,5	» » »
1	VII	»	20	1	» » »
1,5	VIII	»	20	—	Подошла к столу и остановилась
1	IX	»	20	—	Сидит на месте 11
1	33	Метроном	5	0,5	Бежит к кормушке

Note: The Roman numerals indicate the number of times the visual stimulus was not reinforced.

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) metronome; 8) light; 9) went to feeder; 10) started toward table and stopped; 11) remained in place.

V.D. Volkova conducted experiments on the dog Dzhek and Una, in whom she developed a stereotype of conditioned reflexes to two positive stimuli (a bell and a light) and one differential stimulus (a metronome). Each conditioned stimulus acted for 5 sec. The intervals between applications of the stimuli were 1 min. When extinction was begun, the bell had been applied 1215 times and the light 1205 times for Una while for Dzhek the bell had been applied 1210 times and the light 1201 times. Extinction started with the second conditioned reflex in the stereotype, that to the light. It was carried out by repeatedly applying the light alone without reinforcement (at intervals of 1 min) until this stimulus produced no effect at all on three successive applications.

On the first two or three applications of the unreinforced conditioned stimulus the animals, as usual, immediately went to the feeder table (the latent period of the reaction in 0.5-1.0 sec); however, finding no food, they jumped back down to the floor and returned to the mat. They then often went to the mat to adjacent squares or made circling movements on it. After 4-5 nonreinforcements, the latent periods of the conditioned reflexes and the time required to go to the feeder table increased; during the intervals between applications of the conditioned stimuli the animal frequently lay on or near the mat and sometimes went to the door.

The reflexes then became unstable and finally disappeared altogether.

The reflex to the light in Una became unstable on the 11th application and was extinguished on the 22nd spplication; in Dzhek it became unstable on the 19th application and was extinguished on the 24th application.

After a series of ordinary experiments with the entire stereotype being used and the animal displaying normal conditioned-reflex activity, the first conditioned reflex in the stereotype, that to the bell, was extinguished under the same conditions. The reflex to the bell in Una became unstable on the 19th application and was extinguished on the 35th application; in Dzhek it became unstable on the 23rd application and was extinguished on the 37th application.

Thus, in both animals the reflex to the light was extinguished more rapidly than that to the bell, despite the fact that the latter was extinguished after the former, i.e., some training had occurred. Considering that the condtioned reflexes to the light and to the bell in Dzhek and Una were of approximately equal stability, this can be attributed to the fact that the extinction rate of conditioned motor reflexes depends on the physical strength of the conditioned stimulus: the stronger the conditioned reflex, the more slowly is the reflex to it extinguished.

The data cited show that the extinction of conditioned situational reflexes follows the laws discovered in I.P. Pavlov's laboratory for the extinction of conditioned salivary reflexes. Thus, it was established that the rapidity and degree of extinction of conditioned situational reflexes vary in different animals under completely identical experimental conditions (repetition of the unreinforced stimulus at uniform intervals, extinction to the same depth, etc.). The differing rates and degrees of extinction of conditioned motor reflexes in different animals are dependent on the stability of the conditioned reflex, the degree of extinction, the physical strength of the conditioned stimuli, the typological characteristics of the animal's nervous system, etc.

Extinction of the first trip to the feeder table

In experiments conducted by the sancretory method under chamber conditions V.I. Pavlova (1949) observed that feeding the animal before the experiment usually causes some intensification of all conditioned reflexes, but produces the greatest increase in the effect of the following stimulus (the first one in the experiment). Discontinuation of the preexperimental eating caused a disruption of conditioned-reflex activity, which was specifically manifested in a decrease in both conditioned and unconditioned salivation. This disturbance of conditioned-reflex activity lasted about two months.

As was mentioned above, one of the first conditioned situational conditioned reflexes formed required the animal to go from the door of the experimental room to the feeder. Beginning with the 3rd-5th experimental day, the majority of the animals went to the feeder table immediately on entering the room, where they always received their first portion of food before the usual conditioned stimuli were applied. In the experiment of P.S. Kupalov, O.N. Voyevodina, and V.D. Volkova an attempt was made to extinguish the first trip to the feeder table in animals with stable conditioned situational reflexes. This investigation was conducted on four dogs.

The following conditioned-reflex stereotype was induced and fixed in the dog Smirnyy: on entering the room, he went to feeder table 1, ate the first reinforcement, jumped down to the floor, and remained on the mat on square 42. When a positive conditioned stimulus (bell or light) was applied he went to the feeder, ate the reinforcement, and returned to the mat; under the action of the inhibitory stimulus (metronome) he remained on the mat. The conditioned stimuli were applied stereotypically at intervals of 1 min.

In another dog, Belyy, positive reflexes were developed to a metronome and a light and an inhibitory reflex was developed to a bell; the mat was placed on square 17 and the reinforcement was given at table 2.

After formation of a stereotype to a positive and two differential conditioned stimuli, extinction of the first trip to the feeder table was begun (after 44 experiments in Smirnyy and 42 experiments in Belyy). Despite elimination of the first feeding, during the first week the animals continued to go from the door of the experimental room to the feeder table; however, receiving no food, they went to the mat for several seconds and then returned to the table. Thus, during the first 2-3 min of the experiment they made 3-5 such trips and then went to the mat and sat on it until the first conditioned stimulus in the stereotype was applied. During the first 3-5 days after extinction began there was a decrease in the latent period of the conditioned reflex and a slight increase in the rate of the motor reactions in response to application of the first conditioned stimulus in the stereotype; the animal did not always return to the mat immediately after eating and intersignal trips to the feeder were observed. Conditioned-reflex activity was normal on subsequent days.

Beginning with the second week, the animals went to the table on entering the room, but, not receiving food, went to the mat and did not again go to the table until the conditioned stimulus was applied. Only on the 42nd day after elimination of the first reinforcement did Smirnyy go immediately to the mat rather than to the feeder table on entering the experimental room and remain quietly seated until the first positive conditioned stimulus was applied. However, the first trip to the feeder was not stably extinguished in Smirnyy even after 526 reinforcements (experimental days).

The second dog, Belyy, first went directly to the mat on entering the experimental room on the 33rd day after elimination of the first feeding, but this reaction was very rarely observed over the following 700 experiments. When he entered the room Belyy usually went to the table, jumped up onto it, approached the feeder, inspected it for several seconds, sometimes sniffed or licked the empty pan, and then jumped down to the floor and went to the mat. In the rare instances when Belyy went to the mat immediately after entering the room he remained on it for only a few seconds and then began to sniff adjacent squares or drank water from his dish, looking at the feeder from time to time and finally returning to the mat.

More complex conditioned-reflex motor activity was developed in Boy and Dzhek than in Smirnyy and Belyy. Among the factors involved were the following: 1) in addition to employing 8 positive and 3 (rather than 2) differential stimuli in the experiment, positive differentiation of the tables was induced, i.e., the animal received food at table 1 when some positive stimuli were applied and at table 2 when others were applied; 2) the stereotype was fixed over a longer period; 3) reinforcement was discontinued at both tables rather than just one.

The conditioned-reflex activity displayed by Boy and Dzhek proceeded in the following manner: on entering the room the animal received reinforcement first at table 1 and then at table 2 and went to the mat on square 25. The dog went to table 1 when the bell was sounded and to table 2 when the metronome was applied. The positive stimuli a bell and a metronome) were applied from a shelf on the wall to the animal's right, while the inhibitory (differential) metronome was applied to his left. The conditioned stimuli were applied stereotypically at intervals of from 10 to 45 sec.

After the stereotype had been fixed in Boy over 289 experiments and in Dzhek over 97 experiments, investigations involving extinction of the first trip to both feeders were conducted.

Elimination of the first portions of food at both tables led to a clear change in Boy's conditioned-reflex activity on the first day (experiment on 24/X 1957), which was manifested in prolongation of the latent periods of the conditioned reflexes to 2 sec (from the normal 0.5 sec), disruption of the differentiation of the tables, deinhibition of the inhibitory differential stimuli, and appearance of subsequent inhibition. The animals' behavior during the intervals between applications of the conditioned stimuli was also altered: the dog began to remain on the table for 25-40 sec after eating (as compared with the normal 1-3 sec) and did not return to the mat.

On the second and third experimental days (experiment of 26/X 1957) the dog went to the feeder tables immediately on entering the room but, finding no food, began to move aimlessly about the room, sometimes passing over the mat but not stopping on it. Since the conditioned positional reflex was disrupted on these days, the stereotypic conditioned stimuli were not applied.

On the fourth through twelfth experimental days (experiment of 14/XI 1957) Boy continued to make an initial trip to the feeder tables. His movements about the room were still aimless, but he went to the mat a few minutes after the experiment began, which made it possible to apply the stereotypic conditioned stimuli. These experiments showed that the differential reflexes were deinhibited and then successively inhibited during this period.

Record of Experiment on 24/X 1957. Dog Boy
(First day of elimination of first reinforcements at both tables)

1 Число применений условного раздражителя	2 Условный раздражитель	3 Латентный период условного рефлекса (сек)	4 Время побежки к столу (сек)	5 Время еды (сек)	6 Время возвращения на коврик (сек)
1156	Метроном правый 7	0,5	2	20	35
1154	Звонок 8	1	2	21	20
840	Метроном левый 9	2	10	—	37
1157	» правый	1	2	20	35
1155	Звонок	0,5	2	21	40
841	Метроном левый	2	2	—	25
1158	» правый	3	2	20	25
1156	Звонок	0,5	2	20	30
842	Метроном левый	—	—	—	—
1159	» правый	0,5	2	20	30
1157	Звонок	2	2*	—	15

* Dog went to table 1 but not to table 2 and therefore did not receive food.

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) time required to to to table (sec); 5) eating time (sec); 6) time required to return to mat (sec); 7) right-hand metronome; 8) bell; 9) left-hand metronome.

Record of Experiment on 26/X 1957. Dog Boy
(Third day of elimination of first reinforcements at both tables)

On entering the room the dog first went to table 2 and then to table 1, but, finding no food in the feeders, he jumped down to the floor and made random movements about the room for 8 min 50 sec, periodically jumping sometimes onto table 1 and sometimes onto table 2. He occasionally passed over the mat but did not stop on it. Since the conditioned reflex involving the animal's position in the experimental room was clearly disrupted, the stereotypic conditioned stimuli were not applied and the experiment was halted after 9 min.

Elimination of the first feeding thus caused clear and persistent disruptions of conditioned-reflex activity in Boy. The first feeding was subsequently resumed (on the 13th day) in order to restore normal behavior. Nevertheless, the dog periodically exhibited instability of the differential reflexes and subsequent inhibition over the following 2 months and 10 days; disruption of the differentiation of the tables was observed in some experiments. It was only midway through the third month that the animal's entire induced activity returned to normal.

Using the same sequence of experiments for the dog Dzhek, elimination of the first portion of food also caused material disruption of higher nervous activity. It is interesting that, in addition to the changes observed in Boy, Dzhek displayed a pronounced stereotype of impatience, i.e., he made rapid circling movements about the mat but did not sit on it; the motor reactions during the intervals between applications of the conditioned stimuli sometimes had a random character, the dog going to the door, scratching at it, whining, etc. It was necessary to halt the experiment in these cases (experiment of 17, 18, and 21/X 1957).

It was thus impossible to completely extinguish the first trip to the feeder table in any of the four dogs, despite the very prolonged period of nonreinforcement for some of them (526 experiments for Smirnyy and 700 for Belyy); secondly, attempts to extinguish the first trip to the feeder led to disruption of the induced conditioned-reflex motor activity.

There arises the question of why it was more difficult to extinguish the first trip to the feeder from the other reflexes. Let us analyze the data we obtained. Animals with stably developed conditioned situational reflexes went from the door of the experimental room to the feeder table only at the beginning of the experiment, immediately on entering the room. During the intervals between applications of the conditioned stimuli the animal sometimes went to the door but never went from it to the feeder table unless the positive conditioned stimuli were applied. What was the conditioned stimulus for the first conditioned motor reaction — going to the feeder table? It can be assumed that the first feeding reinforced a very complex conditioned stimulus extending over a substantial period of time (a delayed conditioned after-reflex) and including such components as the attendant's entering the vivarium, the animal's path from the vivarium to the door of the experimental room, removal of the leash from the animal's neck, and opening of the door of the experimental room. The strongest components of this system were apparently the two latter stimuli, removal of the leash and opening of the door.

The strongest stimulus of the complex acting on the animal when he entered the experimental room was the sight of the feeder from which he always received the first portion of food at the beginning of the experiment. The stereotypic motor activity induced under the conditions of the experimental room began with the first trip to the feeder table.

In our experiment the entire chain of conditioned stimuli, including the first trip to the feeder table and the subsequent

Record of Experiment on 14/XI 1957. Dog Boy

1 [illegible]	2 Условный раздражитель	3 [illegible]	4 [illegible]	5 [illegible]	6 [illegible]
7 [illegible]					
[illegible]	Метроном правый 8	0,5	2	22	25
1181	Звонок 9	0,5	2	20	20
880	Метроном левый 10	0,5	2	—	20
1184	» правый	2	2	21	20
1182	Звонок	0,5	2	22	2
881	Метроном левый	0,5	2	—	25
1185	» правый	2	2	21	2
1183	Звонок	0,5	2	20	30
882	Метроном левый	0,5	2	—	40
1186	» правый	2	2	21	2
1184	Звонок	0,5	2	21	—

1) Number of applications of conditioned stimulus; 2) conditioned stimulu; 3) latent period of conditioned reflex (sec); 4) time required to go to table (sec); 5) eating time (sec); 6) time required to return to mat (sec); 7) dog went first to table 2 and then to table 1 but, finding no food in the feeders, jumped down to the floor and made aimless movements about the room for 5 min; after 6 min he went to the mat and sat quietly on it for 2 min; 8) right-hand metronome; 9) bell; 10) left-hand metronome.

stereotype of conditioned stimuli, was linked into a single functional system in the animal, disruption of one link of which led to a change in the entire induced system. These changes were transient in some animals (Smirnyy, Belyy), while in others (Boy, Dzhek) they were manifested in a prolonged disruption of the previously developed conditioned-reflex activity. All this apparently depends on the individual properties of the animal's nervous system, the complexity of the experiment, and the stability of the conditioned reflexes.

Extinction of conditioned reflexes by gradual reduction of alimentary-center excitability

It has long been known that conditioned alimentary reflexes are stronger in a hungry animal than in one that is somewhat satiated and that they disappear completely in an animal that is wholly replete, so that he refuses food. Hunger, initially developing in the subcortex, increases the tonus of the cortex, making it capable of conditioned-reflex alimentary activity (I.P. Pavlov, 1927; P.S. Kupalov, 1946).

Record of Experiment on 17/X 1957. Dog Dzhek

1 [illegible]	2 Условный раздражитель	3 [illegible]	4 [illegible]	5 [illegible]	6 [illegible]
344	Звонок 7	0,5	2	19	3
434	Метроном правый 8.	0,5	2	20	4
291	» левый . . 9.	—	—	—	—
435	» правый	0,5	2	19	3
345	Звонок	0,5	2	20	2
292	Метроном левый	—	—	—	—
436	» правый	0,5	2	20	3
346	Звонок	0,5	2	19	4
293	Метроном левый	—	—	—	—
437	» правый	0,5	2	20	4

10 Протокол опыта с обычной условнорефлекторной деятельностью животного.

Note: The action time of each stimulus was 5 sec. The dog remained quietly seated on the mat during the action of the differential left-hand metronome.

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) time required to go to table (sec); 5) eating time (sec); 6) time required to return to mat (sec); 7) bell; 8) right-hand metronome; 9) left-hand metronome; 10) record of experiment involving animal's usual conditioned-reflex activity.

V.D. Volkova set herself the task of determining how and in what sequence the induced conditioned-reflex motor activity of an animal is altered when he is gradually satiated by repeated conjunction of the conditioned stimuli with food on a single experimental day.

These investigations were conducted on 5 dogs with a stably induced system of conditioned reflexes consisting of 8 positive and 2 differential stimuli. The conditioned stimuli were applied stereotypically. The reinforcement was 15z of powdered meat biscuit wetted with water (1:1) and 10z of mea .

On the day of the extinction, after an ordinary experiment had been conducted, the dog was taken from the room for 3-5 min, during which time food was placed in the feeder, and then brought back for another experiment; this was repeated until all the induced conditioned motor reflexes had been completely extinguished.

By way of illustration, let us consider in greater detail the extinction of conditioned situational reflexes in the dog Dzhek by gradual satiation (Table 3; record of experiment on 18/IX 1961).

Record of Experiment on 18/X 1957. Dog Dzhek

1 Число применений условного раздражителя	2 Условный раздражитель	3 Латентный период условного рефлекса (сек)	4 Время побежки к столу (сек)	5 Время еды (сек)	6 Время возвращения на коврик (сек)
	7 (Отменен первый подкорм на обоих столах)				
347	8 Звонок	0,5	2	18	[illegible]
433	Метроном правый	0,5	2	20	[illegible]
294	» левый 10	0,5*	—	—	[illegible]
439	» правый	2	2	20	75
348	Звонок	0,5	2	20	[illegible]
295	Метроном левый	0,5*	—	—	[illegible]
440	» правый	2	2**	—	[illegible]
349	Звонок	1**	—	—	[illegible]
296	Метроном левый	0,5*	—	—	[illegible]
441	» правый	2	2	19	К двери, на коврик не идет. Опыт прекращен 11

* Went to door.
** Positive differentiation of tables disrupted, i.e., dog went to table 2 in response to conditioned stimuli to which a conditioned reflex involving going to table 1 had been formed, and vice versa.

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) time required to go to table (sec); 5) eating time (sec); 6) time required to return to mat (sec); 7) first eating at both tables; 8) bell; 9) right-hand metronome; 10) left-hand metronome; 11) went to door but not to mat. Experiment discontinued.

It can be seen from Table 3 and the experimental record that the extinction of Dzhek's situational conditioned reflexes during gradual satiation began with an increase in the latent periods of the conditioned reflexes and a decrease in the rate of the motor reactions. The reflexes then became unstable and finally were completely extinguished. In this case it became clear that the conditioned reflexes to the weakes conditioned stimulus (the light) were inhibited first, followed by those to the stronger stimuli (the bell and the sound of the feeder). The last to be extinguished were the reflexes to the natural conditioned alimentary stimuli – the sight and odor of the food. After 3-4 consecutive experiments, Dzhek's behavior during the intervals between applications of the conditioned stimuli was altered: he began to remain on the table after eating, did not always go immediately to the mat on jumping down to the floor, began to wander about the room, examining and sniffing the floor and the objects on it, went to the door, sometimes jumped up onto table 2, where he had never before received food, etc.

Record of Experiment on 21/X 1957. Dog Dzhek (Fourth day after discontinuation of first feeding)

1 [illegible]	2 Условный раздражитель	3 [illegible]	4 [illegible]	5 [illegible]	6 Время возвращения на коврик (сек)
[illegible]	Звонок 7	8 0,5	2	19	80
446	Метроном правый	0,5	2	20	10 100
300	» левый	9 0,5	2		Прыгает на стол, но не получив еды, сходит со стола на пол и в течение 5 мин хаотически бегает по комнате, иногда подбегая к двери, нарапая ее и скуля или вскакивая на столы, затем появились манежные движения вокруг коврика, мочеиспускание, дефекация, одышка. Опыт прекращен

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) time required to go to table (sec); 5) eating time (sec); 6) time required to return to mat (sec); 7) bell; 8) right-hand metronome; 9) left-hand metronome; 10) jumped up onto table but, not receiving food, jumped down to floor and moved randomly about room, sometimes going to door, scratching at it, and whining or jumping onto tables; the animal then made circling movements about the mat, urinated, deficated, and panted. The experiment was halted.

These regularities in reflex extinction were also observed in the other four dogs (Table 4).

It was further found that the alimentary excitability at which the conditioned motor reflexes were completely extinguished was not always reduced to the null level, since if the same animals were given food (meat and powdered meat biscuit) outside the experimental room after the experiment involving complete extinction of the conditioned reflexes, they often ate a certain amount of meat (50-100 g).

Different animals behaved differently in the experimental room after complete satiation: Una returned to the mat after eating, lay down on it, rested her head on her front paws, and did not subsequently react either to application of the usual distant conditioned stimuli or to the sound of the feeder. This indicates that the inhibition apparently irradiated from the alimentary center to definite areas of the motor analyzer.

For other dogs the conditioned stimuli did not always become completely indifferent after the conditioned motor reflexes had been extinguished, but often caused various motor reactions: some animals began to sniff the mat or move to adjacent squares or went to the water dish and drank when the conditioned stimuli were

TABLE 3

Extracts from Records of Experiments Conducted on Dog Dzhek on Day of Extinction of Conditioned Situational Reflexes by Gradual Satiation

[1] № опыта в день угашения	[2] Величина латентных периодов условных рефлексов (сек)	[3] Время побежки от коврика до кормушки (сек)	[4] Примечание
1.	0,5—1,0	2—3	[5] При действии звонка или света сразу бежит на стол к кормушке, ест пищу и возвращается на коврик. При действии метронома стоит на коврике. В интервалах между действием усл. раздраж. спокойно стоит на коврике. Время еды 10—15 сек
2	0,5—1,0	2—3	[6] То же
3	0,5—1,0	2—3	» »
4	1,0	2—3	[7] Уменьшилось время еды до 8—12 сек за счет того что собака съедает не весь мясо-сухарный порошок из чашки. После окончания еды не всегда сразу становится на коврик. Отмечаются единичные случаи подхода к выходной двери (на 2—3 сек)
5	1—1,5	2—4	[8] То же. Увеличились латентные периоды условных рефлексов на свет и время побежки.
6	1,0—1,5	2—4	[9] То же, что и в 5-м опыте
7	1,0—2,0	2—4	[10] Рефлекс на свет стал нестойким. Из кормушки ест только мясо. Участились побежки к двери. 2 раза пила воду из чашки. На коврике иногда стоит хвостом к кормушке
8	2—3	3—5	[11] Условный рефлекс на свет отсутствует. В начале опыта увеличились скрытые периоды условных рефлексов на звонок, потом рефлекс на звонок стал нестойким.

1) Experiment No. on day of extinction; 2) latent periods of conditioned reflexes (sec); 3) time required to go from mat to feeder (sec); 4) note; 5) went immediately to feeder table under action of bell or light, ate food, and returned to mat. Remained on mat under action of metronome. Sat quietly on mat during intervals between applications of conditioned stimuli. Eating time 10-15 sec; 6) the same; 7) eating time decreased to 8-12 sec because dog did not eat entire portion of powdered meat biscuit in tray. He did not always immediately return to the mat after eating. In some cases he went to door (for 2-3 sec); 8) the same. Latent periods of conditioned reflexes to light and time required to go to table increased; 9) the same as in 5th experiment; 10) reflex to light became unstable. Dog ate only meat from feeder. Trips to door became more frequent. Twice drank water from dish. Sometimes sat on mat facing away from feeder; 11) conditioned reflex to light absent. Latent periods of conditioned reflexes to bell increased at beginning of experiment and reflexes then became unstable.

Record of Experiment on 18 September 1961. Dog Dzhek (9th Experiment on Day of Extinction)

[1] Интервалы между действием условных раздражителей (мин)	[2] Число применений условного раздражителя в день угашения	[3] Условный раздражитель	[4] Время действия условного раздражителя (сек)	[5] Латентный период условного рефлекса (сек)	[6] Поведение собаки при действии условного раздражителя
1	93	[7] Звонок	5	1,5	[9] Время еды — 3 *сек*. Ест только мясо. После еды в течение 4 *сек* стояла около кормушки, затем, спрыгнув на пол, побежала к выходной двери. Около двери стояла 12 *сек*, затем встала на коврик
1	93	[8] Свет	7	—	[10] Продолжает спокойно стоять на коврике. На 7-й *сек*, на стук кормушки, сразу побежала на стол, ест мясо, возвращается на коврик
1	94	Звонок	5	1,5	[11] Бежит к кормушке, ест, спрыгивает со стола на пол, идет к двери, стоит спокойно у двери 5 *сек*, идет к чашке с водой, пьет, становится на коврик
1	94	Свет	5	3,0	[12] Очень медленно идет к кормушке, ест, прыгает на пол, идет к двери, скребет ее, на 30-й *сек* становится на коврик
1	43	М-120	5	—	[13] Спокойно стоит на коврике
1	95	Звонок	5	2	[14] Медленно бежит к кормушке, смотрит на еду, но так и не дотронувшись до пищи, на 6-й *сек* спрыгнула со стола на пол и пошла к двери. В течение 6 *сек* стояла около двери, затем встала на коврик
1	95	Свет	5	—	[15] Спокойно стоит на коврике 5 *сек*. Затем свет выключается и в тот же момент включается кормушка — на стук кормушки сразу пошла на стол, взяла кусочек мяса из чашки кормушки и сразу вернулась снова на коврик и только там медленно съела его

Continued

1 [illegible]	2 [illegible]	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Поведение собаки при действии условного раздражителя
1	96	Звонок 7	5	—	16 Та же реакция, что и на 94-е применение звонка, т. е. подбежав к кормушке, собака лишь посмотрела на пищу, а затем сразу спрыгнула на пол и побежала к двери, начала скрести ее, скулить — это длилось 2 мин. На этом фоне были даны следующие раздражители стереотипа
2,5	44	М-120	5	—	17 Продолжает стоять у двери, скулит
1	96	Свет 8	10	—	18 Продолжает стоять у двери, скребет дверь лапой. На стук кормушки не реагирует
1	97	Звонок	10	—	19 Яростно скребет дверь, лает. На стук кормушки не реагирует

20 Опыт прекращен

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus on day of extinction; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) bell; 8) light; 9) eating time 3 sec. Ate only meat. Stood near feeder for 4 sec after eating and then jumped to floor and went to door. Stood near door for 1? sec and then went to mat; 10) remained quietly standing on mat. Immediately went to table after 7 sec in response to sound of feeder, ate meat, and returned to mat; 11) went to feeder, ate, jumped from table to floor, went to door, stood quietly near door for 5 sec, went to water dish, drank, and returned to mat; 12) went very slowly to feeder, ate, jumped down to floor, went to door, scratched at it, and returned to mat after 38 sec; 13) sat quietly on mat; 14) went slowly to mat, looked at food but did not touch it, jumped from table to floor after 6 sec, and went to door. Remained near door for 6 sec and then returned to mat; 15) sat quietly on mat for 5 sec. Light was then switched off and feeder simultaneously switched on; the dog went immediately to the table in response to the sound of the feeder, took a piece of meat from the tray, went straight back to mat, and only then slowly ate; 16) the same reaction as on the 94th application of the bell, i.e., dog went to feeder, only looked at food, immediately jumped down to floor, went to door, began to scratch at it, and whined, this occupying 2 min. The subsequent stereotypic stimuli were applied against this background; 17) remained standing at door, whined; 18) remained standing at door and scratched at it. Did not react to sound of feeder; 19) scratched vigorously at door and barked. Did not react to sound of feeder; 20) experiment halted.

TABLE 4

Rate of Extinction of Conditioned Motor Reflexes in Different Dogs

1 [illegible]	2 [illegible]				7 [illegible]
	3 [illegible]		6 [illegible]		
	4 [illegible]	5 [illegible]	[illegible]	[illegible]	
8 Уна	—*	—	41	40	10
9 Спутник	30	18	32	28	8
10 Джек	28	23	37	25	9
11 Белый	25	23	38	38	10
12 Шарик	31	26	43	43	11

*The latent periods of the conditioned reflexes to the light and the bell in Una remained at 1 sec until the reflexes were completely extinguished.

1) Dog's name; 2) with which application of reinforced conditioned stimulus; 3) latent period of conditioned reflex increased; 4) in response to bell; 5) in response to light; 6) reflex extinguished; 7) during which experiment all reflexes were completely extinguished; 8) Una; 9) Sputnik; 10) Dzhek; 11) Belyy; 12) Sharik.

applied. Other animals began to run aimlessly about the room, sometimes went to the door and scratched at it, barked and whined loudly, and sometimes exhibited frequent urination and defecation. The behavior of the animals in the latter group can be said to have been neurotic in character. Similar phenomena were observed by N.P. Murav'yeva (1948) in experiments conducted on dogs by the secretory conditioned-reflex method when the portion of food given the animal was suddenly reduced from 20 to 2 g, as well as by R. Floru and M. Sterescu (1958) in experiments conducted by the situational conditioned-reflex method when the animal was completely satiated. The nervous mechanism of these motors can apparently be regarded as the result of positive induction from the inhibited areas of the cerebral cortex.

On the 2nd-3rd day after complete extinction of the situational conditioned reflexes, conditioned-reflex activity returned to normal in some animals, while others displayed a slight increase in the latent periods of the conditioned reflexes and a decrease in the speed with which they moved to the feeder. At this time the animals ate only the meat and did not touch the powdered meat biscuits; all the dogs exhibited a reduced appetite.

The foregoing shows that gradual satiation, which causes a reduction in the functional level of the alimentary center, leads to gradual disruption of the animal's entire induced alimentary conditioned-reflex motor activity. Overloading of the physiological mechanisms that regulate the ratio of conditioned excitation to unconditioned excitation may also occur in this case. R. Floru and M. Sterescu (1958) had previously arrived at a similar conclusion.

The repetition of stereotypic motor activity observed in some animals when alimentary excitation was absent or at a very low level shows that this activity (at a definite degree of reinforcement) may to some extent be independent of alimentary excitation; the entire experimental setup apparently plays a definite role in the active repetition of this induced motor activity (R. Floru and M. Sterescu, 1958; R. Floru and M. Sterescu-Volanskaya, 1959; I.S. Beritov, 1961; P.S. Kupalov, 1962; et al.).

Moreover, investigations involving extinction and reinforcement of conditioned motor reflexes showed that, when necessary, 3-6 consecutive experiments can be conducted on an animal during the same day, i.e., a comparatively large number of conditioned stimuli (30-50) can be applied without disrupting the animal's induced conditioned-reflex motor activity.

Conditioned situational reflexes can thus be extinguished by a gradual reduction of alimentary excitability. The reflexes to the conditioned stimuli of least physical strengh are inhibited first, followed by those to stronger stimuli. After complete satiation, both artificial and natural conditioned reflexes are inhibited.

Satiation results in overloading of the mechanisms that regulate conditioned and unconditioned excitation; in some animals this is manifested over the following 1-2 days in a change in normal higher nervous activity.

After complete satiation of some animals with stable reflexes, the stimulus furnished by the experimental setup becomes capable of independently activating the induced system of conditioned motor reactions.

Formation of Conditioned Inhibition

During development of conditioned salivary reflexes in I.P. Pavlov's laboratory (1909) it was established that, if an indifferent stimulus was conjoined with a conditioned stimulus to which a stable conditioned reflex had previously been formed and the two stimuli were then no longer conjoined with reinforcement, the action of the new agent had two phases. The stimulus had an active effect during the first phase and took on the role of an inhibitory agent during the second phase.

There have now been many works devoted to the characteristics of the formation of conditioned inhibition in animals (K.N. Krzhishkovskiy, 1909; G.V. Fol'bort, 1912; O.M. Chebotareva, 1913; D.S. Fursikov, 1922, and many others).

In our laboratory, M.M. Khananashvili, V.I. Syrenskiy, and V.D. Volkova have induced conditioned inhibition in dogs by the situational conditioned-reflex method.

In M.M. Khananashvili's experiments, which were conducted on the dog Sharik, conditioned inhibition was induced in the following manner: after a 60 hz tone had sounded for 5 sec, it was conjoined with a 40 watt bulb to which a stable conditioned motor reflex had previously been developed, their joint action lasting 15 sec. This combination of conditioned stimuli was not reinforced. The dog remained quietly standing on the mat during the first three applications of the tone, i.e., it continued to be an indifferent stimulus, and when it was conjoined with the visual stimulus the dog went to the feeder in precisely the same manner as he had done when the light acted alone. After the 5th application of the inhibitory conditioned stimulus, the animal went to the feeder when the tone was sounded alone. The trips to the feeder became less frequent after the 7th application of the inhibitory combination and the conditioned inhibition became stable after the 16th application.

In V.I. Syrenskiy's experiments, which were performed on the dogs Igrun and Trus, a bell was applied first and, after 3 sec, it was conjoined with a crackling noise having a positive signal value when applied separately. These stimuli acted simultaneously for 10 sec without subsequent reinforcement. Igrun failed to go to the table after the second application of these stimuli, while 13 applications were required for this to occur in Trus. The conditioned inhibition became stable in the first dog after 10 applications of the conditioned inhibitory stimulus combination and in the second dog after 49 applications.

Conditioned inhibition was induced in Sharik, Belyy, Dzhek, Una, and Sputnik in the following manner (experiments performed by V.D. Volkova). A new stimulus (a 600 hz tone) was applied 5 sec after the action of a positive conditioned stimulus (a light) began and the new agent was then conjoined with the positive conditioned stimulus. This combination of stimuli continued to act for 15 sec and was not reinforced with food. The conditioned inhibitory stimulus was the second one applied.

Let us discuss the formation of conditioned inhibition in the dog Dzhek in greater detail. He remained quietly on the mat during the first two applications of the tone and went to the feeder table when the light was conjoined with it (the latent period of the reaction being 0.5-1.0 sec). The following reaction was observed on the third application of the conditioned inhibitory stimulus: as soon as the tone was applied the dog jerked forward and left the mat, but he then abruptly slowed down and returned to the mat. When the light was switched on he went to the mat only after 3 sec. The latent periods of the conditioned reflexes to other stimuli were also somewhat prolonged on this day. The reflex became unstable between the 6th and 17th applications of the conditioned inhibitory combination and stable conditioned inhibition developed after the 18th application (Table 5).

Figure 7 shows the change in the latent periods of the conditioned motor reflexes of the dogs under investigation under the action of the conditioned inhibitory stimulus combination. It can be seen from the figure that the rate at which the conditioned inhibition appeared and became stable differed in different animals.

It proved impossible to obtain stable conditioned inhibition in Belyy even after 50 applications of the conditioned inhibitory combination without reinforcement, while in Una conditioned inhibition appeared after the 8th application and became stable after the 10th application.

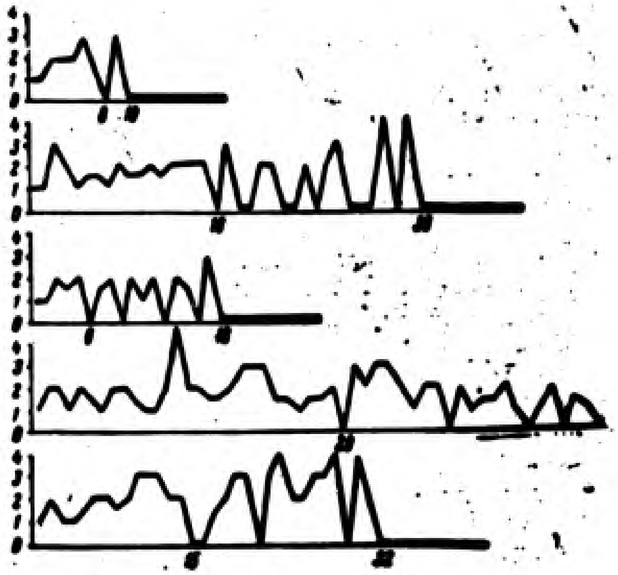

Fig. 7. Change in latent periods of conditioned motor reflexes in dogs Una (a), Sputnik (b), Dzhek (c), Belyy (d), and Sharik (e) during formation of conditioned inhibition. The number of applications of the conditioned inhibitory stimulus is shown along the abscissa and the latent period of the conditioned motor reflex in seconds is shown along the ordinate.

TABLE 5

Rate of Formation of Conditioned Inhibition

1 Кличка собаки	2 С какого применения увеличился латентный период условного рефлекса	3 С какого применения условный тормоз	
		4 появился	5 упрочился
6 Уна	3	8	10
7 Спутник	3	18	26
8 Джек	3	6	18
9 Белый	2	20	72
10 Шарик	2	15	22

1) Dog's name; 2) on which application latent period of conditioned reflex increased; 3) on which application conditioned inhibition; 4) appeared; 5) became stable; 6) Una; 7) Sputnik; 8) Dzhek; 9) Belyy; 10) Sharik.

Thus, the periods required for formation of conditioned inhibition with the animal moving freely about the experimental room were the same as those previously established by the secretory method in I.P. Pavlov's laboratory. The difference in the rates at which conditioned inhibition was formed in the various animals indicates differences in the typological characteristics of their higher nervous activity.

Formation of Delayed Conditioned Reflexes

It was demonstrated in I.P. Pavlov's laboratory (experiments conducted by P.M. Nikiforovskiy) that, if a conditioned reflex to a light with reinforcement after 30 sec was first formed and an unconditioned stimulus (acid) was then applied after 3 min, a so-called delayed conditioned reflex developed, i.e., no saliva was produced during the 1st and 2nd minutes and only during the 3rd minute, before the acid was applied, did saliva appear. Analysis showed that the delay resulted from development of internal inhibition.

A number of works by I.P. Pavlov and his students were subsequently devoted to research on retardive inhibition (I.V. Zavadskiy, 1908; F.S. Grosman, 1909; V.M. Dobrovol'skiy, 1911; N.I. Leporskiy, 1911; S.I. Potekhin, 1911; E.L. Gorn, 1912; G.V. Fol'bort, 1912; M.Ya. Bezbokaya, 1913; V.M. Arkhangel'skiy, 1924; M.K. Petrova, 1929; V.V. Yakovleva, 1926; P.S. Kupalov, 1926b, 1929b; A.G. Ivanov-Smolenskiy, 1932; F.P. Mayorov, 1938; D.I. Soloveychik, 1940; A.O. Dolin, 1940; et al.).

We studied the dynamics of the induction of delayed motor conditioned reflexes, the efficiency of the delay, and its equilibration with the excitation process in 4 dogs.

In V.D. Volkova's investigations on 2 dogs (Dzhek and Una) a system of briefly delayed (by 5 sec) conditioned motor reflexes, including both positive (bell and light) and inhibitory (metronome) stimuli, was induced first. After this system of reflexes had become stable, a delayed reflex with a lag of 1 min was developed to one of the stimuli (the light). It must be kept in mind that reinforcement was always accompanied by the sound of the feeder in our investigations. In forming a delayed conditioned reflex with a lag of 60 sec to the light, V.D. Volkova was thus actually inducing a reflex to a complex stimulus, the light and the noise of the feeder. Let us consider the formation of the delayed conditioned reflex in the dog Dzhek in greater detail.

We observed the following changes in Dzhek's induced conditioned-reflex activity after the delay in reinforcement was increased from 5 to 60 sec: as usual, the dog went immediately to the table when the light was switched on and approached the feeder but, finding no food, he sniffed the tray, scratched at it with a paw, and, after 6 sec, jumped down to the floor and returned to the mat. After remaining on the mat for 5 sec, he returned to the feeder and then went back to the mat. After 60 sec, he went to the table in response to the noise made when the feeder was switched on and received food.

From the second to the seventh applications of the delayed conditioned stimulus, the dog went to the table and, finding no

Record of Experiment on 4 May 1962. Dog Dzhek

1 [illegible]	2 [illegible]	3 Условный раздражитель	4 [illegible]	5 [illegible]	6 Поведение собаки при действии условного раздражителя
1	1216	[7] Звонок	5	1	[10] Сразу бежит к кормушке
1	(25)	[8] Свет	60	—	[11] Повернула голову, смотрит на свет, но продолжает стоять на коврике. На 60-й сек на звук включения кормушки сразу побежала к столу
1	1217	[7] Звонок	5	1	[10] Сразу бежит к кормушке
1	26	[8] Свет	60	—	[12] Вначале спокойно стояла на коврике, а на 43-й сек стала переступать лапами на коврике, смотрит на свет. На 60-й сек на стук кормушки бежит к столу.
1	411	[9] Метроном	5	—	[13] Спокойно стоит на коврике
1	1218	[7] Звонок	5	1	[14] Бежит к кормушке
1	(27)	[8] Свет	60	—	[15] Спокойно стоит на коврике. На стук кормушки бежит к столу
1	1219	[7] Звонок	5	1	[14] Бежит к кормушке
1	412	[9] Метроном	5		[13] Спокойно стоит на коврике
1	(28)	[8] Свет	60	—	[16] Смотрит на свет, стоит на коврике. На 60-й сек на звук включения кормушки бежит к столу

1) Intervals between applications of conditioned stimuli (min); 2) number of applications of conditioned stimulus; 3) conditioned stimulus; 4) action time of conditioned stimulus (sec); 5) latent period of conditioned reflex (sec); 6) dog's behavior under action of conditioned stimulus; 7) bell; 8) light; 9) metronome; 10) immediately went to feeder; 11) turned head, looked at light, but remained on mat. After 60 sec, immediately went to table in response to sound of feeder being switched on; 12) stood quietly on mat at first, but after 43 sec began to shift paws on mat and look at light. After 60 sec, went to table in response to sound of feeder; 13) stood quietly on mat; 14) went to feeder; 15) stood quietly on mat. Went to table in response to sound of feeder; 16) looked at light and stood on mat. After 60 sec, went to table in response to sound of feeder.

food in the feeder, jumped down to the floor and returned to the mat. Remaining on the mat, he attentively looked from the feeder to the sources of the conditioned stimuli; he sometimes made circular movements on the mat or shifted his paws. He went to the table only when he heard the sound of the feeder.

Beginning with the 8th application of the delayed stimulus, the latent period of the conditioned motor reflex increased to 1½-3 sec (as against the normal ½-1 sec); after going to the table, the dog usually stood quietly on the mat until the feeder was switched on.

On the 19th application of the retardive conditioned stimulus, the dog went not to the feeder table but to the door and lay down near it, but he returned to the mat after 40 sec. There was an increase in the latent period of the reaction to the briefly delayed positive conditioned stimulus (the bell), which followed the retardive stimulus. The delayed reflex subsequently became unstable and was totally extinguished after the 24th application; when the light was switched on the dog either remained sitting on the mat or just barely turned his head toward the lamp, looked at it, and sometimes licked his chops, but he did not move from the mat until the feeder was switched on (see the experiment on 4 May 1962).

Despite 100 conjunctions of the retardive conditioned stimulus with reinforcement, the animal remained on the mat when the light was applied and went to the feeder only when he heard it being switched on. However, it must be noted that the animal sometimes took up a more active pose 40-50 sec after the light was applied: if he were sitting or lying on the mat, he stood up, shifted from paw to paw, and began to look from the feeder to the sources of the conditioned stimuli. Similar phenomena were observed in the dog Una.

In O.N. Voyevodina's investigations (1956), which were conducted on the dogs Al'ma and Reni, a conditioned reflex was first formed to a metronome with a delay of 5 sec and a delayed conditioned reflex was then induced to a complex sequential stimulus consisting of a 250 watt bulb (120 sec for Reni and 150 sec for Al'ma), a 10-sec pause (with the light switched off), and the positive conditioned stimulus (metronome) acting for 5 sec. While the first applications of the retardive conditioned stimulus caused the dogs to run to the table and jump up onto it, on subsequent applications they merely went to the table, jumped onto the bench, and returned to the mat. Beginning with the 10th-15th application of the retardive conditioned stimulus, the animals either did not react to the light or took 1-2 steps forward and stopped; they went to the table only when the metronome was switched on. The reaction to the retardive conditioned stimulus subsequently changed: the animals lay down on the mat 20-40 sec after the light was switched off and then left the mat and went to the feeder only when the light was switched on (after 120-150 sec) or when the metronome was sounded.

Analysis of the experimental data thus shows that a dog exhibits a conditioned motor reflex to a retardive conditioned stimulus only in response to the component of the stimulus closest to the reinforcement. The active phase of the delayed motor reflex is manifested in preparation for the execution of the conditioned reflex (the dog gets up from the mat, begins to shift his paws, turns his head toward the conditioned and unconditioned stimuli, etc.).

Conflict of Conditioned Reflexes

It was shown in I.P. Pavlov's laboratory that a so-called conflict, the impingement of stimulatory and inhibitory processes, is one of the factors capable of causing a disruption of higher nervous activity in animals (I.P. Pavlov, 1925; I.P. Razenkov, 1925; M.K. Petrova, 1926; L.N. Fedorov, 1928; D.I. Soloveychik, 1928; V.V. Stroganov, 1928; I.O. Narbutovich, 1928; I.V. Malkiman, 1936; et al.). We became interested in conducting similar investigations during the induction of conditioned situational reflexes.

In investigations conducted on the dogs Akkord and Dzho, O.N. Voyevodina developed positive conditioned reflexes (going to table 1) to the light of a 200 watt bulb and to a 120 bpm metronome located to the right of the feeder table and two inhibitory differentiated reflexes to the light of a 40 watt bulb and to a 120 bpm metronome differing from the positive metronome in its pitch and in its location in the experimental room, being positioned to the left of the feeder. A total of 8 positive and 6 differential conditioned stimuli were applied on each experimental day, acting stereotypically (record of experiment on 11 December 1961). In investigations conducted by V.D. Volkova on the dogs Dzhek, Una, Sharik and Sputnik, positive conditioned reflexes were induced to a bell and a light and an inhibitory differential reflex was induced to a metronome; in Belyy positive conditioned reflexes were developed to a metronome and a light and an inhibitory reflex was developed to a bell. A total of 8 positive and 2 differential conditioned stimuli were applied stereotypically on each experimental day.

After the stereotype of conditioned reflexes became stable, three types of experiments involving conflict among basic nervous processes were conducted.

In the first type of experiment the inhibitory conditioned stimulus was applied one second after the positive stimulus and the two stimuli then acted together for 15 sec. This test was at first conducted once in a single experiment and, after 7-10 days, was repeated on three consecutive days (once in each experiment). The second type of experiment differed from the first only in the fact that the differential stimulus was conjoined with the positive stimulus 0.5 sec after the latter began to act (record of experiment on 12 December 1961). In the third type of experiment the inhibitory stimulus was applied first and then conjoined with the positive stimulus after one second. None of these stimulus combinations were reinforced with food. The intervals between the first and second types of conflict experiments were 7-15 days, while those between the second and third types were approximately one year.

The latent period of the conditioned motor reaction, i.e., the time from application of the conditioned stimulus to the beginning of the motor act, was usually 0.5 sec in all the animals investigated.

The following phenomenon was observed in all the animals as a result of the conflict between excitation and inhibition in the first type of experiment: the animal immediately went to the feeder table when the positive conditioned stimulus was applied; application of the inhibitory conditioned stimulus after 1 sec (while the positive stimulus was still acting) did not disrupt the course of the conditioned motor reaction already in progress and had no effect on subsequent conditioned reflexes or on the animal's general behavior (see the experiment on 15 December 1961, with the dog Akkord).

Similar results were obtained for 5 of 7 animals in the second type of experiment, but two dogs (Akkord and Belyy) exhibited only a prolongation of the latent period of the conditioned motor reflex to 2 sec (see the experiment on Akkord on 12 December 1961).

The dogs displayed different reactions in the third type of experiment, in which the inhibitory conditioned stimulus was applied first and then conjoined with the positive stimulus after one second. Thus, for example, the conflict did not cause any changes in higher nervous activity in Dzhek, Una, or Sputnik: they remained quietly on the mat when the inhibitory stimulus was applied and went to the feeder table when the positive stimulus was applied, but, finding no food in the feeder, they jumped from the table to the floor and returned to the mat. Sharik also remained quietly on the mat when the inhibitory stimulus was applied and went to the feeder table when it was conjoined with the positive stimulus; he looked at the empty feeder tray for 5 sec and then jumped from the table and went back to the mat. However, after standing on the mat for 5 sec, he began to walk around the room and whine; he again returned to the mat after 35 sec. The remainder of Sharik's conditioned-reflex activity was normal both on the day of the conflict and on subsequent days. In Dzhek, Malysh, and Akkord, the conflict caused a prolongation of the latent period of the conditioned motor reflex (to 2-3 sec) and an increase in the time required to reach the feeder table.

Record of Experiment on 11 December 1961. Dog Akkord

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Подкреплено	6 Поведение собаки при действии условного раздражителя
1428	7 +М	5	0,5	9 Да	11 При действии положительных условных раздражителей бежит на стол 1, съедает подкорм и возвращается на коврик; при действии тормозных продолжает стоять на коврике
1071	8 —Св	5	—	10 Нет	
1428	+Св	5	0,5	Да	
1071	—М	5	—	Нет	
1429	+М	5	0,5	Да	
1072	—Св	5	—	Нет	
1429	+Св	5	0,5	Да	
1072	—М	5	—	Нет	
1430	+М	5	0,5	Да	
1073	—Св	5	—	Нет	
1430	+Св	5	0,5	Да	
1073	—М	5	—	Нет	
1431	+Св	5	0,5	Да	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) reinforced; 6) dog's behav-

ior under action of conditioned stimulus; 7) metronome; 8) light; 9) yes; 10) no; 11) under action of positive conditioned stimuli dog went to table 1, ate food, and returned to mat; remained standing on mat under action of inhibitory stimuli.

Record of Experiment on 12 December 1961. Dog Akkord

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Подкрепление	6 Поведение собаки при действии условного раздражителя
1432	7 +М	5	0,5	9 Да	11 На 2-й сек побежала на стол к кормушке, 5 сек стояла на столе и смотрела на пустую чашку, затем спрыгнула на пол и встала на коврик
1074	8 —Св	5	—	10 Нет	
1432	+Св	5	0,5	Да	
1074	—М	5	—	Нет	
1433	+М	0,5+15	2,0	Нет	
1075	—М	15	—	Да	
1075	—Св	5	—	Нет	
1433	+Св	5	0,5	Да	
1076	—М	5	—	Нет	
1434	+М	5	0,5	Да	
1076	—Св	5	—	Нет	
1434	+Св	5	0,5	Да	
1077	—М	5	—	Нет	
1435	+М	5	0,5	Да	
1435	+Св	5	0,5	Да	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) reinforced; 6) dog's behavior under action of conditioned stimulus; 7) metronome; 8) light; 9) yes; 10) no; 11) went to feeder table after 2 sec, stood on table and looked at empty tray for 5 sec, then jumped down to floor and returned to mat.

Our investigations thus showed that if, in setting up the conflict, the inhibitory conditioned stimulus was applied during the first 0.5 sec of the action of the positive stimulus, i.e., during the latent period of the conditioned motor reflex, the conditioned reflex was not altered; its latent period was occasionally somewhat prolonged. If the inhibitory stimulus began to act at the end of the first second, i.e., while the conditioned motor reflex was in progress, it affected the course of the reflex.

If the inhibitory conditioned stimulus was applied first and then conjoined with the positive stimulus after one second, the conditioned-reflex activity of some dogs remained unchanged, others exhibited an increase in the latent period of the conditioned motor reflex and a prolongation of the time required to reach the table, and still others displayed increased motor activity during the intervals between applications of the conditioned stimuli; only one dog (Belyy) failed to respond to the positive stimulus with a conditioned motor reflex. When the positive conditioned stimulus (metronome) was applied while the inhibitory stimulus (bell) was acting, Belyy merely turned his head slightly and looked toward the feeder, but did not leave the mat (see the experiment on 24 April 1963).

The animals' conditioned-reflex activity proceeded normally on subsequent applications of the positive and inhibitory conditioned stimuli (see the experiment on 24 April 1963).

It can be seen from the data presented that, despite repeated conflicts, there were no severe or persistent changes in the higher nervous activity of the experimental animals under the aforementioned experimental conditions, which can evidently be attributed both to the high lability of the nervous processes in the motor analyzer and to the typological characteristics of the animals' nervous systems, which were of the "strong" type.

Record of Experiment on 15 December 1961. Dog Akkord

1	2	3	4	5	6 Поведение собаки при действии условного раздражителя
1442	7 +М	5	0,5	9 Да	11 Сразу побежала на стол 1, 7 ск стояла на столе и смотрела на пустую чашку, затем спрыгнула на пол и встала на коврик
1083	8 —Св	5	—	10 Нет	
1444	+Св	5	0,5	Да	
1084	—М	5	—	Нет	
1443	+М	1+15	0,5	»	
1085	—М	15		»	
1084	—Св	5	—	Да	
1445	+Св	5	0,5	Нет	
1086	—М	5	—	Да	
1444	+М	5	0,5	Нет	
1085	—Св	5	—	Да	
1446	+Св	5	0,5	Нет	
1087	—М	5	—	Да	
1445	+М	5	0,5	Нет	
1447	+Св	5	0,5	»	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) reinforced; 6) dog's behavior under action of conditioned stimulus; 7) metronome; 8) light; 9) yes; 10) no; 11) went immediately to table 1, stood on table and looked at empty tray for 7 sec, then jumped to floor and returned to mat.

Modification of Conditioned Reflexes

In A.T. Selivanova's experiments on the dogs Dzhek and Tobik, situational conditioned reflexes were induced to a bell, a metronome, and a light and an inhibitory differentiated reflex was formed to a buzzer. The conditioned stimuli were applied stereotypically. After the stereotype had become stable, one of the positive conditioned reflexes (to the bell) was converted to a nega-

Record of Experiment on 24 April 1963. Dog Belyy

1 [illegible]	2 [illegible]	3 [illegible]	4 [illegible]	5 [illegible]	6 Поведение животного при действии условного раздражителя
1633	[7] М-120	5	0,5	Да [11]	[13] Бежит к кормушке, ест, возвращается на коврик
1580	[8] Свет	5	0,5	»	[14] То же
1634	М-120	5	0,5	»	» »
1581	Свет	5	0,5	» [12]	» »
422	[9] Звонок	5	—	Нет	[15] Спокойно стоит на коврике
1634	М-120	5	0,5	Да	[16] Бежит к кормушке
1582	Свет	5	1,0	»	» » »
423	Звонок	1+15	—	Нет	[17] Чуть повернула голову и смотрит то на кормушку, то на условные раздражители, но с коврика не сошла
1636	М-120	15	—	—	
1583	Свет	5	1,0	Да	[16] Бежит к кормушке
424	Звонок	5	—	Нет	[15] Спокойно стоит на коврике
1637	Метроном [10]	5	1,0	Да	[16] Бежит к кормушке

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) reinforced; 6) animal's behavior under action of conditioned stimulus; 7) 120 bmp metronome; 8) light; 9) bell; 10) metronome; 11) yes; 12) no; 13) went to feeder, ate, and returned to mat; 14) the same; 15) remained quietly on mat; 16) went to feeder; 17) turned head slightly and looked from feeder to conditioned stimuli, but did not leave mat.

tive reflex and the negative reflex (to the buzzer) was converted to a positive reflex.

In Dzhek, the positive conditioned stimulus (the bell) was converted to a negative stimulus after 7 unreinforced applications, while the negative stimulus (the buzzer) was converted to a positive stimulus after 19 reinforced applications; the latent period of the conditioned reflexes to the buzzer was 3-4 sec between the 19th and 29th applications (as against the normal 1 sec) and 1 sec after the 30th application.

The negative conditioned stimulus was converted to a positive stimulus for Tobik after 10 reinforced applications, but complete differentiation to the bell could not be induced even by 300 applications of this stimulus without reinforcement.

Since it is known that the rate at which a positive conditioned reflex is converted to an inhibitory reflex or an inhibitory reflex is converted to a positive reflex characterizes the lability of the nervous processes in the animal in question, it can be assumed that the differing rates observed for modification

Record of Experiment on 25 April 1963. Гog Belyy

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Подкрепление	6 Поведение животного при действии условного раздражителя
1638	[7] М-120	5	0,5	[10] Да	[12] При действии метронома и света сразу бежит на стол к кормушке; при действии звонка спокойно стоит на коврике
1584	[8] Свет	5	0,5	»	
1639	М-120	5	0,5	»	
1585	Свет	5	1,0	[11] ь	
425	[9] Звонок	5	—	Нет	
1640	М-120	5	0,5	Да	
1586	Свет	5	1,0	»	
1641	М-120	5	0,5	»	
426	Звонок	5	—	Нет	
1587	Свет	5	1,0	Да	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) reinforced; 6) animal's behavior under action of conditioned stimulus; 7) 120 bpm metronome; 8) light; 9) bell; 10) yes; 11) no; 12) went immediately to feeder table under action of metronome and light; remained quietly on mat under action of bell.

of conditioned situational reflexes in different dogs resulted from differences in their type of higher nervous activity.

The qualitative changes in the significance of the conditioned stimuli (modification) for the animals we investigated did not produce any disruptions of higher nervous activity.

FORMATION OF SITUATIONAL CONDITIONED REFLEXES BASED ON IMITATION

Imitation plays an important role under the natural conditions of animal life, since it forms the basis for expansion of individual experience by learning nonhereditary adaptive reactions from other individuals. This process has been studied by many researchers (P.F. Kapterev, 1898; L.T. Hobhouse, 1901; A.D. Kinneman, 1902; H.S. Berry, 1906 and 1908; E.L. Thorndike, 1911; W. Keller, 1930; V.M. Borovskiy, 1936; A.N. Promptov, 1944, 1947 and 1948; G.Z. Roginskiy, 1945 and 1948; B.I. Khotin, 1947; A.G. Polyakova, 1956 and 1958; et al.).

The Pavlovian conditioned-reflex method has substantially expanded our opportunities for the experimental study of imitation. This technique has been employed to study imitation in fish (L.G. Voronin, 1957; L.B. Kozarovitskiy, 1961; et al.), birds (N. Popov, 1927; B.I. Bayandurov, 1928; M. Akhmeteli, 1940 and 1941; et al.), dogs (V.Ya. Kryazhev, 1928, 1940 and 1955; M.P. Shtodin, 1941 and 1947; et al.), and monkeys (V.Ya. Kryazhev, 1940 and 1955; M.P. Shtodin, 1941 and 1947; L.G. Voronin, 1947 and 1957; L.G. Voronin and G.I. Shirkova, 1948; G.I. Shirkova, 1961; et al.).

V.Ya. Kryazhev's investigations on dogs are of particular interest to us. Kryazhev (1955) showed that the sight of an alimentary action by another animal causes changes in respiration, general motor reactions, and salivation; similar reactions are displayed to certain components of the act of eating, e.g., the sight of a human making chewing movements. It was also established that an "observer dog" responds to a protective reaction on the part of another animal with motor restlessness, panting, whining, humoral changes, etc.

Kryazhev referred to the reactions produced in response to the sight of another animal eating or effecting a protective reaction as natural imitative reflexes. He established that an artificial conditioned imitative reflex can be induced by reinforcing such natural reflexes with an indifferent stimulus.

Kryazhev found that natural imitative alimentary and defensive reflexes are difficult to extinguish even when they are not reinforced by unconditioned stimuli. According to his data, artificial conditioned imitative reflexes also have considerable stability. This author noticed a similarity between natural imitative reflexes and first-order reflexes on the one hand and artificial imitative reflexes and second-order reflexes on the otner hand. At the same time, he considers imitative reflexes to be the result of a further complication of conditioned-reflex activity.

Our investigations were intended to establish whether it is possible to induce conditioned situational reflexes based on imitation in dogs.

The first attempt to develop conditioned situational reflexes based on imitation was undertaken by O.N. Voyevodina and O.P. Yaroslavtseva. The methodological features of these experiments reduced to the following. The dog in which the conditioned situational reflex was to be induced was placed in a special cage in the experimental room.* The cage was located in the room in such fashion that the animal in it could observe the movements of the active dog. In order to systematically follow the course of the induction of the conditioned situational reflex, the active animal was removed from the room at the end of each experiment and the passive animal was released from the cage and subjected to an individual test.

Conditioned reflexes based on imitation were developed in two dogs, Dzhenni and Dzhek; Boy was the active animal.

The following complex conditioned-reflex activity was induced in Boy: on entering the experimental room, the animal went first to one feeder and then to the other, where he received the first portion of food. He then went to the mat and remained on it, going to one of the feeders and receiving food in response to the positive stimulus. A bell and a 120 bpm mechanical metronome on the left side of the room served as the positive stimuli. Boy went to feeder 2 in response to the bell and to feeder 1 in response to the metronome (see Fig. 1). A 120 bpm metronome on the right side of the room served as the negative stimulus and the animal remained on the mat when it was sounded. Each positive stimulus was applied four times and the negative stimulus three times during the course of each experiment. Boy's conditioned-reflex activity was quite clear and stable.

The first experimental day showed that the presence of a strange animal in the experimental room had a negative effect on Boy's conditioned-reflex activity. The active dog periodically went to the cage holding the passive animal, moved about the room a great deal, and often went to the door and attempted to get out. Boy's conditioned-reflex activity was somewhat improved on the second and third experimental days and was almost normal on the fourth day.

Observation of the behavior of the passive dogs over the first few days of the investigation showed that conditioned reflexes had not developed in them. After being released from the cage, the passive animal moved about the room a great deal, but did not approach the feeders. Dzhenni first went to the feeders on the fourth experimental day, i.e., the same day on which Boy's conditioned-reflex activity was completely restored. Dzhek first exhibited a similar reaction during the sixth experiment. The dogs were given reinforcement only on the first trip to each feeder during the experimental day. Dzhenni and Dzhek each participated in 13 experiments with Boy, but they did not go to the mat and remain on it.

The investigation conducted by O.N. Voyevodina and O.P. Yaroslavtseva thus showed that the dogs could be induced to approach the feeders by imitation, but a reaction involving remaining on the mat could not be produced.

G.A. Shichko made a subsequent (1959) study of imitation in dogs, in which the passive animal was not isolated by placing it in a cage. Depending on specific conditions, the passive dogs were leashed in some experiments and were not restricted in others. An electrical feeder, positive and differential loudspeakers (loudspeakers 1 and 2) of different sizes, and a water dish were placed on the floor of the experimental room during the experiments. The conditioned signal was the sound of a 120 bpm metronome originating at loudspeaker 1. The reinforcement was pieces of meat, each portion being 15-20 g. The passive dogs were not given reinforcement even when they went to the feeder in response to the conditioned signal. As in the investigation conducted by O.N. Voyevodina and O.P. Yaroslavtseva, periodic control experiments were performed on the passive dog in order to observe the development of the conditioned reflex.

A comparatively simple conditioned situational reflex consisting of the following components was induced in the active dogs: going to the positive loudspeaker, striking it with a paw (Fig. 8), going to the feeder in response to the sound of the metronome, eating the food, and returning to the loudspeaker. The dog generally did not touch the differential loudspeaker or even approach it.

This investigation was conducted on six dogs, three of whom (Zor'ka, Kashtanka, and Pal'ma) were 6-8 months old, while the others were three or more years old. The active animal in the experiments on Dzhek was Dzhul'bars; when the conditioned situational reflex had been induced and become stable in Dzhek, he served as the active animal for the other dogs.

Fig. 8. Active motor reaction in Dzhek, directed at switch 1.

The setup for the first experiment on Dzhek and Dzhul'bars was as follows: the feeder was placed on square 46, loudspeaker 1 on square 34, loudspeaker 2 on square 24, and the water dish on square 20. Dzhek was leashed on table 1, while Dzhul'bars could move freely about the room.

The presence of a passive dog in the experimental room had little effect on Dzhul'bars' behavior, essentially causing only a slight prolongation of the latent period of the trip to the feeder in response to the sound of the metronome, periodic trips to table 1, and sniffing of Dzhek.

After the ninth reinforced application of the metronome, Dzhul'bars was taken from the room and Dzhek was unleashed. The latter dog moved about the experimental room a great deal, sniffed the floor and the objects on it, and sometimes went to the feeder, which no longer contained food. On the first application of the metronome, he exhibited an orientation reaction and subsequently went to the feeder; receiving no reinforcement, he began to scratch at it. He did not go to the feeder when the metronome was applied a second time. As Table 6 shows, he usually went to the feeder in response to the sound of the metronome in subsequent test experiments. It can be seen from the table that the metronome was tested 19 times during the course of the investigation and the dog went to the feeder 14 times. A conditioned motor reflex involving going to the feeder in response to the sound of the metronome appaared on the first application of this stimulus and became stable on the sixth application.

It is of some interest that Dzhek was leashed in the first experiment, so that he could not go to the feeder after Dzhul'bars

TABLE 6

Tests with 120 bpm Metronome. Dog Dzhek

[1] Порядковый номер применения метронома	[2] № опытов	[3] Реакция животного на звуки метронома	[4] Подкрепление
1	1	[5] Слабая ориентировочная реакция, собака подошла к кормушке, царапает ее, приблизилась к динамику 1, обнюхала его, вернулась к кормушке и вновь начала царапать ее	[22] Нет
2	1	[6] Двигательная реакция отсутствует	»
3	5	[7] Собака подошла к кормушке	»
4	7	[8] К кормушке не пошла	»
5	7	» » » »	»
6	14	[9] Собака подошла к кормушке, заглянула в открытую чашку и обнюхала ее	»
7	14	[10] Собака подошла к кормушке, заглянула в открытую чашку и стала царапать ее	»
8	14	[11] В момент включения метронома находилась на столе 1 и обнюхивала расположенную на нем кормушку. На звук метронома продолжала обнюхивать кормушку	»
9	15	[12] В момент включения метронома находилась на столе 1. На условный сигнал подошла к краю стола, посмотрела на кормушку, затем спрыгнула на пол и подошла к ней	»
10	15	[13] Перед включением метронома была на столе 1. На звук метронома подошла к краю стола, посмотрела на кормушку, облизалась, спрыгнула на пол, подошла к кормушке	»
11	15	[14] Собака сразу подошла к кормушке и заглянула в открытую чашку ее	»
12	16	[15] Сначала появилась ориентировочная реакция, затем собака приблизилась к динамику 1, обнюхала его и подошла к кормушке	»
13	16	[16] Собака сразу пошла к кормушке и обнюхала ее . .	»
14	16	[17] Собака посмотрела в сторону кормушки, через 10 *сек* пошла к ней	»
15	17	[18] Двигательная реакция не появилась	»
16	17	[19] Сначала видимой реакции не было, затем собака подошла к кормушке	
17	18	[20] Перед включением метронома находилась на столе 1. На звук метронома повернулась к кормушке, посмотрела на нее, облизалась, спрыгнула со стола и подошла к ней	»
18	18	[21] В течение 5 *сек* прислушивалась, потом попила воду и сразу же пошла к кормушке	[23] »
19	18	7 Собака побежала к кормушке	20 *г* мяса

1) Sequential number of application of metronome; 2) number of experiments; 3) animal's reaction to sound of metronome; 4) reinforcement; 5) weak orientation reaction, dog went to feeder, scratched at it, approached loudspeaker 1, sniffed it, returned to feeder, and again scratched at it; 6) motor reaction absent; 7) dog went to feeder; 8) did not go to feeder; 9) dog went to feeder, looked into open tray, and sniffed it; 10) dog went to feeder, looked into open tray, and began to scratch at it; 11) was on table 1 when metronome was switched on, sniffed feeder. Continued to sniff feeder in response to sound of metronome; 12) was on table 1 when metronome was switched on. Went to edge of table in response to conditioned signal, looked at feeder, then jumped to floor and went to it; 13) was on table 1 before metro-

nome was switched on. Went to edge of table in response to sound of metronome, looked at feeder, licked his chops, jumped to floor, and went to feeder; 14) dog immediately went to feeder and looked into open tray; 15) first exhibited orientation reaction, then approached loudspeaker 1, sniffed it, and went to feeder; 16) dog immediately went to feeder and sniffed it; 17) dog looked toward feeder, went to it after 10 sec; 18) no motor reaction; 19) no visible reaction at first, dog then went to feeder; 20) was on table 1 before metronome was switched on. Turned toward feeder in response to sound of metronome, looked at it, licked his chops, jumped down from table, and went to feeder; 21) listened for 5 sec, then drank water and went immediately to feeder; 22) none; 23) 20 g of meat.

in response to the sound of the metronome. This means that the motor analyzer did not play an active part in the formation of the conditioned motor reflex in Dzhek. The following stimuli acted on Dzhek when he was on the table: Dzhul'bars' going to loudspeaker 1 and striking it with his paw, the sound of the metronome, the active animal's going to the feeder in response to this sound, the noise of the feeder, and the act of eating. All these stimuli were addressed to the visual and auditory analyzers. It is quite natural that, as a result of the periodic repetition of the action of these stimuli in the same sequence, corresponding temporal associations were formed in Dzhek's cerebral cortex. When the dog was unleashed, these associations dictated the functioning of the motor analyzer, which was manifested in periodic trips to the feeder during the intersignal pauses and in response to the sound of the metronome. Here it is pertinent to recall the investigation conducted by O.N. Voyevodina and O.P. Yaroslavtseva, in which the passive animal was kept in a cage and could not repeat the movements of the active animal, so that his motor analyzer did not participate directly in the formation of the reaction involving going to the feeders. As test experiments showed, such a reaction was nevertheless formed in the passive dogs, who periodically followed the movements of the active dog with their eyes. All this demonstrates that there is a close relationship and interaction between the motor analyzer and other analyzers, particularly the visual and auditory analyzers. It also indicates that the temporal associations formed in these two analyzers can activate the motor analyzer on the basis of existing interanalyzer temporal associations.

The investigation conducted on Dzhek showed that the feeder and loudspeaker 1 became positive alimentary stimuli for this dog during the first few experiments. This was manifested both in the fact that Dzhek periodically went to the feeder and to loudspeaker 1 in the control experiments and in his aggression toward Dzhul'bars when the latter went to loudspeaker 1 and struck it with his paw or when he approached the feeder and ate from it. Thus, at the beginning of the second experiment, Dzhek, whose movements were no longer restricted, chased Dzhul'bars from the feeder. This reaction was subsequently observed on numerous occasions. The passive dog first growled at the active dog in the fifth experiment, when the latter struck loudspeaker 1 with his paw. Dzhek subsequently growled and sometimes barked when Dzhul'bars pawed loudspeaker 1 (record of experiment 15). In some cases, Dzhek also attacked Dzhul'bars when he executed the active motor reaction (record of experiment 15 on 22 February 1960). That loudspeaker 1 and the feeder acquired the significance of alimentary stimuli for Dzhek was also indicated by the fact that he sometimes licked his chops while the active dog was striking loudspeaker 1, going to the feeder, and eating from it. Similar reactions were also observed in other dogs.

Record of Experiment No. 15 on 22 February 1960. Dogs Dzhek and Dzhul'bars[1]

[1] Время суток		[4] Условный раздражитель				[9] Подкрепление	[10] Поведение животных после дачи пищи и в межсигнальные паузы
[2] часы	[3] минуты	[5] название	[6] порядковый № применения	[7] время действия (сек)	[8] реакции животных		
15	36						[17] В комнату впущен Джек. Он ходит по комнате, обнюхал кормушку, прыгнул на стол 1
15	37,5	[11] Метроном 120 ударов в мин.	9	5	[13] Подошел к краю стола, смотрит на кормушку, облизывается, подошел к кормушке	[16] Нет	[18] Ходит по комнате, обнюхивает пол, забрался на стол 1, обнюхивает кормушку этого стола
15	39	[12] То же	10	5	То же	»	[19] От кормушки Джек пошел к динамику 1, обнюхал его, ходит по комнате. Пришел на 70-й квадрат, обнюхивает пол
15	40	» »	11	5	[14] Сразу идет к кормушке, заглянул в открытую чашку ее	»	[20] Отошел от кормушки, ходит по комнате
15	41						[21] Впущен Джульбарс. Он подошел к воде, пьет, затем осторожно подошел к динамику 1, сюда же подошел и Джек. Джульбарс ушел в сторону, вскоре и Джек удалился. Джульбарс вернулся к динамику 1 и стал ударять лапой по нему, Джек идет к кормушке и стоит около нее
15	45	» »			[15] Джек у кормушки, Джульбарс продолжает ударять по динамику	»	[22] Джульбарс отошел в сторону, вернулся к динамику, ударяет по нему. Джек стоит у кормушки. Джульбарс отошел в сторону, вновь ударяет по динамику 1.

Continued

[1] Время суток		[4] Условный раздражитель						
[2] часы	[3] минуты	[5] название	[6] порядковый № применения	[7] время действия (сек)	[8] реакция животных	[9] Подкрепление	[10] Поведение животных после дачи пищи и в межсигнальные паузы
15	45	[11] Метроном 120 ударов в минуту			[15] Джек у кормушки, Джульбарс продолжает ударять по динамику	[16] Нет	[25] Джек у кормушки, Джульбарс пришел в возбуждение, побежал к двери, пытается выйти из комнаты
15	46	[12] То же					[26] Кормушка перенесена на стол 1. Джек сразу же забрался на стол 1 и встал около кормушки. Джульбарс ударяет лапой по динамику 1 резко и часто. В результате сбил его на 35-й квадрат. Джульбарс отошел в сторону, ходит, идет к двери, вернулся к динамику, стоит и смотрит на Джека, возобновил удары. Джек спрыгнул со стола и напал на Джульбарса
15	47						[27] Джек привязан к передней ножке стола 2, динамик 1 положен на 27-й квадрат. Джульбарс ударяет по динамику 2, осторожно подошел к динамику 1 и легко ударяет по нему
15	48	» »	909°	5	[23] Джульбарс прыгнул на стол 1, подошел к кормушке, ест	[24] 20 г мяса	[28] Джульбарс съел мясо, подошел к динамику 1, но его не тронул, ударяет по динамику 2, подошел к столу 1, затем к динамику 1, ударяет по нему. Джек облизывается

Continued

Время суток		Условный раздражитель				Подкрепление	Поведение животных после дачи пищи и в межсигнальные паузы
часы	минуты	название	порядковый № применения	время действия (сек)	реакция животных		
15	49	Метроном 120 ударов в минуту	910	5	Джульбарс прыгнул к кормушке, ест. Джек смотрит и облизывается	20 г мяса	Джульбарс съел мясо, подошел к динамику 2 и ударил по нему, подошел к динамику 1 и 3 раза осторожно ударил лапой по нему
15	50	То же	911	5	То же	То же	Джульбарс, съев мясо, дважды подходил к динамику 2 и ударял по нему, три раза ударил по динамику 1
15	51	» »	912	5	» »	» »	Джульбарс, съев мясо, начал ударять по динамику 1. Джек лежит, отвернулся
15	52	» »	913	5	» »	» »	Съев мясо, Джульбарс сильно ударил по динамику 1 и сбил его на 28-й квадрат. Джек лежит
15	53	» »	914	5	» »	» »	Съев мясо, Джульбарс 3 раза ударил по динамику 1 и побежал к кормушке, вернулся, еще три раза ударил и опять побежал к кормушке, ударяет по динамику 1
15	54	» »	915	5	Джульбарс бежит к кормушке. Джек смотрит на него	» »	Джульбарс съел мясо, ходит, идет к кормушке, подошел к динамику 1, ударяет по нему. Джек смотрит на него
15	55	» »	916	5	То же	» »	Джульбарс съел мясо, ходит по комнате, подошел к динамику 1 и ударяет по нему. Джек начал лаять

Continued

1 Время суток		4 Условный раздражитель					
2 часы	3 минуты	5 название	№ 6 порядковый применения	время действия (сек) 7	8 реакции животных	9 Подкрепление	Поведение животных после дачи пищи и в межсигнальные паузы 10
15	56	11 Метроном 120 ударов в минуту	917	5	38 Джульбарс бежит к кормушке, Джек смотрит на него	24 20 г мяса	39 Джульбарс ест, Джек лает 40 Джульбарс ходит по комнате, осторожно приблизился к динамику 1. Джек усиленно лает. Джульбарс осторожно три раза ударил по динамику 1

[1]Experimental setup: the feeder was on square 55, loudspeaker 1 on square 27, loudspeaker 2 on square 35, and the water dish on square 19. *909 is the sequential number of the reinforced application of the metronome for Dzhul'bars.

1) Time of day; 2) hours; 3) minutes; 4) conditioned stimulus; 5) designation; 6) sequential number of application; 7) action time (sec); 8) animals' reactions; 9) reinforcement; 10) animals' behavior after receiving food and during intersignal pauses; 11) 120 bpm metronome; 12) the same; 13) went to edge of table, looked at feeder, licked his chops, and went to feeder; 14) immediately went to feeder, looked into open tray; 15) Dzhek went to feeder, Dzhul'bars continued to paw loudspeaker; 16) none; 17) Dzhek entered room. Walked about room, sniffed feeder, jumped up onto table 1; 18) walked about room, sniffed floor, jumped up onto table 1, and sniffed feeder on this table; 19) Dzhek went from feeder to loudspeaker 1, sniffed it, and walked about room. Went to square 70 and sniffed floor; 20) left feeder and walked about room; 21) Dzhul'bars entered room, went to water dish and drank, and then carefully approached loudspeaker 1, as did Dzhek. Dzhul'bars turned aside and Dzhek soon moved away. Dzhul'bars returned to loudspeaker 1 and began to strike it with his paw. Dzhek went to the feeder and stood near it; 22) Dzhul'bars withdrew, returned to loudspeaker, and pawed it. Dzhek stood near feeder. Dzhul'bars withdrew and then again pawed loudspeaker 1; 23) Dzhul'bars jumped up onto table 1, went to feeder, and ate; 24) 20 g of meat; 25) Dzhek remained near feeder, Dzhul'bars became excited, ran to door, and tried to leave room; 26) the feeder was transferred to table 1. Dzhek immediately jumped up onto table 1 and stood near feeder. Dzhul'bars rapidly and roughly pawed loudspeaker 1. This caused it to move to square 35. Dzhul'bars withdrew, walked about, went to the door, returned to the loudspeaker, stood and looked at Dzhek, and resumed his pawing. Dzhek jumped down from table and attacked Dzhul'bars; 27) Dzhek was tied to front leg of table 2 and loudspeaker 1 was placed on square 27. Dzhul'bars pawed loudspeaker 2, cautiously approached loudspeaker 1, and gently pawed it; 28) Dzhul'bars ate meat, went to loudspeaker 1 but did not

touch it, pawed loudspeaker 2, went to table 1 and then to loudspeaker 1, and pawed the latter. Dzhek licked his chops; 29) Dzhul'bars jumped up to feeder and ate. Dzhek watched him and licked his chops; 30) Dzhul'bars went to feeder and Dzhek watched him; 31) Dzhul'bars ate meat, went to loudspeaker 2 and pawed it, then went to loudspeaker and carefully touched it with his paw 3 times; 32) Dzhul'bars ate meat, went twice to loudspeaker 2 and pawed it, and went to loudspeaker 1 and pawed it three times; 33) Dzhul'bars ate meat and began to paw loudspeaker 1. Dzhek lay down and turned away; 34) ate meat. Dzhul'bars pawed roughly at loudspeaker 1 and moved it to square 28. Dzhek remained lying; 35) ate meat. Dzhul'bars pawed 3 times at loudspeaker 1 and went to feeder, returned, pawed loudspeaker three times more, again went to feeder, and again pawed loudspeaker 1; 36) Dzhul'bars ate meat, walked about, went to feeder, approached loudspeaker 1, and pawed it. Dzhek watched him; 37) Dzhul'bars ate meat, walked about, went to loudspeaker 1, and pawed it. Dzhek began to bark; 38) Dzhul'bars went to feeder, Dzhek watched him; 39) Dzhul'bars ate and Dzhek barked; 40) Dzhul'bars walked about room and cautiously approached loudspeaker 1. Dzhek barked vigorously. Dzhul'bars gently struck loudspeaker 1 three times with his paw.

The sound of the metronome, the noise made by the feeder when its trays were shifted, and Dzhul'bars pawing at loudspeaker 1 all became signals for Dzhek to go to the feeder during the experiments conducted with the active dog. During the eighth experiment, Dzhek, who was in the room together with Dzhul'bars, thus began to go to the feeder when the active dog pawed loudspeaker 1 and often remained near it. In such cases, Dzhul'bars did not approach the feeder, but pawed at the loudspeaker for a long time, withdrew, or tried to leave the room. As a result, Dzhek was leashed on certain experimental days. If loudspeaker 1 was placed comparatively near the tied dog, Dzhul'bars approached it cautiously or pawed loudspeaker 2 (record of experiment 15). Dzhek, being leashed, sometimes barked when Dzhul'bars pawed the loudspeaker or ate the food given him (record of experiment 15). Dzhek did not exhibit aggression when the active dog drank water, remained near or even pawed loudspeaker 2, as in experiment 15, went to the other objects on the floor, jumped up onto one of the tables, or sniffed the feeder, constantly standing near it.

A total of 18 experiments were performed on Dzhek, but he did not touch loudspeaker 1 in any of them. Nevertheless, when a transition was subsequently made to systematic alimentary reinforcement of the sound of the metronome, Dzhek actively pawed loudspeaker 1.

Thus, as a result of the fact that he was in the room together with Dzhul'bars when the latter was executing the induced motor activity, Dzhek displayed: a positive reaction to the feeder and loudspeaker 1 and conditioned-reflex trips to the feeder in response to its noise, the sound of the metronome, and the pawing of loudspeaker 1 by the active animal. Despite the fact that the passive dog received no reinforcement, his conditioned-reflex trips to the feeder in response to the metronome were stably main-

*Record of Experiment No. 1 on 1 September 1960. Dogs Kashtanka and Dzhek**

[1] Время суток		[4] Условный раздражитель					
[2] часы	[3] минуты	[5] название	[6] порядковый номер применения	[7] время действия (сек)	[8] реакция животных	[9] Подкрепление	[10] Поведение животных после дачи пищи и в межсигнальные паузы
16	13						[16] Впущена Каштанка, она немного ходила по комнате, большую часть времени находилась у двери. К кормушке и динамику не подходила
16	16						[17] Впущен Джек, собаки обнюхались и начали играть. На 2 *сек* включен метроном, при этом Джек подошел к динамику 1 и начал ударять по нему лапой
16	20	[11] Метроном 120 ударов в минуту	364	5	[13] Джек побежал к кормушке	[15] 20 *г* мяса	[18] Джек съел мясо, ходит по комнате, приближался к динамику 1, ударяет по нему. Каштанка пытается обнюхать динамик, но Джек оттолкнул ее. Она подошла к кормушке, Джек подошел сюда же и оттолкнул ее, затем вернулся к динамику и возобновил удары по нему. Каштанка смотрит на Джека
16	24	[12] То же	365	5	То же	То же	[19] Джек съел мясо, стоит у кормушки, идет к динамику 1, ударяет по нему. Каштанка смотрит
16	25	» »	366	5	[14] Джек побежал к кормушке, за ним последовала Каштанка	» »	[20] Джек ест, подошла Каштанка, он начал рычать. Каштанка отошла в сторону. [21] Джек подошел к динамику, к нему приближалась Каштанка и ударила лапой по динамику 1. Собаки начали играть, причем Джек так возбудился, что не реагировал на провоцирующие включения метронома.

Continued

Время суток [1]		Условный раздражитель [4]				Подкрепление [9]	Поведение животных после дачи пищи и в межсигнальные паузы [10]
часы [2]	минуты [3]	название [5]	порядковый номер применения [6]	время действия (сек) [7]	реакция животных [8]		
16	25	[11] Метроном 120 ударов в минуту	366	5	[14] Джек побежал к кормушке, за ним последовала Каштанка	20 г мяса	[22] Собаки одновременно пьют воду из чашки. Джек начал ударять по динамику 1, Каштанка смотрит на него
16	29	[12] То же	367	5	[13] Джек побежал к кормушке	То же	[23] Джек съел мясо, ходит, подошел к динамику и 3 раза ударил по нему. Каштанка обнюхивает пол
16	30	» »	368	5	То же	» »	[24] Джек съел мясо, собаки начали играть

*Experimental setup: the feeder was on square 54, loudspeaker 1 on square 25, loudspeaker 2 on square 27, and the water dish on square 20.

1) Time of day; 2) hours; 3) minutes; 4) conditioned stimulus; 5) designation; 6) sequential number of application; 7) action time (sec); 8) animals' reactions; 9) reinforcement; 10) animals' behavior after receiving food and during intersignal pauses; 11) 120 bpm metronome; 12) the same; 13) Dzhek went to feeder; 14) Dzhek went to feeder, Kashtanka followed him; 15) 20 g of meat; 16) Kashtanka entered room, walked about a bit, spent most of her time near door. She did not approach the feeder or the loudspeaker; 17) Dzhek entered room and the two dogs sniffed each other and began to play. The metronome was applied after 2 sec, whereupon Dzhek went to loudspeaker 1 and began to paw it; 18) Dzhek ate meat, walked about room, approached loudspeaker 1, and pawed it. Kashtanka tried to sniff loudspeaker, but Dzhek drove her off. She went to feeder. Dzhek also went to feeder and drove her off, then returned to loudspeaker and resumed pawing it. Kashtanka watched him; 19) Dzhek ate meat, stood near feeder, went to loudspeaker 1, and pawed it. Kashtanka watched him; 20) Dzhek ate, approached Kashtanka, and began to growl. Kashtanka withdrew; 21) Dzhek went to loudspeaker 1, Kashtanka approached it nd began to paw it. Dogs began to play and Dzhek became so excited that he did not react to the next application of the metronome; 22) dogs drank water together from dish. Dzhek began to paw loudspeaker 1, Kashtanka watched him; 23) Dzhek ate meat, walked about, went to loudspeaker, and pawed it 3 times. Kashtanka sniffed floor; 24) Dzhek ate meat and dogs began to play.

tained (see Table 6).

The results of the experiments on the other adult animals were as follows. Nord developed a conditioned motor reflex to the sound of the feeder and the metronome and sometimes licked his chops, growled, and barked while the active dog was pawing loudspeaker 1 and eating his food from the feeder.

The following reactions were observed in the experiments on Dik: the passive dog licked his chops when Dzhek pawed loudspeaker 1 and in response to the sound of the metronome and made periodic trips to the feeder, attempting to obtain food from it. When the noise of the feeder and the sound of the metronome were applied in test experiments, Dik exhibited only an orientation reaction and did not go to the feeder, even the former reaction sometimes being lacking. This phenomenon can probably be attributed to the fact that Dzhek exhibited pronounced aggression Dik and did not permit him to approach either the feeder or loudspeaker 1. It is possible that, as a result, Dik's positive motor reaction to the noise of the feeder and the sound of the metronome was inhibited and did not appear.

The data cited show that none of the three adult dogs developed an active reaction involving pawing the loudspeaker and that they generally exhibited no motor activity with respect to the positive loudspeaker. In contrast to the adult dogs, the young animals displayed active motor reactions.

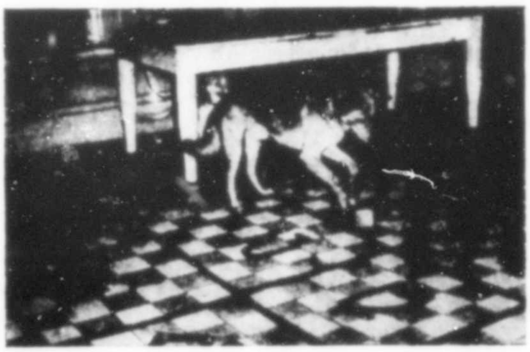

Fig. 9. Zor'ka watches movements of active animal from beneath table 2.

As can be seen from the record, Kashtanka repeated the active reaction involving pawing loudspeaker 1 in the first experiment. It is noteworthy that Dzhek drove off Kashtanka if she approached the feeder or loudspeaker 1, yet drank water with her from the same dish.

Since Kashtanka had a material influence on Dzhek's behavior and confused him in executing the induced activity, she was tied to one leg of table 2 for a number of subsequent experiments. In the third experiment loudspeaker 1 was so arranged that the passive dog could come to within 0.5 m of it. The animal made several unsuccessful attempts to reach the loudspeaker, sometimes moving her paw in front of her as though she were tapping it. In the fifth experiment Kashtanka, still leashed, was able to reach loudspeaker 1. At one point in this experiment, when Dzhek was some distance away, Kashtanka took loudspeaker 1 in her teeth, but Dzhek attacked her and she jumped aside with a yelp. Nevertheless, as soon as Dzhek went to the feeder in response to the next application of the metronome, Kashtanka grasped loudspeaker 1 in her teeth, picked it up, dropped it on the floor, and struck it with her paw. Dzhek then returned, stood over the loudspeaker, and began to growl. Kasntanka subsequently took loudspeaker 1 in her teeth on numerous occasions. At the end of this experiment, Kashtanka, who remained alone in the room, immediately went to the feeder and sniffed it, although she had never received food from it. On the first application of the metronome she went to the feeder and licked her chops, but, receiving no food, she whined, went to the door, and began to scratch at it. On the second application of the metronome, she went to the feeder, but soon returned to the door and resumed her efforts to leave the room. She did not go to the feeder on subsequent applications of the metronome.

Somewhat different data were obtained for two other dogs, Zor'ka and Pal'ma. Zor'ka usually stayed under table 2 during the first few experiments, from which vantage point she watched Dzhek's movements (Fig. 9). From the second experiment onward, she began to go to the feeder after Dzhek left it. It was during this same experiment that Zor'ka first licked loudspeaker 1 and began to lick her chops when Dzhek pawed the loudspeaker. In some cases, she went to the feeder while Dzhek was pawing. Pal'ma exhibited a similar reaction, but she went to the feeder more frequently in response to the sound of the metronome than to Dzhek's pawing at the loudspeaker. In experiments without Dzhek present, Zor'ka and Pal'ma went to the feeder in response to the sound of the metronome and the noise of the feeder. They sometimes went to loudspeaker 1 and to the feeder and sniffed them during the intersignal pauses. In addition, Zor'ka often stayed near the loudspeaker, tilting her head slightly and looking at it. During the thirteenth experiment, Zor'ka, who was tied to a leg of table 2, succeeded in reaching loudspeaker 1 with great difficulty (by moving the table), sniffed it, and then struck it with a paw. This dog displayed a distinct positive alimentary reaction to the feeder and loudspeaker 1, which was manifested in the fact that, although she was substantially weaker than Dzhek, at times she did not permit him to approach either loudspeaker 1 or the feeder. Thus, at one point in the eighth experiment, when Dzhek was pawing loudspeaker 1, Zor'ka struck out at him with a growl. In another case she lay between the loudspeaker and the feeder and growled when Dzhek approached either of them.

Pal'ma exhibited periodic trips to loudspeaker 1 and sometimes sniffed it. This reaction was first noted after the first application of the metronome.

Neither Pal'ma nor Zor'ka pawed loudspeaker 1.

It must be noted that the passive dogs did not approach the differential loudspeaker and displayed no visible reaction in cases where the active animal went to this loudspeaker or drank water from the dish. The active dogs did not display aggression toward the passive dogs if the latter approached the differential loudspeaker or drank water. These data indicate that the feeder and loudspeaker 1 had a positive alimentary significance for both the passive and active animals, while loudspeaker 2, the water dish, and the other objects in the experimental room had no such significance.

Comparison of the data obtained in the experiments on adult and young dogs shows that imitation was more highly developed in the latter than the former. This is in accord with certain of the data in the literature (G.Z. Roginskiy, 1945 and 1948; B.I. Khotin, 1947; et al.).

Our data indicate that, when a passive animal is learning from an active animal, the former does not simply mimic certain motor reactions on the part of the latter, but associates them with the concrete situation, principally the periodic changes in it, so that a situational reflex develops. In the experiments described above, the trips to the feeder by the passive animals were evoked by the stimuli that generally preceded eating by the active animal. These stimuli included the active animal's pawing at loudspeaker 1, the sound of the metronome, this animal's going to the feeder, the noise of the latter, and, finally, the act of eating. These stimuli acquired a positive signal value for certain animals, thus causing them to go to the feeder. Thus, for example, Pal'ma went to the feeder when Dzhek pawed loudspeaker 1 and in response to the sound of the metronome and the noise of the feeder. This indicates that, in learning from the active animal, the passive animals developed a motor reflex to the sequential set of stimuli preceding the act of eating by the active dog.

It is of great biological significance that the passive animals did not simply reproduce the motor reaction of the active animal, but reproduced it in connection with the changes in the environment that dictated the active animal's motor act. If, during learning, animals merely mimicked the motor reactions of another animal in isolated form, this would be of little value in the struggle for survival. Comparatively few of the motor reactions acquired by animals on the basis of imitation are completely new. In our experiments, the reaction involving going to the feeder that was reproduced by the passive animals was not new to them. Under nonexperimental conditions, dogs quite often have occasion to approach or go to a place where food is located, another animal, etc.

Formation of a new temporal association or a system of such associations is generally an important result of imitation. In our experiments, temporal associations were formed in the passive dogs between the cortical points to which the sight of loudspeaker 1 and the feeder, the active animal's pawing the loudspeaker, the sound of the metronome, and the noise of the feeder were addressed and the cortical points that perceived the active animal's eating. When the movements of the passive animal were restricted by a cage or a leash, the visual and auditory analyzers participated in the formation of the temporal associations; later, after the animal was unleashed, these associations resulted in the appearance of an adequate motor reaction, this being an example of the close interaction between the visual and auditory analyzers and the motor analyzer. In those cases where the passive animal was not restricted at the beginning of the experiment and followed the active dog to the feeder, as was sometimes done by the young animals, the motor and possibly the olfactory analyzers participated in forming the system of temporal associations.

Analysis of our experimental data enables us to assume that so-called imitative conditioned reflexes are induced by the same mechanism as second-order conditioned reflexes. This can easily be seen if we consider that a reflex involving going to the feeder in response to the sound of the metronome developed in the passive animal. This animal periodically perceived the sound of the metronome, the active animal's trip to the feeder, and the act of his eating. Corresponding temporal associations were consequently formed in the passive dog's cerebral cortex. This animal received conditioned rather than unconditioned reinforcement (the sight of the other dog eating rather than food). The act of eating by the other animal is a first-order conditioned stimulus, so that reflexes induced on this basis to any other stimuli, e.g., the sound of the metronome, must be regarded as second-order reflexes.

The motor reaction involving pawing the loudspeaker is unusual for dogs, this possibly being the reason why only one young dog repeated it. It is also possible that this animal sometimes made similar movements under natural conditions. The other two young animals also exhibited such active motor reactions as licking and pawing loudspeaker 1, tilting their heads toward it, and striking it with a paw. The active dog did not execute reactions of this sort, so that they cannot be regarded as the result of imitation. Neither can we claim that their appearance in the passive animals was fortuitous; they were produced by the influence of the active dog's behavior. The passive dogs did not exhibit such reactions before the experiments conducted jointly with the active animal; loudspeaker 1 was an indifferent stimulus for them and they did not approach it.

Our experimental data thus demonstrate that conditioned situational reflexes can be induced in dogs on the basis of imitation.

In conclusion, attention must be called to the fact that imitation, which plays an important role under natural conditions, has not yet been the subject of an extensive and probing physiological study. This is one reason why certain complex forms of animal behavior are considered to be incomprehensible and sometimes interpreted from the false standpoint of anthropomorphism.

CONCLUSION

The experimental data presented above show that, when the experimental animal can move freely about the room, conditioned associations are readily and rapidly formed to a definite place where food is found and to the entire experimental setup. The rate at which the first conditioned motor reflex is formed to ordinary conditioned stimuli differs in different animals, depending on the physical strength of the conditioned stimuli applied, the amount and nature of the unconditioned stimulus, the functional state of the dog's cerebral cortex, the individual characteristics of the dog's nervous system, and a number of other factors. Conditioned motor reflexes induced by the situational conditioned-reflex method are distinguished by strength and stability.

From the point where the first conditioned motor reflexes are formed, the animal's behavior during the experiment is determined by the conditioned stimuli. The animal's position in a definite area of the room and his pose also become positive conditioned agents during the intervals between applications of the conditioned stimuli and he voluntarily goes to this area and, adopting a definite pose, remains in it until the next positive conditioned stimulus is applied.

Development of the second, third, and subsequent conditioned motor reflexes is more rapid as training proceeds.

The "force law" established by the classical salivary method in I.P. Pavlov's laboratory is also fully manifest in studying the natural motor activity of animals. In this case, the appearance of the "force law" depends to a large extent on the functional state of the cerebral cortex, which in turn depends on the animal's alimentary excitability. A decrease in alimentary excitability promotes manifestation of the "force law," while an increase in excitability masks it. Extraneous stimuli, being external inhibitory factors, readily suppress the motor reaction to a weak conditioned stimulus, but have difficulty doing so for a strong stimulus. The "force law" may weaken and disappear as training proceeds. It is more clearly displayed when the motor activity is complicated.

In studying the differentiation of conditioned stimuli in different types of experiments, we established that the course of this process depends to a substantial extent on the spatial factor.

We made a special study of the differentiation of positive stimuli reinforced by food supplied from feeders located in different areas of the experimental room. This method proved to be convenient for studying the role of the spatial factor in stimulus differentiation and in the animals' behavior as a whole. It was found that differentiation of stimuli located in different areas of the experimental room occurred substantially more rapidly than differentiation of the same stimuli when they were located in the same area. Moreover, we noticed that gradual approximation of the sources of the stimuli to be differentiated could cause material disruptions of higher nervous activity, reaching the point of neurosis.

In studying the formation of inhibitory differentiation, we demonstrated the significance of positive induction in the development of the motor reactions observed in response to the inhibitory stimuli.

Both our investigations and those conducted by V.V. Yakovleva and other authors made it possible to establish the conditioned-reflex significance of different areas of the experimental room. Thus, it was found that the place in the room occupied by the animal when the positive conditioned stimuli were applied acquired the character of a positive conditioned agent, while the place he occupied when the inhibitory stimuli were applied acquired the character of a negative agent. Different spatial areas thus became conditioned stimuli of differing significance and, together with the other conditioned and unconditioned stimuli, determined the animal's complex motor activity. It was found that the differentiation of different spatial areas followed the general rules for higher nervous activity established in I.P. Pavlov's laboratory.

The formation and extinction of situational conditioned reflexes, the formation of inhibitory differential reflexes and conditioned inhibition, the modification of reflexes, and so forth also obey the rules previously established in I.P. Pavlov's laboratory.

It was established that the decisive condition in the formation of complex motor activity in a free-moving animal was the spatial factor: the animal's position in the experimental room, the location of the food, and the location of the conditioned stimuli. Together with the other conditioned and unconditioned stimuli, the spatial factor determined the animal's complex motor activity. This factor is open to physiological analysis on the basis of the general mechanisms of higher nervous activity.

The conditioned-reflex activity of the free-moving animals was governed by the functional state of the cerebral cortex, the physical strength of the conditioned stimuli, and the character of the unconditioned stimulus.

The data that have now been amassed enable us to surmise that the complex conditioned-reflex motor activity of animals is facilitated by very complex, protracted nervous processes linking many components. These components, determined by the conditioned stimuli applied, the animal's spatial position, his pose, his movements, etc., are combined into a highly organized functional structure in the higher elements of the brain and, interacting, govern the manifest reaction produced. It can be specifically assumed that, through positive induction, inhibition of one focus in this functional structure of nervous processes causes excitation of other elements functionally linked to the inhibited point. The movement of an animal from a negative area of the room to an area having a positive alimentary significance can serve as a concrete example of such nervous activity.

The foregoing experimental data thus show that, by using the conditioned-reflex method and permitting the animal to move freely about the experimental room, it is possible to form complex conditioned-reflex motor activity, a process effected on the basis of the mechanisms established by I.P. Pavlov and his students and followers through the classical salivary method.

The situational conditioned-reflex method expanded the opportunities for experimental study of imitation in dogs. Employing this technique, we demonstrated that it is sufficient for a dog to be present in the experimental room while another animal is carrying out conditioned-reflex activity for the former to develop conditioned motor reflexes. The experimental data obtained show that the "passive" animal does not simply repeat motor reactions executed by the "active" animal, but associates them with a specific setup, particularly the periodic changes in the situation. As a result, the "passive" dog develops a conditioned motor reflex to a sequential complex of stimuli rather than to a single stimulus.

Analysis of the experimental data enables us to assume that imitative conditioned reflexes are induced by the same mechanism as second-order conditioned reflexes. One of their special features is the fact that they are formed rapidly and maintained with comparative stability, despite the fact that the "passive" animal receives no alimentary reinforcement. This is due to the fact that the "active" animal and his behavior are powerful biological stimuli for the "passive" animal.

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FOOTNOTES

70 For convenience in reporting the material, an animal in which a conditioned reflex has been elaborated on the basis of imitation will be referred to as "passive," while the imitated animal will be called "active."

Chapter 2

INFLUENCE OF CHANGES IN LOCATION OF CONDITIONED AND UNCONDITIONED STIMULI ON SITUATIONAL CONDITIONED REFLEXES

INFLUENCE OF CHANGES IN LOCATION OF CONDITIONED VISUAL AND AUDITORY STIMULI ON CONDITIONED-REFLEX ACTIVITY

The following conditioned-reflex activity was induced in V.V. Yakovleva's experiments on the dog Ledi. On entering the experimental room, the dog went to the mat on square 34. She kept her head and torso pointed toward the conditioned stimuli, which were usually located on a shelf on the right-hand wall, above squares 35 and 28 (see Fig. 1). The dog turned to the left and went to table 1 when the 120 bpm metronome was switched on, while when the bell was switched on she turned to the right and went to table 2. She remained on the mat during the intervals between applications of the conditioned stimuli.

In one experiment, the bell and metronome were shifted from the right-hand to the left-hand shelf, which was located on the opposite wall above squares 43 and 36. As usual, the dog turned to the left when the metronome was applied, but she went to table 2 rather than to table 1; her conditioned reflex remained unchanged when the bell was applied.

Returning the conditioned stimuli to their prior location on the following day led to normalization of conditioned-reflex activity.

A similar disruption of higher nervous activity was observed in Ledi when the conditioned stimuli were moved to other areas of the room.

N.I. Khudryashova (1955) induced conditioned-reflex activity in which the dog went to table 1 and received food in response to application of a 120 bpm metronome and went to table 2 and also received food in response to application of a bell. The conditioned stimuli were on a shelf to the animal's right. After these reflexes had become stable, the position of the conditioned stimuli was periodically changed. Only one stimulus was moved in a single experiment. The metronome was placed in its usual spot on the following day. However, application of either conditioned stimulus altered the animal's behavior. The dogs began to remain at the tables for longer periods after eating, the time required to return to the mat increased, and the latent period of the conditioned reaction was prolonged. In some cases, the animals began to whine, ran about the room, and sometimes stopped near the door and attempted to open it. These disturbances were more pronounced if the conditioned stimuli were moved behind the animals. The disruption of higher nervous activity was far more severe the first few times the conditioned stimuli were moved, repeated shifting of the stimuli having a far less substantial effect.

V.I. Syrenskiy's experiments showed that the extent to which conditioned-reflex activity was disrupted when the conditioned stimuli were moved depended on other factors. Differentiation of two auditory stimuli reinforced with food at different tables and located at equal distances from the latter (on squares 44 and 51) was induced in his investigations. The conditioned-reflex activity developed in the animal (Una) consisted in going to table 1 in response to a tone and to table 2 in response to a bell. The tone source, a loudspeaker, was first shifted after differentiation had just been established. The conditioned-reflex reaction to the tone was altered when the loudspeaker was moved 80 cm closer to table 2: the animal went to table 2 rather than to table 1 (record of experiment on 3 November 1959).

The position of the tone source was changed for a second time when the conditioned reflex had become essentially stable (after more than 200 reinforcements). In this case, moving the loudspeaker by the same amount (80 cm) did not disrupt the induced conditioned-reflex activity: the dog went immediately to table 1 (record of experiment on 8 May 1961).

The position of the conditioned stimulus was then altered to a greater extent. In one experiment, the loudspeaker was transferred from the floor to table 2 and placed next to the feeder. The character of the conditioned motor reaction to application of the tone nevertheless remained the same: the animal went to table 1 (experiment on 12 May 1961). Thus, during the period when the reflexes were becoming stable, Una exhibited the correct reaction to the tone when the conditioned stimulus that produced one reflex was placed next to the unconditioned stimulus that evoked the other reflex.

Similar experiments were conducted on the dog Grom. Shifting the loudspeaker to a distance of 80 cm from its prior place during the initial period of stabilization of the reflexes also caused a change in this animal's higher nervous activity. When, after the reflexes had become relatively stable, the loudspeaker was transferred from the floor to table 2 and placed near the feeder, there were no changes in the dog's induced conditioned-reflex activity; however, placing the loudspeaker next to the feeder, i.e., next to the unconditioned stimulus for the other reflex, caused Grom's previously induced activity to be disrupted: he did not go to this table. Thus, Grom exhibited the correct reaction when the loudspeaker was placed a short distance from the unconditioned stimulus for the other reflex, but he displayed an erroneous motor reaction when the loudspeaker was placed beside the feeder, i.e., the positive differentiation of the tables was disrupted.

Changing the location of the conditioned stimuli after the conditioned reflexes had become stable thus had absolutely no ef-

Change in Conditioned-Reflex Activity after Shifting of Conditioned Auditory Stimuli (Differentiation of Positive Stimuli). *Dog Una*

Число применений условного раздражителя [1]	[2] Условный раздражитель	Латентный период условного рефлекса (сек) [3]	Время пробежки (сек) [4]	[5] Поведение собаки при действии условного раздражителя
	[6] **Выписка из протокола опыта от 3/XI 1959 г.** (Динамик находится на расстоянии 80 *см* от стола 2)			
19	[7] Зуммер (стол 2)	0,4	1,8	[9] Бежит к столу 2
19	[8] Тон (стол 1)	0,3	1,9	» » » 2
20	Тон (стол 1)	0,8	2,0	» » » 1
20	Зуммер (стол 2)	0,4	1,9	» » » 2
	[10] **Выписка из протокола опыта от 8/V 1961 г.** (Динамик находится на расстоянии 80 *см* от стола 2)			
102	[11] Треск (стол 2)	0,5	1,9	Бежит к столу 2
224	Тон (стол 1)	0,9	1,7	» » » 1
64	[12] «Писк» (стол 2)	0,6	1,8	» » » 2
150	«Музыка», детская игрушка (стол 1)	0,8	1,8	» » » 1
	[13] **Выписка из протокола опыта от 12/V 1961 г.** [14] (Динамик поставлен на стол 2 рядом с кормушкой)			
108	Треск (стол 2)	0,5	2,0	Бежит к столу 2
230	Тон (стол 1)	1,0	1,8	[16] Поворот головы к раздражителю, топчется, бежит к столу 1
88	[15] «Бом» (стол 2)	0,9	2,0	Бежит к столу 2
	[17] **Выписка из протокола опыта от 20/X 1959 г.** (Динамик поставлен ближе к столу 2 на 50 *см*)			
617	[18] Метроном 240 (стол 2)	0,5	1,8	Бежит к столу 2
647	[19] Метроном 180 (стол 1)	0,6	1,9	» » » 2
648	Метроном 180 (стол 1)	0,8	1,9	» » » 2
618	Метроном 240 (стол 2)	0,7	1,8	» » » 2

Note: The table to which the animal should have gone when the stimulus was applied is indicated in parentheses.

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) time required to reach table (sec); 5) dog's behavior under action of conditioned stimulus; 6) extract from record of experiment on 3 November 1959 (loudspeaker 80 cm from table 2); 7) buzzer (table 2); 8) tone (table 1); 9) went to table 2; 10) extract from record of experiment on 8 May 1961 (loudspeaker 80 cm from table 2); 11) crackling noise (table 2); 12) "squeak" (table 2); 13) "music," child's toy (table 1); 14) extract from record of experiment on 12 May 1961 (loudspeaker on table 2, next to feeder); 15) "boom" (table 2); 16) turned head toward stimulus, trod in place, went

to table 1; 17) extract from record of experiment on 20 October 1959 (loudspeaker placed 50 cm closer to table 2); 18) 240 bpm metronome (table 2); 19) 180 bpm metronome (table 1).

fect on the character of the conditioned-reflex reaction of the first dog (Una), while the reaction of the second dog (Grom) was disrupted only when the conditioned stimulus was placed beside the unconditioned stimulus for the other reflex. These slight differences in the animals' behavior can apparently be attributed to the individual characteristics of their nervous systems.

The data obtained indicate that the extent to which conditioned-reflex activity is disrupted as a result of relocation of the conditioned stimuli depends on the extent to which differentiation has been fixed: changing the location of the conditioned stimuli leads to more substantial changes in higher nervous activity during the initial period of conditioned-reflex formation than after the reflexes have become relatively stable. The significance of the temporal associations induced to the spatial relationships of the conditioned stimuli is thus particularly clear during the initial period of the formation of conditioned situational reflexes. Moreover, the greater the extent to which the spatial relationships between the conditioned and unconditioned stimuli are altered, the more probable is a disruption of higher nervous activity and the more substantial it will be when it occurs. Under these conditions, experiments involving shifting of the conditioned stimuli by less than 1 m from their prior location during the reflex-formation period lead to a change in the animal's normal behavior. After the reflexes have become stable, higher nervous activity is most frequently disrupted if the source of the conditioned stimulus that evokes one reflex is brought close to the unconditioned stimulus that produces the other reflex.

It was further found that, if differentiation is induced to stimuli of similar character (e.g., metronomes of different frequencies), conditioned-reflex activity is disrupted when the conditioned stimuli are shifted by smaller amounts. Thus, differentiation of a 240 bpm metronome reinforced at table 2 and a 180 bpm metronome reinforced at table 1 was disrupted in Una when the sound source (loudspeaker) was moved 50 cm closer to one table or the other. Consideration must be given to the fact that, in this case, stable differentiation of the conditioned stimuli occurred as a result of repeated application (see the experiment on 20 October 1959).

V.I. Syrenskiy and V.D. Volkova studied the influence of relocation of the conditioned stimuli after formation of inhibitory differentiation.

In V.D. Volkova's experiments, inhibitory differentiation was induced to a metronome, while the positive conditioned stimulus was a bell; the metronome was placed on a shelf to the left of the dog and the bell on a shelf to his right. The bell was reinforced from feeder 1. The dog remained on square 42 during the intervals between applications of the conditioned stimuli. In one experiment, the differential metronome was transferred from the left-hand to the right-hand shelf, beside the positive conditioned stimulus (the bell). When the metronome was applied at its new location, the dog immediately turned his head toward the feeder table, licked his chops, but did not move from the spot, i.e., a weak positive reaction was observed (experiment on 31 January 1959). It must be noted that this test was conducted after the stimuli to be differentiated had been applied more than 600 times.

This same dog had previously been subjected to relocation of a conditioned stimulus (experiment on 20 February 1958). The positive conditioned stimulus, a 200 watt bulb hung from a stand, was transferred from square 28 to square 25. The dog normally went to table 1 and received food when the 200 watt bulb was switched on. When this stimulus was applied at its new location, the animal turned his head toward it but remained on the mat. He went to the table only in response to the sound of the feeder trays being shifted. The conditioned reactions to application of the other stimuli were normal. Thus, relocation of a positive visual stimulus closer to the "inhibitory zone" led to a change in the character of the conditioned motor reaction, which was inhibited when the light first acted.

G.A. Shichko also investigated the influence of shifting of conditioned stimuli on higher nervous activity. In his experiments, the feeder was located on the floor and two loudspeakers of differing size and shape were placed at some distance from it. These loudspeakers supplied sounds of different timbres and strengths, but of the same frequency (120 bpm). A positive conditioned reflex was developed to the sound produced by one speaker and an inhibitory differential reflex to the sound produced by the other. The dog went to the feeder when the positive loudspeaker was applied and remained on the mat when the negative loudspeaker was applied. The positive loudspeaker was switched on only when the animal went to it and pawed it several times. On one experimental day (7 June 1962), the positive loudspeaker was shifted to another area of the room, at a distance of 3 m from its usual location. As a result, at the beginning of the experiment the animal went to the negative rather than the positive loudspeaker, struck it twice with a paw, and then withdrew. The animal then walked about the room for 7 min, went toward the positive loudspeaker several times, but never stopped near it and did not paw it. Only after the positive loudspeaker was returned to its prior location was the animal's normal behavior restored.

A similar change in the induced activity was observed when the loudspeaker was repeatedly moved to a distance of 1-2 m from its inicial location. The changes in the animal's behavior then gradually became less and less pronounced from experiment to experiment. A point was finally reached where the animal reacted properly to the conditioned stimulus even if the loudspeaker was suspended at a height of 1 m above the floor (see Fig. 14).

A change in the location of conditioned visual and auditory stimuli thus leads to a disruption of conditioned-reflex activity. The extent of the disruption depends on the following factors:

1) the stability of the reflexes. Relocation of the conditioned stimuli leads to more pronounced disruptions if the conditioned reflexes are not sufficiently stable. At the same time, such relocation may not at all affect the animal's behavior if the conditioned stimuli have not been applied at least a hundred times;

2) the amount by which the conditioned stimuli are moved. The farther from their initial location the conditioned stimuli are shifted, the more probable is a change in conditioned-reflex activity and the more severe it will be;

3) the complexity of the induced conditioned-reflex activity. The more complex the animal's activity, the more clearly and severely it is altered when the conditioned stimuli are relocated.

Change in Conditioned-Reflex Activity after Relocation of Conditioned Stimuli (Inhibitory Differentiation)

[1] Число применений условного раздражителя	[2] Условный раздражитель	[3] Латентный период условного рефлекса (сек)	[4] Поведение собаки при действии условного раздражителя	[5] Примечание
		[6] **Выписка из протокола опыта от 20/II 1958 г.** (Местоположение условных раздражителей изменено)		
710	[7] Звонок	1,0	[9] Бежит к столу	
390	[8] Свет	—	[10] Повернула голову к раздражителю, смотрит на него	[11] Бежит к столу на стук чашки
711	Звонок	1,0	Бежит к столу	
		[12] **Выписка из протокола опыта от 31/I 1960 г. Собака Смирный** (Местоположение условных раздражителей изменено).		
1308	Звонок	0,9	Бежит к столу	
1080	Свет	1,0	» » »	
613	[13] Метроном	—	[14] Повернула голову к столу, облизалась, стоит на коврике, глядя на стол	
1309	Звонок	1,0	Бежит к столу	
1070	Свет	1,0	» » »	
		[15] **Выписка из протокола опыта от 7/VI 1962 г. Собака Пальма** (Местоположение положительного раздражителя изменено)		
			[16] Войдя в комнату, собака ходит некоторое время, обнюхивая пол, затем подошла к кормушке, оттуда направилась к отрицательному динамику, подошла и ударила по нему два раза лапой. Отходит в сторону, снова идет к кормушке, пытается влезть на стол 2. Идет к квадрату 53, затем к кормушке. Рычит и ударяет по ней лапой. Отходит в сторону, проходит мимо положительного динамика, но не касается его. Ходит по комнате, временами задерживаясь у кормушки и отрицательного динамика. Ни разу не остановилась у положительного динамика и не сделала попыток ударить по нему лапой. Собака подходит к положительному динамику и ударяет по нему лапой	

Continued

Число применений условного раздражителя [1]	Условный раздражитель [2]	Латентный период условного рефлекса (сек) [3]	Поведение собаки при действии условного раздражителя [4]	Примечания [5]
[17] Положительный раздражитель перенесен на свое обычное место				
157	Метроном	1,0	Бежит к кормушке	[18] После еды сразу идет к положительному динамику и ударяет по нему лапой
158	»	0,9	» » »	После еды сразу идет к положительному динамику и ударяет по нему лапой
159	»	1,0	» » »	

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) dog's behavior under action of conditioned stimulus; 5) notes; 6) extract from record of experiment on 20 February 1958 (location of conditioned stimuli changed); 7) bell; 8) light; 9) went to table; 10) turned head toward stimulus, looked at it; 11) went to table in response to sound of feeder; 12) extract from record of experiment on 31 January 1959. Dog Smirnyy (location of conditioned stimuli changed); 13) metronome; 14) turned head toward table, licked chops, stood on mat, and looked at table; 15) extract from record of experiment on 7 June 1962. Dog Pal'ma (location of positive stimulus changed); 16) on entering the room, the dog walked about for a short time, sniffing the floor, then went to feeder, whence she approached the negative loudspeaker and pawed it twice. She withdrew, again went to the feeder, and attempted to climb up onto table 2. She went to square 53 and then to the feeder. She growled and struck it with a paw. She withdrew and approached the positive loudspeaker, but did not touch it. She walked about the room, periodically remaining near the feeder and the negative loudspeaker. She did not stop near the positive loudspeaker and did not attempt to paw it. She went to the positive loudspeaker and pawed it; 17) positive stimulus returned to its usual location; 18) went to positive loudspeaker and pawed it immediately after eating.

INFLUENCE OF CHANGE IN POSITION OF MAT ON CONDITIONED-REFLEX ACTIVITY

If an unconditioned or conditioned stimulus is applied when a dog is accidentally in a definite area of the experimental room (on a definite square), the animal will independently go to this square after several such applications; if a mat is placed on this spot, the dog will stand on it.

This behavior is dictated by the fact that such areas of the experimental room or a mat placed on any of them acquire conditioned alimentary significance, i.e., become conditioned stimuli.

In the preceding section we presented data showing that relocation of the sources of conditioned auditory and visual stimuli affects induced conditioned-reflex activity.

We became interested in determining how changing the location of the mat, i.e., one of the stimuli governing the animal's spatial position, affected conditioned-reflex activity. V.V. Yakovleva and P.S. Kupalov made the first observations in this direction.

It was established that, if the mat was transferred from its usual location to some other spot, the normal course of conditioned-reflex activity was disrupted.

In an experiment on the dog Ledi, the mat was shifted from square 33 to square 19. On entering the experimental room under these conditions, the dog went to take up her usual position on square 33. After a short time, she moved over to the mat. The 120 bpm metronome evoked the usual conditioned motor reaction: the dog went to table 1. She also went to this table in response to the bell, i.e., made an error. During the intervals between applications of the auditory stimuli, the dog went to her usual position and stood there for awhile, went to the mat, and then returned to the conditioned place (square 33). Toward the end of the experiment, she began to go to table 2 in response to the bell, i.e., the conditioned reaction was normalized.

V.I. Syrenskiy's investigations established that conditioned-reflex activity was usually not disrupted if the mat was moved to a distance of 0.5 m from its usual location (experiment on 10 November 1959). Definite changes in the animal's behavior appeared if the mat was shifted by 1-1.5 m from its usual place (experiment on 3 December 1959).

It can be seen from the latter experiment that, on entering the room, the dog went to the mat and stood on it. After remaining there for a short time (10 sec), the dog went and stood on the portion of the floor where the mat had been previously located; after 5 sec, he went to the table and jumped up onto it. Jumping down from the table, the animal returned to the mat, but, remaining there for only a short time, went to the portion of the floor where the mat had previously been positioned. He exhibited the normal behavior pattern when the positive and inhibitory conditioned stimuli were applied. On the following day, the mat was placed in its former location and the dog's conditioned-re..ex activity was normal. Moving the mat over the same distance (1-1.5 m) caused similar changes in the behavior of other animals.

O.N. Voyevodina's investigations were conducted on the dogs Al'ma and Reni. The animals' conditioned-reflex activity consisted in the following. They went to table 1 and received food in response to a 120 bpm metronome on a shelf to their right. Inhibitory differentiation was induced to application of a 120 bpm metronome on a shelf to their left. In addition, a delayed conditioned reflex was formed to a complex stimulus consisting of a 200 watt bulb acting for 140 sec and a metronome following it after a 10-second interval. The metronome acted for 5 sec. All the stimuli were applied only when the animal was on the mat located on square 45. A total of 8 positive, 3 negative, and one retardive stimuli were applied in each experiment.

In one day of experiments on Al'ma, the mat was shifted from square 45 to square 39, i.e., 1 m from its usual position (experiment on 15 May 1957). It must be noted that this animal had been subjected to experimental neurosis 14 months previously in another set of experiments. After the mat had been shifted and the positive conditioned stimulus applied, the dog jumped down from the table, went to square 45 and stood on it for 10 sec, went to the mat, walked about it for a short time, and then stood on it. As a result of this behavior, the time required for the animal to return to the mat and stand on it increased to 50 sec. The animal's behavior during the intersignal pauses had the same character after all subsequent applications of the positive conditioned stimuli. It must be added that the character of the conditioned motor reaction was also altered after the second application of the positive conditioned stimulus. Thus, when the stimulus was applied, the animal did not go immediately to the table, but went first to square 45, i.e., the usual location of the mat, and only then to the feeder. After the sixth application of the positive metronome, the dog went to the door and did not leave it for 10 min, so that the experiment had to be discontinued. The mat was placed in its usual position on the following day and this led to restoration of conditioned-reflex activity.

The other dog, Reni, whose nervous system was of the weak type, had an even more difficult time when the location of the mat was changed. She developed severe disruptions of higher nervous activity accompanied by autonomic reactions unusual under the experimental conditions in question (hiccuping, vomiting, and defecation). These disturbances continued for several days, even after the mat was returned to its usual place. I. Ungher and E. Ciurea (1959) observed similar autonomic disturbances when the location of the mat was changed during their investigations. Reni's conditioned-reflex activity became normal only after an interval of five days.

In V.I. Syrenskiy's investigations, the mat was transferred from its usual place (square 27) to a distance sufficiently great that it was outside the animal's field of vision (square 51) when he stood in the mat's normal location. The following changes in conditioned-reflex activity were noted in this case (experiment on 19 November 1959). On entering the room, the animal began to move about the floor, sometimes stopping in the vicinity of square 27, i.e., the usual location of the mat. In several instances, the animal stopped on this square and then spontaneously went to the table and jumped onto it. Behavior of this type was observed for 4 min, but the animal never attempted to approach the mat. As a result, it was decided to modify the experiment. For this purpose, the experimenter entered the room and approached the mat. The animal immediately went to him and thus to the mat. When the experimenter was certain that the dog had seen the mat and even stood on it, he left the room. The animal remained near the mat for a short time, but then went from it to the usual place (square 27). The dog subsequently made no attempt to return to the mat. The character of his behavior was also altered: he began to move aimlessly about the room, whine, turn in circles, etc. In order to prevent any possible disruption of higher nervous activity, the experimenter entered the room and changed the position of the mat so that it was at a distance of 1.5 m (squares 39-46) from its usual place. As soon as this had been done, the animal went to the mat and stood near it. He went to the table when the positive stimulus was applied and exhibited the proper motor reactions on subsequent applications of the positive and negative conditioned stimuli. During the pauses between applications of the stimuli, he stood sometimes on the mat, sometimes on its usual location, and sometimes between these two spots.

It follows from the experiment described above that shifting the mat so that it was outside the animal's field of vision when he stood in the usual place did not evoke a reaction involving going to the mat. The animal at first stood in the usual place and then moved aimlessly about the room, went to the door, and whined near it.

The data obtained give us grounds for reaching the following conclusion. When a conditioned reflex was formed to a mat always located at a definite place in the room, it was produced to a complex stimulus consisting of two components: objective and spatial. The animal exhibited the proper conditioned-reflex motor activity only if these components acted simultaneously or almost simultaneously. Let us clarify this. When the mat was located in its usual place, the spatial and objective components of the conditioned stimulus acted simultaneously. If the mat was placed in a different position, even directly beside its prior position, the excitations produced by the two components did not develop simultaneously, one following the other by a certain time interval. The greater the interval separating the two excitations, the more severe was the disruption of higher nervous activity. The fact that, when the mat was shifted from its usual place by only a small amount, the animal generally stood on its former location and not on the mat itself indicates that the spatial component had greater physiological force than the objective component. This hypothesis is also supported by the following observation. When the mat was shifted by a substantial amount, the animal generally went to the vicinity of its usual place and made no attempt to stand on the mat.

Influence of Change in Mat Location on Conditioned-Reflex Activity

Число применений условного раздражителя [1]	[2] Условный раздражитель	Время действия условного раздражителя (сек) [3]	Латентный период условного рефлекса (сек) [4]	[5] Поведение собаки при действии условного раздражителя	[6] Примечания
[7] **Выписка из протокола опыта от 10/XI 1959 г. Собака Пегий (Коврик перенесен на 0,5 м)**					
159	[8] Тон (стол 1)	5,0	0,2	[11] Бежит к столу 1	[13] В паузе, соскочив со стола, встает на коврик через 6—20 *сек*
153	[9] Метроном (стол 2)	5,0	0,4	» » » 2	
154	Метроном (стол 2)	5,0	0,2	» » » 2	
57	[10] Зуммер	5,0	—	[12] Стоит	
160	Тон (стол 1)	5,0	0,2	Бежит к столу 1	
[14] **Выписка из протокола опыта от 3/XII 1959 г. Собака Пегий (Коврик перенесен на 1 м)**					
					[15] Идет к коврику и становится на него, затем переходит на то место, где коврик помещался ранее. С этого места без включения условного сигнала побежала к столу. Соскочив со стола, вернулась на коврик
180	Тон (стол 1)	5,0	0,3	Бежит к столу 1	[16] Идет на квадрат 27, ложится, через 40 *сек* встает и идет к коврику, откуда бежит без сигнала к столу 2, возвращается на коврик, через 10 *сек* идет на квадрат 27, через 42 *сек* опять идет на коврик

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1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Поведение собаки при действии условного раздражителя	6 Примечания
176	Метроном (стол 2)	5,0	0,4	[18] Бежит к столу 2	Идет [20] на коврик, через 5 *сек* на квадрат 27, где ложится, через 90 *сек* бежит без сигнала к столу, возвращается на коврик
77	[17] Зуммер (тормоз)	5,0	—	[19] Лежит	Лежит на коврике [21]
177	Метроном (стол 2)	5,0	0,5	Бежит к столу 2	Идет [22] на коврик, затем бежит к двери, оттуда идет на квадрат 27, через 120 *сек* переходит на коврик
181	Тон (стол 1)	5,0	0,3	» » » 1	Бежит [23] к двери, скулит

[24] **Выписка из протокола опыта от 15/V 1957 г.**
Собака Альма
(Коврик перенесен с квадрата 45 на квадрат 39, т. е. на расстояние 1 *м*)

3084	[25] Метроном (положительный)	5,0	0,5	Бежит к столу 1	[26] Войдя в комнату, бежит к столу 1 и вскакивает на него, соскочив, идет на квадрат 45, затем к коврику. [27] Соскочив со стола, идет к квадрату 45, оттуда через некоторое время идет к коврику. Делает несколько кругов возле коврика и затем встает на него
3085	Метроном (положительный)	5,0	0,5	» » » 1	[28] Поведение в паузе аналогичное

Continued

Числа применений условного раздражителя [1]	[2] Условный раздражитель	Время действия условного раздражителя (сек) [3]	Латентный период условного рефлекса (сек) [4]	[5] Поведение собаки при действии условного раздражителя	[6] Примечания
3086	[25] Метроном (положительный)	5,0	2,0	[30] Идет на квадрат 45, оттуда к столу 1	[32] Соскочив со стола, идет на коврик, затем направляется к квадрату 45, стоит на нем некоторое время, идет на коврик
201	[29] Лампа (пауза) Метроном (положительный)	140 10 5,0	2,0	[31] Стоит [18] Бежит к столу 2	[33] Соскочив со стола, идет на квадрат 45, затем на коврик
3087	Метроном (положительный)	5,0	2,0	Идет на квадрат 45, оттуда к столу 1	[34] Поведение аналогичное
3088	Метроном (положительный)	5,0	2,0	Идет на квадрат 45, оттуда к столу 1	[34] Поведение аналогичное
253	Метроном (отрицательный)	5,0	—	Стоит	
3089	Метроном (положительный)	5,0	2,0	Идет на квадрат [illegible], затем бежит к столу [illegible]	[35] Соскочив со стола, идет к двери, делает попытки открыть ее, затем ложится около нее на полу, где и находится в течение 10 *мин*

[36] **Выписка из протокола опыта от 19/XI 1959 г.**
Собака Пегий
(Коврик перенесен с квадрата 27 на квадрат 51, т. е. вне поля зрения животного)

					[37] Вбежав в комнату, собака вскочила на стол 1. Соскочив со стола, идет к чашке с водой и пьет. Идет на квадраты 20—21, где стоит 15 *мин*, опять подходит к чашке с водой и пьет.

Continued

1 Число применений условного раздражителя	2 Условный раздражитель	3 Время действия условного раздражителя (сек)	4 Латентный период условного рефлекса (сек)	5 Поведение собаки при действии условного раздражителя	6 Примечание
					Идет в квадрат 27, стоит там 140 *сек*, бежит на стол 1 без сигнала. Соскочив со стола, идет к чашке с водой, оттуда на квадрат 27, на квадрат 34, лежит на нем 15 *сек* и затем идет на квадрат 21, где остается 40 *сек*. Затем в течение 2 *мин* животное осуществляет аналогичное поведение, переходя с одного квадрата на другой и не делая попыток встать на коврик. Несколько раз подходит к двери, у которой скулит и вертится. 3 8 В комнату вошел экспериментатор и направился к коврику, собака пошла за ним. 3 9 Экспериментатор вышел из комнаты, собака же некоторое время оставалась у коврика, а затем перешла на квадрат 27. В районе этого квадрата животное находилось 4 *мин*. 4 0 В комнату опять вошел экспериментатор и перенес коврик на квадраты 32—30. Животное подошло к коврику и стало на него

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[1] Число применений условного раздражителя	[2] Условный раздражитель	[3] Время действия условного раздражителя (сек)	[4] Латентный период условного рефлекса (сек)	[5] Поведение собаки при действии условного раздражителя	[6] Примечания
157	[8] Тон (стол 1)	5,0	0,5	[11] Бежит к столу 1	[42] Соскочив со стола, идет на квадраты 7, 21, 10, на квадрате 27 ложится, через 16 *сек* встает и идет к коврику [40]
153	[9] Метроном (стол 2)	5,0	0,6	» » » 2	Соскочив со стола, сразу идет на коврик
65	[17] Зуммер (тормоз)	5,0	—	[41] Сидит на коврике	—
138	Тон (стол 1)	5,0	0,4	Бежит к столу 1	[44] Соскочив со стола, идет на коврик, через 10 *сек* идет к столу 2, возвращается на коврик, оттуда к двери

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) action time of conditioned stimulus (sec); 4) latent period of conditioned reflex (sec); 5) dog's behavior under action of conditioned stimulus; 6) notes; 7) extract from record of experiment on 10 November 1959. Dog Pegiy (mat shifted by 0.5 m); 8) tone (table 1); 9) metronome (table 2); 10) buzzer; 11) went to table 1; 12) stood still; 13) during pause jumped down from table and stood on mat after 6-20 sec; 14) extract from record of experiment on 3 December 1959. Dog Pegiy (mat shifted by 1 m); 15) went to mat and stood on it, then moved to spot where mat had previously been. Went to table from this spot without application of conditioned signal. Jumped down from table and returned to mat; 16) went to square 27, lay down, stood up and went to mat after 40 sec, went to table 2 without signal, returned to mat, went to square 27 after 10 sec, returned to mat after 42 sec; 17) buzzer (inhibitory); 18) went to table 2; 19) lay down; 20) went to mat, moved to square 27 after 5 sec and lay down, went to table without signal after 90 sec, and returned to mat; 21) lay down on mat; 22) went to mat, then to door, then to square 27, went to mat after 120 sec; 23) went to door, whined; 24) extract from record of experiment on 15 May 1957. Dog Al'ma (mat shifted from square 45 to square 39, i.e., by 1 m); 25) metronome (positive); 26) on entering room went to table 1 and jumped up onto it, jumped down, went to square 45 and then to mat; 27) jumped down from table, went to square 45, then went to mat after short time. Made several circles near mat and then stood on it; 28) exhibited similar behavior during pause; 29) bulb (pause); 30) went to square 45 and then to table 1; 31) stood still; 32) jumped down from table, went to mat and then to square 45, stood on this square for short time, then went to mat; 33) jumped down from table, went to square 45 and then to mat; 34) similar behavior; 35) jumped down from table, went to door, attempted to open it, lay down near it on floor, and remained there for 10 min; 36) extract from record of experi-

ment on 19 November 1959. Dog Pegiy (mat shifted from square 27 to square 51, i.e., outside animal's field of view); 37) on entering room, jumped up onto table 1. Jumped down from table, went to water dish, and drank. Went to squares 20-21, remained there 15 min, again went to water dish and drank. Went to square 27, remained there 140 sec, and ran to table 1 without signal. Jumped down from table, went to water dish, then to square 27, and then to square 34, lay down on latter square for 15 sec, then went to square 21, remaining there for 40 sec. Then exhibited similar behavior for 2 min, moving from one square to another and not attempting to stand on mat. Went to door several times, whining and turning in circles; 38) experimenter entered room and went to mat, dog following him; 39) experimenter left room, dog remained near mat for short time and then went to square 27, remaining in vicinity of this square for 4 min; 40) experimenter again entered room and shifted mat to squares 32-39; animal went to mat and stood on it; 41) sat on mat; 42) jumped down from table, went to squares 7, 21, and 10, lay down on square 27, and went to mat after 16 sec; 43) jumped down from table and immediately went to mat; 44) jumped down from table, went to mat and to table 2 after 10 sec, returned to mat, and went to door.

INFLUENCE OF CHANGE IN LOCATION OF FEEDER TABLE ON CONDITIONED-REFLEX ACTIVITY

The first observations in this area were made by P.S. Kupalov on the dog Nayda, in whom a positive reflex involving going to table 1 in response to a metronome was induced. On one experimental day, the table was removed from the room. On entering the room, the dog ran to the usual location of the table, sat down, prepared herself to jump, and then turned aside.

Influence of Change in Location of Feeder Table on Conditioned-Reflex Activity

1 Число применений условного раздражителя	2 Условный раздражитель	3 Латентный период условного рефлекса (сек)	4 Поведение собаки при действии условного раздражителя	5 Примечание
6 Выписка из протокола опыта от 18/VIII 1962 г. Собака Уна (Стол 1 с квадратов 66—68 перенесен на квадраты 42—38)				
				7 Как только собака была впущена в комнату, она сразу побежала к месту обычного нахождения стола, на квадрате 53 она сделала резкий поворот и побежала к столу, где съела первый подкорм. Затем прыгнула на стол 2, соскочила на пол. Ходит по комнате, обнюхивая пол. Прыгает на стол 1, соскакивает с него и становится на коврик. Через 5 сек уходит с коврика, перемещается по комнате, останавливаясь в различных ее местах и оглядываясь по сторонам. Затем становится на коврик и смотрит в направлении квадрата 38

Continued

[1] Число применений условного раздражителя	[2] Условный раздражитель	[3] Латентный период условного рефлекса (сек)	Поведение собаки при действии условного раздражителя [4]	Примечания [5]
3058	[8] Звонок	1,5	[10] Повернулась к столу 1 и вскочила на него. Остановилась, повернула голову в сторону прежнего местонахождения стола, к чашке подошла на стук кормушки	[14] Ходит по комнате, затем встает на коврик. В положении на коврике голова и туловище вначале повернуты к квадрату 46, а затем к квадрату 43
3008	[9] Свет	1,5	[11] Двинулась в направлении прежнего местонахождения стола 1, на квадрате 47 повернулась к столу 1 и вскочила на него	[15] Соскочив со стола, идет на коврик, откуда без сигнала бежит на стол 1, опять встает на коврик и опять без сигнала бежит на стол. Еще раз встает на коврик, причем голова и туловище оказываются повернутыми к столу 1
3059	Звонок	1,0	[12] Поворачивается к столу 1 и вскакивает на него	[16] Спрыгнув со стола, некоторое время ходит по комнате, затем встает на коврик, голова и туловище повернуты к столу 1
3009	Свет	1,0	[13] То же	[17] Встает на коврик, повернувшись к квадрату 40, затем поворачивается к квадрату 37

1) Number of applications of conditioned stimulus; 2) conditioned stimulus; 3) latent period of conditioned reflex (sec); 4) dog's behavior under action of conditioned stimulus; 5) notes; 6) extract from record of experiment on 18 August 1962. Dog Una (table 1 moved from squares 66-68 to squares 42-28); 7) on entering room immediately went to usual location of table, made a sharp turn on square 53, and went to table, there eating first portion of food. Then jumped onto table 2 and back to floor. Ran about room, sniffing floor. Jumped onto and down from table 1 and stood on mat. Left mat after 5 sec, moved about room, stopping in different areas and looking to all sides. Then stood on mat and looked at square 38; 8) bell; 9) light; 10) returned to table 1 and jumped up onto it. Remained on table, turned head toward prior location of table, and approached tray in response to noise of feeder; 11) moved toward prior location of table 1, turned back toward table 1 from square 47, and jumped onto table; 12) turned toward table 1 and jumped onto it; 13) the same; 14) walked about room and then

stood on mat. Turned head and torso at first toward square 46 and then toward square 43 while standing on mat; 15) jumped down from table, went to mat, went to table 1 without signal, returned to mat, and again went to table without signal. Again returned to mat, but kept head and torso turned toward table 1; 16) jumped down from table, walked about room for short time, then stood on mat, with head and torso turned toward table 1; 17) stood on mat, turning toward square 40 and then toward square 37.

V.V. Yakovleva observed similar behavior in the dog Ledi when the location of the feeder table was changed.

Analogous investigations were subsequently conducted by other researchers (O.N. Voyevodina, V.D. Volkova, G.A. Shichko, and others).

The following conditioned-reflex activity was formed in V.D. Volkova's investigations on the dog Una. At the beginning of the experiment, the animal entered the room and went to table 1, where she received food. Then, jumping down from the table, she went to the mat located on squares 18-25 and did not leave it until the conditioned stimuli were applied. She went to table 1 when a bell or a light (the positive conditioned stimuli) was switched on.

In one experiment, table 1 was shifted from squares 66-68 to squares 42-48 (see Fig. 1). The other experimental conditions were as before. On entering the experimental room, the dog ran rapidly toward the usual location of table 1, but she slowed down abruptly on square 53. She then turned toward the table in its new location and ran to it. Jumping up onto the table, she received her first portion of food. She did not immediately return to the mat after eating. She walked about the room for a short time, sniffing the floor and looking about her. She approached the mat in some instances, but she never stood on it. This type of movement about the room alternated with intersignal trips to table 1. On the first application of the conditioned stimulus (bell), the dog immediately went to table 1 and jumped up onto it. However, on leaving the table, she first turned her head toward the usual location of the table and stood in this position for several seconds. Only in response to the sound of the feeder did she go to the tray and begin to eat. She returned to the mat after eating. When the next conditioned stimulus (light) was applied, she first moved toward the place where the table had previously been and then, changing direction, she went to table 1 and jumped up onto it. The dog's path from the feeder to the table was consequently a curved rather than a straight line. However, the animal adapted very rapidly to the new situation and began to run to the table by the shortest path, i.e., along a straight line, on subsequent applications of the conditioned stimuli. At the beginning of the experiment, the animal did not immediately stand on the mat during the intervals between applications of the conditioned stimuli, but walked about it for some time. Having taken up a position on the mat, the dog turned first toward the usual location of the table and then toward its new location. At the end of the experiment, the animal generally began to move toward the new location of the table (experiment on 18 August 1962).

It can be seen from the foregoing that changing the location of the feeder table led to disruptions of conditioned-reflex activity. These disruptions were more substantial at the beginning of the experiment, for the most part having disappeared by the end of the experiment.

If the feeder table was returned to its usual place on the following day, the animal's conditioned-reflex activity proceeded without material changes, only an intensification of the orientation reaction during the pauses between applications of the conditioned stimuli being noted in certain cases.

In V.D. Volkova's experiments on Sharik, the dog entered the room and ran toward the prior location of feeder table 1 so rapidly that he had to turn his body in mid air in order to avoid striking his head on the wall. The other changes in his conditioned-reflex activity were the same as those noted in Una.

Changing the location of the feeder table thus led to prolongation of the time required for the animal to reach the mat, a change in his usual pose on the mat, and disruption of his conditioned motor reflexes. It must be emphasized that all these disruptions were more pronounced at the beginning of the experiment and gradually disappeared toward its end.

CONCLUSION

Relocation of the sources of conditioned visual and auditory stimuli, the mat, and the feeder table at different distances from their usual locations led to marked disruptions of induced conditioned-reflex motor activity. These disruptions entailed changes in both the animal's conditioned motor reflexes and his behavior during the intervals between applications of the conditioned stimuli.

The extent to which conditioned-reflex activity was disrupted was a direct function of:

1) the strength of the conditioned reflexes;

2) the amount by which the locations of the conditioned and unconditioned stimuli were altered;

3) the complexity of the induced conditioned-reflex activity;

4) the individual characteristics of the animal's nervous system.

More substantial disruptions were observed during the initial period of conditioned-reflex formation, when the conditioned-reflex activity was more complex, when the conditioned stimuli were shifted by greater distances from their initial locations, and in animals with weak or weakened nervous systems.

The data obtained indicate that the central nervous system is more sensitive to changes in the spatial relationships of the stimuli in an animal's environment. For example, changing the position of the conditioned stimulus by only 50 cm during formation of differentiation leads to a change in higher nervous activity.

It must be noted that similar data have been obtained by other authors in investigations conducted on various living organisms under natural conditions. Thus, for example, V.A. Vagner (1913) established that a bee cannot find its hive if it has been moved by only 50 cm. According to the data of G.Z. Roginskiy (1948), a murre cannot find its egg if it has been moved by 30-50 cm, etc.

It follows from the foregoing that animals at different levels of evolutionary development react in similar ways to the spatial relationships of environmental stimuli.

Chapter 3

INVOLUNTARY AND VOLUNTARY MOVEMENTS AS COMPONENTS OF ANIMAL BEHAVIOR

It has long been customary to classify the activity of animals and man as voluntary or involuntary. Many noted physiologists have adhered to this division (I.M. Sechenov, 1863, 1878, and 1884; N.O. Kovalevskiy, 1892; I.P. Pavlov, 1933, 1934, and 1935; et al.).

Involuntary reactions are those that regularly appear in response to a given stimulus under definite circumstances. As examples we can cite salivation on stimulation of the oral cavity, constriction of the pupils in bright light, jerking back of an extremity subjected to severe painful stimulation, etc. Voluntary reactions are those that are actively effected by the animal and are not responses to a specific stimulus. I.M. Sechenov (1884) stated* that voluntary movements are movements learned under the influence of vital needs. Essentially the same view was held by I.P. Pavlov, who wrote: "It is quite easy for us to execute any movement, since we are continually doing so, and all our movements are under the influence of permanent cortical associations; this is very rarely the case for the functions we term 'involuntary'."** Pavlov regarded movements originating in the cerebral cortex as voluntary.*** Examples of voluntary reactions include the dog's approaching the mat and standing on it, jumping up on the table during the intersignal pauses, so-called random movements, etc.

Involuntary reactions, in the form of unconditioned reflexes, have long been a subject of physiological study. The conditioned-reflex method substantially expanded opportunities for experimental investigation of involuntary movements and opened up new prospects for objective study of voluntary movements. Voluntary movements are associated principally with the activity of the skeletal musculature, so that it is readily seen why I.P. Pavlov and his students and followers devoted a great deal of attention to studying the motor activity of animals (N.I. Krasnogorskiy, 1911; V.M. Arkhangel'skiy, 1922; Yu.P. Frolov, 1924; E. Asratyan, 1934 and 1935; V.P. Protopopov, 1935 and 1950; Yu. Konorskiy and S. Miller, 1936; I.S. Rozental', 1936, 1938, and 1940; M.K. Petrova, 1941; K.S. Abuladze and I.S. Rozental', 1948; et al.).

I.P. Pavlov assigned special importance to the work of N.I. Krasnogorskiy and of Yu. Konorskiy and S. Miller (1936), whose data he used as a basis for an attempt to interpret the physiological mechanism of so-called voluntary movements. Analysis of experimental data enabled Pavlov to reach the following conclusions: 1) "The cortical motor region is related to voluntary activity, continually undergoing successive inhibition and stimulation. The salivary reaction, although its cortical projection must be acknowledged, is obviously constructed on a different pattern and is an involuntary activity: we do not control the saliva and cannot halt its flow. It must be recognized that the functional characteristics of salivary and motor reactions are totally different; the former are involuntary functions, while the latter are voluntary. All processes should be weaker in a salivary cortical projection than in a motor projection"*; 2) "...a kinesthetic cell stimulable by a definite passive movement produces this movement when stimulated centrally rather than peripherally"**; 3) "...the cortical kinesthetic cells may be and actually are linked with all the cortical cells that are projections of internal influences and of the body's internal processes. This is the physiological basis for the so-called voluntariness of movements, i.e., the fact that they are dictated by total cortical activity."*** These hypotheses advanced by Pavlov are an important contribution to a physiological understanding of the mechanism of involuntary and voluntary movements.

A great deal of interesting material on the problem of involuntary and voluntary actions has been gathered in connection with the study of the higher nervous activity of dogs under free-movement conditions. Systematic investigations in this area have been conducted in the laboratories of I.S. Beritov (I. Beritov, 1934a,b,c, 1935, 1947, 1961, and 1962; I. Beritov, N. Beburishvili, and M. Tsereteli, 1934; I. Beritov and M. Tsereteli, 1934; et al.), L.G. Voronin (L.G. Voronin, 1947, 1952, and 1957; L.N. Norkina, 1951; N.A. Rokotova, 1954 and 1957; et al.), and P.S. Kupalov (P.S. Kupalov, 1946, 1948, 1949, and 1962; V.K. Fedorov, 1948 and 1955; V.V. Yakovleva, 1948 and 1952; et al.). Many interesting data have also been amassed by N.A. Shustin (1959) and certain other researchers.

So-called food-procuring reactions involving pressing a lever or pedal with a paw have been exgensively studied in L.G. Voronin's laboratory. In order to develop such reactions, the experimenter takes the animal's paw, presses it on the lever or pedal, and gives the animal food.**** An indifferent stimulus is subsequently conjoined with pressing on the lever and this leads to induction of a conditioned motor reflex. In these investigations, the combination of passive pressure on the lever and an alimentary reward caused the animal to develop a voluntary reaction in the form of active repetition of the appropriate motor act. The conjunction of an indifferent stimulus with active pressure on the lever resulted in induction of a conditioned motor reflex, so that the voluntary movement acquired the character of an involuntary action. The technique employed by L.G. Voronin and his colleagues thus makes it possible to study voluntary and involuntary reactions simultaneously and to trace the conversion of one type of reaction to the other.

In the laboratories of I.S. Beritov, L.G. Voronin, and other researchers, a definite motor reaction was generally induced by the experimenter's intervening directly in the animal's behavior. For example, in I.S. Beritov's investigations (1934), a conditioned motor reflex involving going to a feeder was developed in the following manner. The dog was first forced to lie in a given place in the experimental room (on a couch) and then trained to go to the feeder, for which purpose he was periodically called to it and given food. He was then forcibly led back to the couch. After finishing this "preliminary training," an indifferent stimulus was conjoined with going to the feeder, which completed the development of the appropriate conditioned motor reflex.

As has been frequently mentioned above, one feature of our investigations* was the fact that the animal was completely isolated from the experimenter during the experiment: conditioned behavior was induced on the basis of active rather than passive movements. Moreover, the conditioned signal was usually applied after the animal had independently carried out the motor reaction (standing in a definite pose on the mat, shaking himself, pawing a loudspeaker, etc.) and not before. The behavior we induced proceeds in accordance with the following scheme: R-S-D-P, where R is an active motor reaction in the form of shaking, scratching, etc., S is the conditioned signal, D is movement toward the feeder, and P is eating. In many authors' investigations, motor activity proceeded in accordance with the scheme S-R-D-P or S-D-P. Conducting investigations with the first procedure ensures better conditions for studying involuntary and voluntary reactions, as is rather well shown by the experimental data that we will now discuss.

ACTIVE EXECUTION OF INVOLUNTARY REACTIONS

Our laboratory studied the active repetition of involuntary (shaking, sneezing, and scratching) and voluntary (pressing a rubber bulb, licking a lightbulb, and pawing a loudspeaker) reactions by dogs. In a special series of experiments conducted by V.K. Fedorov and L.S. Gorshkova, we also determined the characteristics of conditioned shaking and scratching reflexes formed by conjoining an indifferent stimulus with an appropriate unconditioned stimulus.

Active repetition of a shaking reflex was studied by V.V. Yakovleva, by R. Floru, and by V.K. Fedorov and L.S. Gorshkova.

In the experiments of V.V. Yakovleva (P.S. Kupalov, 1948, 1958, and 1962; V.V. Yakovleva, 1948 and 1952), a conditioned reflex involving going to the feeder in response to a metronome operating at 120 beats per minute was developed in the dog Ledi. During this investigation it was found that, on several days, the dog shook herself after eating the first portion of food. This reaction was not observed during the remainder of the experiments. These fortuitous shakings were subsequently accompanied by application of the metronome followed by feeding. The animal consequently began to execute this reaction at the beginning of each day, at first only once, after eating the first portion of food, but then 3-4 times during the experiment. At other times during the experiment, she made persistent unsuccessful attempts to shake, wagging her head, gnashing her teeth, tossing her head, and bouncing several times on her front paws. Ledi began to pant after such fruitless attempts and, in some cases, lay down in complete exhaustion or moved sluggishly about the room, toward the door.

R. Floru obtained similar data in his experiments (1952).

In the investigations conducted by V.K. Fedorov and L.S. Gorshkova (P.S. Kupalov, 1948; V.K. Fedorov, 1955) on 12 dogs, the animal was not isolated from the experimenter and active repetition of the reaction was induced not on the basis of fortuitous scratching, but on the basis of scratching purposely evoked by the experimenter, who sprinkled water on the animal's coat. The experiments were conducted in the following manner. One of the experimenters sprayed the dog's coat with a fine stream of water, while the other gave him bread moistened in milk after he shook himself. At the beginning of the investigation, all the animals exhibited a defensive reaction to the first experimenter and an alimentary reaction to the second. The defensive reaction then became positive, so that the dogs not only did not run from the experimenter who did the sprinkling, but came up to him when he picked up the syringe he used to spray them. The number of shakings caused by the sprinkling subsequently increased by a factor of 1½-3, but active execution of this reaction was rarely observed. There were often incomplete shaking movements, which substantially exceeded the complete reactions in number even though they were not reinforced. Thus, in one experiment, the dog Sharik executed 6 complete and 19 incomplete shakings. It is interesting that each complete repetition of this reflex was followed by several incomplete ones. For example, Sharik executed 11 incomplete shakings after his first complete shaking and 2 and 5 incomplete ones after his second and third complete ones, respectively.

Experimental data indicate that "Shaking is a complex reaction with voluntary and involuntary components. It begins with placement of the legs in a suitable position for supporting the torso. This is the voluntary component and the dog can readily repeat it. The actual act of shaking, with its sharp, powerful, frequent vibratory movements of the head, torso, and cutaneous musculature, is an involuntary action and the dog cannot perform it without specific unconditioned stimuli that evoke the shaking reflex."* However, if accidentally or purposely evoked shaking is reinforced with food, the dogs begin to actively repeat it, as our experimental data show. This indicates that even an involuntary reaction is not rigidly fixed and inalterable and that it can, under certain conditions, acquire the character of a voluntary reaction.

As V.V. Yakovleva correctly noted (1948, page 108), active repetition of the shaking reflex requires great nervous tension. This explains the fact that the animal effects the complete action comparatively infrequently, yet often repeats its voluntary components without visible difficulty. Certain observations made on humans also indicate the difficulty of active repetition of an involuntary reaction. Thus, I.R. Tarkhanov (1881) reported that a subject capable of voluntarily raising his heart rate had a hard time doing so and became tired when the experiments were frequently repeated.

The experimental data of V.V. Yakovleva, R. Floru, V.K. Fedorov, and L.S. Gorshkova show that active repetition of shaking is more readily and frequently effected when the skin is first stimulated by wetting the coat, putting a chain around the animal's neck, etc. For example, in V.V. Yakovleva's investigation (1952), the dog's coat was wetted on his muzzle and back before the experiments; this made the shakings particularly strong and they increased markedly in number, reaching as many as 13 in a single experiment. When the coat was not preliminarily wetted, the shakings were weaker and were often incomplete, abortive, and preceded by such movements as jumping on the front paws, tossing the head, and scratching.

According to the data of these researchers, some dogs voluntarily engaged in autostimulation by scratching, rolling on the mat, etc., which facilitated shaking. Thus, one of the dogs in the experiments conducted by V.K. Fedorov and L.S. Gorshkova rolled on the floor if he was not sprinkled with water and he then "demonstratively shook."

In analyzing the data cited, it is impossible to overlook the fact that the cutaneous stimuli that facilitated shaking were addressed to the receptive field of the shaking reflex. They increased the excitability of the cortical projection of the unconditioned shaking reflex, so that active repetition of this reflex became markedly easier. It is for precisely this reason that the animals readily and frequently shook after preliminary cutaneous stimulation.

In a special series of investigations, V.K. Fedorov and L.S. Gorshkova showed that the shaking reflex is comparatively easily induced and stably maintained in dogs when an indifferent stimulus is conjoined with sprinkling of the coat or with feeding. Thus, in an investigation conducted in a soundproof chamber with the dog Tarzan, only 30 conjoint applications of a bell and wetting of the coat were required to develop a strong and stable conditioned shaking reflex. Its stability is indicated by the fact that pronounced conditioned shaking was produced in response to 68 of 70 applications of the bell. In two other animals, a conditioned shaking reaction was induced after 49 and 61 applications of an indifferent stimulus in combination with sprinkling of the coat and feeding and was then stably maintained.

These data show that a conditioned shaking reflex evoked by a definite conditioned stimulus differs in induction rate, stability, and strength from active shaking, which, as was mentioned above, develops comparatively slowly, is rarely manifested in complete form, and requires great nervous tension.

The data obtained in studying sneezing (V.V. Yakovleva, 1952; V.K. Fedorov, 1955) are in basic agreement with those gathered in investigating shaking.

In V.V. Yakovleva's investigation, the conditioned alimentary stimulus (a metronome) was applied only when the dog was at the stimulus site. When the pauses between the conditioned signals were lengthened, the animal began to exhibit various motor reactions, including sniffing and sneezing. The act of sneezing was reinforced by switching on the metronome and giving the dog food, so that he began to actively sneeze. The animal was not always able to actively repeat the sneezing reflex; in many cases he unsuccessfully attempted to sneeze, raising and tossing his head, then lowering it and snorting. This indicates that, like shaking, active sneezing is a difficult task for a dog's nervous system.

In the investigation conducted by V.K. Fedorov and L.S. Gorshkova, sneezing was induced in the active form on the basis of passive sneezing intentionally evoked by an unconditioned (cigarette smoke) or conditioned stimulus. Active sneezing was infrequently observed and was not consistent. At the same time, the animals made numerous "sneeze-like" movements, shaking their heads and baring their teeth. Different results were obtained when a classical conditioned reflex was induced by conjoining an indifferent stimulus with an unconditioned stimulus. The conditioned reflex was readily formed, stable, and quite pronounced. Thus, in experiments on the dog Tarzan, a conditioned sneezing reflex appeared on the ninth application of a square while blowing smoke at the animal and became stable on the twentieth application. A sneezing reflex was also readily developed in the dog Chertenok and remained stable for seven years.

The investigations described above showed that, under certain conditions, an involuntary sneezing reaction can take on the character of a voluntary reaction and be actively executed by the animal, although not always in its full form. They also indicated that, in contrast to active sneezing, conditioned-reflex sneezing induced to a definite stimulus is easily developed and persists for prolonged periods.

Study of the active repetition of a sneezing reflex induced by alimentary reinforcement of fortuitous sneezes (V.K. Fedorov, 1955; R. Floru, 1952) showed that it was readily formed and stably maintained. Thus, according to R. Floru's data, the dogs began to actively execute the sneezing reflex after it had been reinforced with food 5-6 times. According to V.K. Fedorov's data, the dogs exhibited both complete sneezes and a large number of incomplete sneezes, in which they shook a paw to one side or raised it.

V.V. Yakovleva's experiments established that dogs execute active sneezing more easily than active shaking, while the investigations conducted by V.K. Fedorov and R. Floru showed that dogs have substantially less difficulty in repeating the scratching reflex than the shaking reflex. Thus, active execution of the shaking reflex is a substantially more difficult task for the dog's nervous system than repetition of the sneezing or particularly the scratching reflex. The comparative ease with which an animal scratches is due to the fact that this reflex is less complex than shaking or sneezing. The scratching reflex consists in taking up a definite pose, touching a paw to the skin, and making rapid movements with it. These components of the act of scratching are voluntary movements and this is obviously why they are easily effected. However, as an integral reaction under natural conditions, scratching is executed by an unconditioned mechanism and has an involuntary character.

Shaking and sneezing consist of involuntary and voluntary components, this being why animals execute the latter readily and frequently but perform the entire act comparatively rarely.

Thus, the investigations conducted by V.V. Yakovleva, R. Floru, and V.K. Fedorov and L.S. Gorshkova showed that involuntary scratching, sneezing, and shaking under experimental conditions can acquire the character of voluntary acts and be actively executed by the animal; the ease and consistency with which a given reflex is repeated depends on its complexity.

A special investigation conducted by R. Floru (1952) and involving extirpation of the cutaneous and motor analyzers showed that active execution of shaking and scratching reflexes is associated principally with cortical activity and that the motor analyzer plays an important role. Thus, removal of the cutaneous analyzer caused more frequent appearance of active scratching, while repetition of the scratching reflex ceased and could not be restored after extirpation of the motor analyzer.

ACTIVE EXECUTION OF VOLUNTARY REACTIONS

The active execution of motor reactions customarily assumed to be voluntary has been studied by V.K. Fedorov, I.A. Alekseyeva, O.N. Voyevodina, P.S. Kupalov, and G.A. Shichko.

V.K. Fedorov conducted an investigation on 12 puppies, in which he studied a motor reaction involving pressing a paw on a rubber bulb. The experiments were carried out on an experimental table, with both the animal and the rubber bulbs on it. One of the bulbs was connected pneumoelectrically to a light and the other to a bell. Pressing a bulb automatically switched on the conditioned-signal source connected to it. The animals, moving about the table or lying on it, accidentally pressed a bulb, a definite conditioned stimulus was consequently applied, and the experimenter provided alimentary reinforcement.

All the puppies first developed a conditioned reflex involving going to the reinforcement site in response to the conditioned stimuli (the light of the lamp and the sound of the electric bell) and those motor acts that more frequently led to application of a conditioned signal and provision of food then became fixed. The dogs consequently exhibited diverse active motor reactions at the beginning of the experiment: some animals shifted from paw to paw, others periodically lay down on the table, pressing their chest and abdomen against it, and still others alternately sat and stood. The motor reactions observed were at first directed not at the rubber bulb but at the area of the table where the animal was most frequently able to activate the conditioned signal. Later, as the number of experiments increased, the bulb was differentiated from the other stimuli and the random motor acts were replaced by a reaction involving pressing the bulb with a paw. Some puppies directed their active motor activity at the bulb from the beginning of the experiment, grasping it in their teeth and pressing it with their paws. All the animals eventually exhibited an active motor reaction involving pressing the bulb with a paw; as this reaction became stable, the induced activity proceeded more rapidly and consisted of approaching the bulb, pressing it with a paw, going to the reinforcement site in response to the conditioned xignal, and eating the food. As a result of the rapid course of the motor activity, the duration of the experiments was greatly reduced. Thus, for example, one of the puppies required 18 min to carry out the usual four cycles of motor activity (pressing the bulb, going to the reinforcement site, eating the food, and returning to the bulb) at the beginning of the investigation, a time that subsequently decreased to 1½ min. The puppies often went to the bulb and pressed it even without eating the next portion of food. This indicates that the animals were able to effect the motor reaction with comparative ease.

The portion of V.K. Fedorov's investigation described above showed that formation of the reaction involving actively pressing a paw on a rubber bulb occurred gradually: a conditioned motor reflex was first formed to the conditioned signal, various motor acts directed at a definite place appeared, and only then was the bulb isolated from the over-all experimental situation and the paw-pressing reaction fixed, the other active motor actions being extinguished (including sitting and standing, etc.).

I.A. Alekseyeva (1953), I.A. Alekseyeva and O.N. Voyevodina (1953), O.N. Voyevodina and P.S. Kupalov (1954), and O.N. Voyevodina (1962) studied a voluntary reaction involving licking an electric bulb.

I.A. Alekseyeva conducted her experiments on two dogs, Chernyavka and Tsezar. A conditioned reflex involving going to the feeder in response to a 120 bpm metronome was induced and, after it had become stable, a new reflex, the light of an electric bulb, was added. The lamp was hung on a stand, which was placed in the middle of the room during the experiment. The stimulus-application sequence was as follows: the electric light was applied first and then replaced by the metronome, which was conjoined with alimentary reinforcement. Chernyavka did not react to the electric bulb at the beginning of the investigation, but she then began to remain near the stand, look at the bulb, and even paw it. She subsequently touched the bulb with her muzzle and soon began to make licking movements in connection with the reinforcement. The dog's behavior at this point consisted of the following components: approaching the stand, licking the bulb, going to the metronome (in response to the light), going to the feeder in response to the metronome, and eating the food.

Essentially the same data were obtained for Tsezar as for Chernyavka. The most important difference lay in the fact that Tsezar began to lick the bulb suddenly. This reaction was first noted and immediately reinforced after 81 applications of the light and began to appear systematically after 92 applications. The animals repeated the licking reaction readily, consistently, and frequently. Thus, O.N. Voyevodina, who continued I.A. Alekseyeva's investigations on the same dogs, established that active licking of the bulb was stably maintained for more than ten years. The ease with which this reaction was repeated is shown by the investigation conducted by O.N. Voyevodina and P.S. Kupalov (1954), in which the animal executed the full cycle of motor activity whose first component was the licking reaction 12 times during a single experiment without any noticeable difficulty.

Of greatest interest in the experiments of I.A. Alekseyeva, O.N. Voyevodina, and P.S. Kupalov was the active licking of the bulb that appeared spontaneously, without any special intervention on the part of the experimenter. Such active motor acts have long been known and were repeatedly noted by I.P. Pavlov. For example, in an article entitled "The Physiological Mechanism of So-Called Voluntary Movements" he wrote: "A conditioned stimulus is a signal that 'substitutes' for an unconditioned stimulus. Thus, for example, a dog will go to a bulb and even lick it if it is a conditioned alimentary stimulus when lit."*

Like V.K. Fedorov, I.A. Alekseyeva, O.N. Voyevodina, and P.S. Kupalov, G.A. Shichko studied the active repetition of a voluntary reaction, the only difference being that he made a more detailed investigation of the formation of the active motor act.

The experiments were conducted on three dogs (Dzhul'bars, Dzhek, and Pal'ma) under the following conditions. An electric feeder, a water dish, and two loudspeakers were placed on the floor of the exper'mental room; one loudspeaker was subsequently converted to a positive stimulus (loudspeaker 1), while the other was converted to a differential stimulus (loudspeaker 2). The loudspeakers were placed a short distance apart and were 105 × × 95 × 80 and 75 × 65 × 45 mm in size (Fig. 10). Each of them was connected by wires to an electric metronome. The positive and differential auditory stimuli were the sound of a 120 bpm metronome. The unconditioned alimentary stimuli were powdered meat biscuits in the experiments on Dzhul'bars and pieces of meat in the experiments on the other two dogs. Each reinforcement portion was 15-20 g.

Fig. 10. View of loudspeakers and feeder.

There was no preliminary induction of a conditioned trip to the feeder in the form previously employed in this method.

The site of the feeder and loudspeakers, the noise of the feeder, and the sounds of the positive and negative metronomes were checked for indifference during the first experiment. A conditioned reflex involving going to the feeder in response to the positive metronome was then induced. This reflex was developed on the basis of imitation in Dzhek and Pal'ma. After the conditioned reflex involving going to the feeder had become stable, a reflex was induced to the location of loudspeaker 1.

In the investigation on Dzhul'bars, the feeder was generally on square 54, loudspeaker 1 on square 34, loudspeaker 2 on square 32, and the water dish on square 20. It was established on the first day of experimentation that the site of the feeder and loudspeakers, the noise of the feeder, and the sound of the positive and negative metronomes were indifferent stimuli for the dogs. Induction of the conditioned reflex involving going to the feeder in response to the positive metronome was then begun. The metronome was switched on when the animal was near the feeder and he was given reinforcement. The first conditioned-reflex trip to the feeder was noted on the fourth application of the metronome reinforced by powdered meat biscuit and the reflex began to appear systematically on the twenty-first application. At the beginning of the investigation, when the conditioned reflex to the metronome was not adequately stable, Dzhul'bars moved about the room a great deal, jumped up onto the tables, sniffed the floor and the objects on it, and often went to the door. Then, as the reflex became stable, his general motor activity began to decrease and he spent most of his time in the right-hand path of the room, where loudspeaker 1 was located, and exhibited a positive reaction to this loudspeaker. The latter reaction was manifested in the fact that, when he was near the door, Dzhul'bars in some cases went to the feeder in response to the sound of the metronome along a curved rather than a straight line, passing near loudspeaker 1. This reaction was first noted on the 59th reinforced application of the metronome (9th experiment). That loudspeaker 1 had ceased to be an indifferent stimulus was shown by the fact that the animal approached it and sometimes watched it during the intersignal pauses. He did not approach the differential loudspeaker, but went to the feeder in response to the sound of the metronome emanating from it.

After the 95th conjunction of the positive metronome with reinforcement with powdered meat biscuit (13th experiment), the conditioned reflex involving going to the feeder was sufficiently stable that it was possible to move on to induction of a conditioned reflex to the animal's taking up a position near loudspeaker 1 (square 34). In order to develop this reflex, the metronome was applied only when the dog was on or near square 34. The animal's general motor activity during the intersignal pauses decreased after induction of the reflex to the position of loudspeaker 1 began, the decrease being larger than that observed while the reflex involving going to the feeder was becoming stable. At the same time, Dzhul'bars began to approach loudspeaker 1 more frequently and, if it was not immediately switched on, remained near it. From the 108th reinforced application of the metronome onward, the conditioned signal was given only when the animal had been near loudspeaker 1 for 3-10 sec. The dog now remained near the loudspeaker for longer periods, watching it, occasionally lying down in front of it, and sometimes attempting to actively manipulate it. Thus, Dzhul'bars tilted his head toward loudspeaker 1 for the first time after the 110th application. This reaction was subsequently observed during the pauses after the 112th, 113th, 120th, and certain other applications. The dog gently touched the positive loudspeaker with his nose after the 129th application (17th experiment) and cautiously pushed it with his nose after the 132nd application (record of experiment 17 on 25 February 1959). During the pause after the 145th application (19th experiment), the loudspeaker was not switched on for 5 min, despite the fact that the animal repeatedly approached it and remained near it. During this pause, the dog went to the loudspeaker, cautiously put a paw on it, held it there for a short time, and then slowly lay down. During the pause after the 148th application (19th experiment), the dog very carefully placed his left front paw on loudspeaker 1. During the 20th experiment (record of experiment 20 on 10 March 1959), Dzhul'bars made several attempts to touch loudspeaker 1 with a paw, sometimes holding his paw over it and then letting it drop to the floor. In two cases he struck the loudspeaker, in one case he touched it with his paw, and in one case he withdrew his paw. The dog approached loudspeaker 2 three times, in which case the differential metronome was applied but not reinforced. As can be seen from the record of the experiment, the dog went to the feeder in response to this stimulus.

Active motor reactions, in the form of touching or pawing loudspeaker 1, were subsequently frequently observed and they gradually increased in number.

Over the next six experiments (21-26), there was an increase in the number of active motor reactions involving touching or pawing loudspeaker 1. Thus, while the dog touched the loudspeaker with his paw only four times during the 20th experiment, he touched it seven times during the 25th experiment (185th-193rd applications). Since these active reactions were intentionally unreinforced, they were markedly extinguished over the following three experiments (27-29). Thus, Dzhul'bars did not touch the loudspeaker at all during the 28th experiment and touched it only once during the first half of the 29th experiment. In order to avoid permanent extinction of the active motor reaction, reinforcement was resumed with the 215th application. As a result, the dog again began to touch the loudspeaker on the 218th application and to strike it with his paw on the 224th application. From this point onward, the dog no longer tilted his head toward loudspeaker 1, made incomplete attempts to touch it, or cautiously poked at it with his nose or paw. In the 31st experiment, it was found that the dog resumed striking the loudspeaker if the metronome was not switched on in response to his first tap. After the 32nd experiment (242nd application), the metronome was switched on only when Dzhul'bars struck loudspeaker 1 at least 3 times. As a result, the animal began to tap the loudspeaker several consecutive times. The dog sometimes rested one or both of his front legs on the loudspeaker during the intersignal pauses. He maintained this pose until loudspeaker 1 was switched on. If there was a great delay in its retardation, he began to paw at it. He did not touch the differential loudspeaker.

Record of Experiment No. 17 on 25 February 1959. Dog Dzhul'bars

Время суток [1]		Условные раздражители [4]				Подкрепление [9]	Поведение собаки после дачи пищи и в межсигнальные паузы [10]
часы [2]	минуты [3]	название [5]	порядковый № применения [6]	время действия (сек) [7]	реакция собаки [8]		
							[15] Впущена в комнату, пьет воду, идет к кормушке, прыгнула на стол 1, стоит на 40-м квадрате, идет к кормушке, стоит перед динамиком 1
15	11	[11] Метроном 1	126	5	[13] Бежит к кормушке	[14] Мясо-сухарный порошок	[16] Съела, идет на 34 й квадрат, отсюда к кормушке, вернулась к динамику 1, стоит перед ним
15	13	[12] То же	127	5	То же	То же	[17] Съела, подошла к динамику 1, наклонила к нему голову (возможно обнюхала), пошла к кормушке, от нее к динамику, снова идет к кормушке, затем к динамику 1, стоит
15	15	» »	128	4	» »	» »	[18] Съела, сразу подошла к динамику 1, от него побежала к кормушке, вернулась к динамику, стоит, идет к кормушке, отсюда к динамику 1, стоит
15	17	» »	129	4	» »	» »	[19] Съела, прыгнула на стол 1, подошла к кормушке, затем к динамику 1, наклонила к нему голову и смотрит на него, подняла голову, стоит неподвижно, снова наклонила голову и смотрит на динамик (как бы замерла в такой позе). Идет к динамику 2, от него к кормушке, затем к динамику 1, на 41 й квадрат, вернулась к динамику 1, стоит, коснулась его носом, пошла к кормушке, затем к чашке с водой, пьет. В дальнейшем трижды подходила к динамику и кормушке.

Continued

Время суток 1		Условные раздражители 4					
2 часы	3 минуты	5 название	порядковый № применения 6	время действия (сек) 7	8 реакция собаки	9 Подкрепление	Поведение собаки после дачи пищи и в межсигнальные паузы 10
15	21	Метрогом 1	130	4,5	Бежит к кормушке	Мясо-сухарный порошок	[20] Съела, идет на 56, 28-й квадраты, отсюда к кормушке, на 42-й квадрат и к динамику 2, остановилась перед ним, подошла к динамику 1, от него к кормушке, немного постояла, обнюхала ее, вернулась к динамику 1, стоит около него
15	24	То же	131	4	То же	То же	[21] Съела, забралась под стол 2, отсюда идет к динамику 1, к столу 2, к динамику 1, стоит перед ним, подошла к кормушке, заглянула в открытую чашку ее, подошла к динамику 1, стоит перед ним и периодически посматривает на него
15	26	» »	132	5	» »	» »	[22] Съела, пошла на 52-й квадрат, затем на 21-й, вернулась к кормушке, обнюхала ее, подошла к динамику 1, остановилась, подошла к кормушке, вернулась к динамику 1, стоит перед ним, смотрит на него, толкнула носом динамик, продолжает стоять
15	28	» »	133	5	» »	» »	[23] Съела, опыт прекращен

1) Time of day; 2) hours; 3) minutes; 4) conditioned stimuli; 5) type; 6) number of application; 7) action time (sec); 8) dog's reaction; 9) reinforcement; 10) dog's behavior after eating and during intersignal pauses; 11) metronome 1; 12) the same; 13) went to feeder; 14) powdered meat biscuit; 15) entered room, drank water, went to feeder, jumped up onto table 1, stood on square 40, went to feeder, stood in front of loudspeaker 1; 16) ate, went to square 34 and then to feeder, returned to loudspeaker 1 and stood in front of it; 17) ate, went to loudspeaker 1, tilted head toward it (perhaps sniffing), went to feeder and then to loudspeaker, again went to feeder and back to loudspeaker 1, stood still; 18) ate, immediately went to loudspeaker 1 and then to feeder, returned to loudspeaker, stood for a while, went to feeder and back to loudspeaker 1, stood still; 19) ate, jumped up onto table 1, went to feeder and then to loudspeaker 1, tilted head toward it and watched it, raised head, stood immobile, again tilted head and looked at loudspeaker (as though frozen in this pose). Went to loudspeaker 2, then to feeder, then to loudspeaker 1, then to square 41, returned to loudspeaker 1, stopped, touched it with his nose, went to feeder and then to water dish, drank. Then made three trips to loudspeaker and feeder; 20) went to squares 56 and 28, thence to feeder, square 42, and loudspeaker 2, stopped in front of latter, went to loudspeaker 1 and then to feeder, stood for a short time, sniffed it, returned to loudspeaker 1, and stood near it; 21) ate, went beneath table 2 and then to loudspeaker 1, table 2, and loudspeaker 1, stood in front of latter, went to

feeder, looked into open tray, went to loudspeaker 1, stood in front of it, and periodically looked at it; 22) ate, went to square 52 and then to square 21, returned to feeder, sniffed it, went to loudspeaker 1, stopped, approached feeder, returned to loudspeaker 1, stood in front of it and looked at it, touched it with his nose, and remained standing; 23) ate, experiment discontinued.

Thus, the dog's behavior at the end of the investigation reduced to the following: going to loudspeaker 1, pawing it no less than three times, going to the feeder in response to the positive metronome, eating, and returning to the loudspeaker.

The experiments conducted on Dzhul'bars showed that, during the induction and stabilization of the conditioned alimentary reflex to the sound of the metronome, both this stimulus and the loudspeaker from which it emanated acquired positive significance. It was for precisely this reason that the dog approached loudspeaker 1 comparatively often and sometimes remained near it. Later, as a result of the intentional development of a reaction involving going to loudspeaker 1 and staying near it, the dog began to fix his gaze on the loudspeaker and to bring his nose or paw close to it. These incomplete movements gradually culminated in cautious touches with his nose or paw. The factor underlying these incomplete movements differs from that underlying incomplete shaking or sneezing. In the latter case, the animals clearly tried to actively reproduce the shaking or sneezing reflex and even executed the voluntary components of these reactions, but it can be assumed that they were unable to complete the acts because of the reduced excitability of the cortical projection of the corresponding unconditioned reflexes. As for Dzhul'bars, there was no doubt that he could readily execute such voluntary reactions as touching the loudspeaker with his nose or paw. It is possible that the incomplete active movements in the experiments on Dzhul'bars were the result of an orientation reflex. Only this can explain such phenomena as the gradual approximation of the dog's paw to the loudspeaker, which was followed by rapid withdrawal, or his very cautious and gentle touching of it, which was also followed by rapid withdrawal.

It must be noted that the dog made incomplete and sometimes complete active movements on numerous occasions (see the record of experiment 20), although they were intentionally not reinforced at first. This indicates that the active movements in question were far from accidental and that they were regularly evoked by the experimental situation and the induction and stabilization of the conditioned alimentary reflex to the sound of the metronome and the animal's taking up a position near loudspeaker 1. This is also shown by the fact that the basic results of the investigation conducted on Dzhul'bars corresponded to those of the experiments on Dzhek and Pal'ma.

As was noted above, the conditioned reflex involving going to the feeder in response to the sound of the metronome was induced in Dzhek by imitation and subsequently became stable (after the

Record of Experiment No. 20 on 10 March 1959. Dog Dzhul'bars

Время суток [1]		Условные раздражители [4]				Подкрепление [9]	Поведение собаки после дачи пищи и в межсигнальные паузы [10]
[2] часы	[3] минуты	[5] название	порядковый № применения [6]	время действия (сек) [7]	[8] реакция собаки		
15	35						[16] Собака впущена в комнату. Побежала к кормушке, заглянула в открытую ее чашку и обнюхала. Ходит по комчате (34—48—34—48—44—стол 1—34—48—34 кв.). Остановилась около динамика 1, обнюхала его, потом ударила по нему правой лапой. Отошла в сторону
15	37	[11] Метрономом 1	149	5	[14] Побежала к кормушке	[15] Мясо-сухарный порошок	[17] Съела, идет по 40—46—34-му квадратам, наклонила голову к динамику 1, пошла на 47-й квадрат, отсюда к воде, пьет, подошла к кормушке, прыгнула на стол 1, идет на 34—48—34-й квадраты, стоит около динамика 1, наклонила к нему голову, отвернулась
15	40	[12] То же	150	4	То же	То же	Съела, остановилась на 34-м квадрате
15	41	[13] Метрономом 2	8	5	[14] Идет к кормушке	0	[19] Идет к динамику 1, отсюда на 40-й квадрат, вернулась к динамику 1, осторожно подняла лапу над ним, опустила ее на пол, пошла к кормушке, вернулась, наклонила голову к динамику, идет по 44—48 и 24-му квадратам, подняла левую лапу над динамиком 1, опустила ее, подняла правую лапу над тем же динамиком, пошла к кормушке, вернулась, стоит около динамика 1
15	45	Метрономом 1	151	6	То же	Мясо-сухарный порошок	[20] Съела, идет на 36-й квадрат, отсюда к динамику 1, затем пошла на 48-й квадрат, вернулась к динамику, постояла, отошла, вновь вернулась, подняла левую лапу над динамиком, но его не коснулась, отошла, вернулась к динамику 1, подошла к динамику 2

Continued

Время суток		Условные раздражители				Подкрепление	Поведение собаки после дачи пищи и в межсигнальные паузы
часы	минуты	название	порядковый № применения	время действия (сек)	реакция собаки		
15	47	Метроном 2	9	10	Идет к кормушке	0	От кормушки сразу пошла к динамику 1, подняла левую лапу над ним, медленно стала опускать, но скоро отдернула ее и поставила на пол, наклонила голову над динамиком 1, пошла на 64-й квадрат, отсюда к динамику 1, пытается поставить лапу на динамик, но скоро отдернула ее, несколько раз после этого наклоняла голову к динамику 1
15	50	Метроном 1	152	4	То же	Мясо-сухарный порошок	Съела, идет по 40, 64, 34-му квадратам, наклонила голову к динамику 1, подняла над ним левую лапу, опустила, постояла около 1 *сек* и снова подняла ту же лапу над динамиком, опустила ее на пол, наклонила голову к динамику 1, фиксирует его глазами, подняла левую лапу над динамиком, но его не коснулась. Идет на 44-й квадрат, вернулась к динамику 1, наклонила к нему голову, фиксирует глазами, подняла над динамиком левую ногу, отдернула, идет по 20, 48 и 34-му квадратам, стоит перед динамиком 1
15	53	То же	153	5	Бежит к кормушке	То же	Съела, ходит по комнате, подошла к динамику 1, ходит, приблизилась к динамику 2
15	55	Метроном 2	10	10	Идет к кормушке, от нее к динамику 1	0	Наклонила голову к динамику 1, подняла левую лапу, опустила, идет на 16-й, затем на 40-й квадраты, задержалась у динамика 2

Continued

Время суток [1]		Условные раздражители [4]					
часы [2]	минуты [3]	название [5]	порядковый № применения [6]	время действия (сек) [7]	реакция собаки [8]	Подкрепление [9]	Поведение собаки после дачи пищи и в межсигнальные паузы [10]
15	56	Метроном 2 [13]	11	10	Идет к кормушке [14]	0	[26] От кормушки сразу пошла к динамику 1, вернулась к кормушке, пьет воду, обнюхала динамик 1, отошла, вернулась, подняла над динамиком 1 левую лапу, опустила на пол, стоит
15	58	Метроном 1 [11]	154	5	Бежит к кормушке [14]	Мясо-сухарный порошок	[27] Съела, остановилась на 47-м квадрате, забралась на стол 1, идет к кормушке, отсюда к динамику 1, дважды наклоняла голову к динамику, прыгнула на стол 2, подошла к динамику 1, слегка и очень осторожно прикоснулась к нему лапой, стоит спокойно
16	03	То же	155	6	То же	То же	[28] Съела, идет на 15-й квадрат, затем на 34-й, дважды пыталась тронуть динамик 1, но не коснулась его, стоит
16	06	» »	156	4	» »	» »	[29] Съела, сразу к динамику 1, подняла левую лапу над ним, но не коснулась его, ходит, наклонила к динамику 1 голову, отошла, вернулась, повторила это, отошла, толкнула левой лапой динамик 1, ходит, подошла к динамику 1, смотрит на него, левой лапой потянула динамик на себя, стоит
16	08	» »	157	7	» »	» »	[30] Съела. Опыт прекращен

1) Time of day; 2) hours; 3) minutes; 4) conditioned stimuli; 5) type; 6) number of application; 7) action time (sec); 8) dog's reaction; 9) reinforcement; 10) dog's behavior after eating and during intersignal pauses; 11) metronome 1; 12) the same; 13) metronome 2; 14) went to feeder; 15) powdered meat biscuit; 16) dog entered room, went to feeder, looked into open tray, and sniffed it. Walked about room (squares 34, 48, 34, 48, and 44, table 1, and squares 34, 48, and 34). Remained near loudspeaker 1, sniffed it, then struck it with right front paw. Withdrew; 17) ate, walked over squares 40, 46, and 34, tilted head toward loudspeaker 1, went to square 47 and then to water dish, drank, went to feeder, jumped up onto table 1, went to squares 34, 48, and 34, stood near loudspeaker 1, tilted head toward it, and turned away; 18) ate, stayed on square 34; 19) went to loudspeaker 1 and then to square 40, returned to loudspeaker 1, carefully rested paw on it and then dropped it to floor, went to feeder, returned to loudspeaker, tilting head toward it, went over squares 44, 48, and 24, rested left front paw on loudspeaker 1, dropped it, raised right front paw over loudspeaker, went to feeder, returned and stood near loudspeaker 1; 20) ate, went to square 36, then to loudspeaker 1, and then to square 48, returned to loudspeaker, stood awhile,

withdrew, returned, raised left front paw over loudspeaker but did not touch it, withdrew, returned to loudspeaker 1, went to loudspeaker 2; 21) went to feeder and then to loudspeaker 1; 22) went immediately from feeder to loudspeaker 1, raised left front paw over it, slowly began to lower it but soon withdrew it, lowering it to floor, tilted head toward loudspeaker 1, went to square 64 and then to loudspeaker 1, tried to place paw on loudspeaker but soon withdrew it, then tilted head toward loudspeaker 1 several times; 23) ate, walked over squares 40, 64, and 34, tilted head toward loudspeaker 1, raised left front paw over it, lowered paw, stood for about 1 sec, again raised same paw over loudspeaker, dropped it to floor, tilted head toward loudspeaker 1, fixed his gaze on it, raised left front paw over it but did not touch it. Went to square 44, returned to loudspeaker 1, tilted head toward it, gazed at it, raised left front paw over loudspeaker, withdrew it, went over squares 20, 48, and 34 to stand in front of loudspeaker 1; 24) ate, walked about room, went to loudspeaker 1, walked about, approached loudspeaker 2; 25) tilted head toward loudspeaker 1, raised left front paw, left it drop, went to squares 40 and 16, remained near loudspeaker 2; 26) went immediately from feeder to loudspeaker 1, returned to feeder, drank water, sniffed loudspeaker 1, withdrew, returned, raised left front paw over loudspeaker 1, let paw drop to floor, stood still; 27) ate, stood on square 47, went to table 1, then to feeder, and then to loudspeaker 1, twice tilted head toward loudspeaker, jumped up onto table 2, went to loudspeaker 1, very gently touched it with a paw, stood quietly; 28) ate, went to square 15 and then to square 34, twice attempted to touch loudspeaker 1 but did not do so, stood still; 29) ate, went immediately to loudspeaker 1, raised left front paw over it but did not touch it, walked about, tilted head toward loudspeaker 1, withdrew, returned, repeated this process, withdrew, touched loudspeaker 1 with left front paw, walked about, went to loudspeaker 1, looked at it, drew it toward him with left front paw, stood still; 30) ate, experiment discontinued.

18th experiment). After this reflex had become stable, induction of an active reaction involving approaching loudspeaker 1 and remaining near it was begun. Hence it can be seen that the investigation conducted with Dzhek took essentially the same form as that conducted with Dzhul'bars. The only difference lay in the method of inducing the conditioned trip to the feeder in response to the metronome.

The experimental setup during the investigation with Dzhek was usually as follows: the feeder was on square 54, loudspeaker 1 on square 27, loudspeaker 2 on square 25, and the water dish on square 20. In contrast to Dzhul'bars, Dzhek did not immediately react to the metronome when the reflex involving going to the feeder was being stabilized. The metronome often failed to cause the animal to halt the movement he was making. This movement was completed within 1-5 sec after the metronome was applied and only then did the dog go to the feeder. Thus, for example, if the signal was given while the dog was going to the door, he continued his movement and turned around to go to the feeder only after 1-2 sec. If Dzhek was drinking water when the metronome was switched on, he continued drinking for several (up to 5) seconds and then went to the feeder. The latent period of the conditioned reaction was 1-5 sec and even as long as 10 sec in isolated cases during this period.

The conditioned reaction involving going to the feeder became stable on the 12th reinforced application of the metronome, which made it possible to move on to induction of a conditioned reflex involving the animal's taking up a position near loudspeaker 1. This reflex appeared after ten applications, taking the form of comparatively frequent trips to loudspeaker 1, but the animal did not stay near the loudspeaker at first. At this time, Dzhek exhibited many intersignal trips to the feeder, which were often preceded by a sudden cessation of a movement he had already begun. Thus, in some cases, the dog moved toward loudspeaker 1 or the water dish, but abruptly stopped, turned, and went to the feeder. He occasionally withdrew to 1.5-3 m from the feeder or gingerly approached loudspeaker 1 and rapidly turned back.

The dog first left the positive loudspeaker and went to the feeder during the pause after the 34th reinforced application of the metronome. Similar reactions were then frequently observed. He also made circling movements about loudspeaker 1, sometimes repeating this process 2 or 3 times during an intersignal pause. This reaction persisted until the 110th application (31st experiment), despite the fact that it was reinforced only 9 times (on the 43rd, 51st, 52nd, 77th, 82nd, 85th, 86th, 88th, and 93rd applications). In a number of instances Dzhek circled the differential loudspeaker when his circling of loudspeaker 1 was not reinforced; in this case, the negative metronome was switched on but not reinforced. As a result, the dog soon stopped circling loudspeaker 2.

After the 82nd application, Dzhek began to remain near loudspeaker 1 substantially more often than before and this reaction became consistent after the 96th application. While near the positive loudspeaker, the dog usually watched it and remained "frozen" in this pose. When the metronome was applied, he stayed in this position for 1-5 sec and only then went to the feeder. When Dzhek remained near loudspeaker 1, he often wagged his tail, licked his chops, and salivated (the duct of one parotid gland had been led out in this dog).

The development of the active motor reactions (touching and pawing the loudspeaker) took a totally different course from that observed in Dzhul'bars. The dog first touched loudspeaker 1 with his nose at the beginning of the 28th experiment and made his first attempt to paw it during the 33rd experiment (126th application; he raised a paw over the loudspeaker, held it in this position for a short time, and then lowered it to the floor). Dzhek pushed loudspeaker 1 with his nose during the pause after the 127th application and attempted to lick it after the 139th application (34th experiment; he looked at the loudspeaker, licking his chops and wagging his tail, then tilted his head toward it, and made licking movements in the air). He again pushed the loudspeaker with his nose during the pause after the 142nd application and subsequently repeated this action quite frequently. He first licked loudspeaker 1 during the pause after the 155th application. This reaction subsequently occurred infrequently. Dzhek first cautiously placed a paw on loudspeaker 1 during the pause after the 164th application; the metronome was then applied and the animal received food. During the pause after the 166th application (38th experiment), the dog stood for a long time near the positive loudspeaker, wagged his tail, licked his chops, and pushed the loudspeaker with his nose several times; however, as in previous cases, no reinforcement was given. Toward the end of this pause, the dog struck the loudspeaker sharply with a paw, in connection with which the metronome was switched on and the dog given reinforcement. Dzhek thenceforth usually pawed the loudspeaker and also pushed it with his nose. The former reaction was always reinforced. From the 39th experiment onward, the dog pawed the loudspeaker 2-4 consecutive times. Reinforcement was given only when he struck it at least three times. On the first such occasions, the animal sometimes struck the loudspeaker once or twice, withdrew from it toward the feeder by 0.5-1 m, stopped, and looked at the loudspeaker. Since the metronome was not switched on in such cases, he returned to the loudspeaker and resumed pawing it. Such reactions were very rarely observed after the 40th experiment. Dzhek's conditioned-reflex activity now began to take a very distinct and rapid course, the latent periods of the trip to the feeder in response to the metronome not exceeding 2 sec. Intersignal trips from the loudspeaker to the feeder soon almost completely disappeared. The dog went for reinforcement only in response to the conditioned signal. Even after the conditioned reflex had become rather stable, Dzhul'bars still sometimes struck the loudspeaker only once or twice and then went to the feeder. Toward the end of the investigation, Dzhek made comparatively few extraneous movements, i.e., movements that were not components of the induced activity. As a rule, he immediately returned to loudspeaker 1, sometimes running, after receiving food, began to paw it, went to the feeder in response to the metronome, etc. Like Dzhul'bars, Dzhek sometimes placed one or both of his front paws on the positive loudspeaker. In a second variant, the free paw was suspended in the air, extended under great tension, or periodically used to touch the loudspeaker. In some cases, Dzhek placed one paw on loudspeaker 1 and began to press or scratch at it. However, striking the loudspeaker remained the typical active reaction.

After the conditioned-reflex motor activity became stable, the dog went to the differential loudspeaker extremely rarely, looking at it and immediately going to the positive loudspeaker when he did so.

The experiments on Pal'ma yielded essentially the same data as those on Dzhek. During the first eight experiments, Pal'ma learned by imitation and a conditioned reflex involving going to the feeder in response to the sound of the metronome was formed.

In contrast to the other dogs, Pal'ma exhibited a positive reaction to loudspeaker 1 from the very outset: she made periodic trips to it, fixed her gaze on it, sniffed it, and even pushed it with her nose. Thus, during the pause after the ninth application, which lasted 3 min rather than the usual 1-2 min, the dog moved about the room a great deal at first and then went to loudspeaker 1 and pushed it with her nose. During the next intersignal pause, which was prolonged to 5 min, Pal'ma spontaneously attempted to get food from the feeder and, when she was unable to do so, began to bite its lid; she then whined, withdrew, returned, and roughly struck the feeder. During the 12th experiment (20th-26th applications), the dog pushed loudspeaker 1 with her nose in three cases and tilted her head toward it and looked at it in four cases. Since Pal'ma displayed a positive attitude toward loudspeaker 1 from the first reinforced applications of the metronome, this being a result of the prior experiments involving imitation, a conditioned reflex was not induced to the position of the loudspeaker. At the same time, in contrast to the experiments on Dzhul'bars and Dzhek, Pal'ma was given reinforcement when she tilted her head toward loudspeaker 1 and touched or pushed it with her nose.

The dog sometimes approached loudspeaker 2 at the beginning of the investigation, looked at it, and, in one case (after the 18th application), struck it with a paw. Motor activity directed at loudspeaker 2 was never reinforced and the dog consequently soon stopped approaching this stimulus.

Until the 39th application, when Pal'ma was near loudspeaker 1 she usually looked at it or attempted to touch it with her nose, sometimes being successful in doing so. She then began to paw loudspeaker 1, at first infrequently and then (after the 44th application) systematically. In contrast to the other dogs, Pal'ma initially pawed in front of the loudspeaker, slightly brushing one wall of its housing with her paw or even failing to touch it at all. She never rested a paw on the loudspeaker, as Dzhul'bars and Dzhek had occasionally done. When near loudspeaker 1, Pal'ma often licked her chops or growled at it; she did not go immediately to the feeder in response to the positive metronome, but waited 5-7 sec. She sometimes pawed the loudspeaker once or twice, looked at it and listened, then pawed it again, etc. When the active motor reaction (pawing the loudspeaker) became stable, the animal stopped going to the differential loudspeaker. There was also a sharp curtailment of her movements about the experimental room. On entering the room, Pal'ma usually went immediately to the feeder or the loudspeaker, began to paw it, went for reinforcement in response to the sound of the metronome, ate the meat, returned to the loudspeaker, resumed pawing it, etc.

The investigation conducted on Dzhek and Pal'ma confirmed the basic results obtained in the experiments on Dzhul'bars. The individual peculiarities of the animals' behavior presented no obstacle to development of the main reaction, i.e., active pawing of the loudspeaker.

The experiments on Dzhek rather conclusively showed that the site of loudspeaker 1 evoked an alimentary reaction, which was manifested in salivation, chop-licking, and tail-wagging. This means that both the reinforced conditioned stimulus (the sound of the metronome) and its source (the loudspeaker) acquired the capacity to evoke conditioned alimentary reactions.

As our experiments showed, the active pawing of the loudspeaker was not an accidental movement but a regular motor reaction; this indicates that *new* movements can be induced in an animal under the influence of his environment. Striking a loudspeaker three times in succession is naturally a new reaction for a dog, since he does not exhibit it under natural circumstances. However, we cannot overlook the fact that striking a loudspeaker is an action composed of old, well-mastered movements – raising and lowering of a paw. In Dzhek and particularly in Dzhul'bars, formation of the motor act in question began with the raising of a paw; the dogs then began to try to lower it in order to touch the loudspeaker. Only at this juncture were single taps on the loudspeaker observed. That animals can develop new, more complex motor acts on the basis of existing movements is elegantly shown by the following experimental data.

In experiments conducted on Dzhul'bars, Dzhek, and Pal'ma after induction and stabilization of the conditioned motor reaction involving pawing loudspeaker 1, this loudspeaker was moved to new locations. The results of this change in the experimental setup were described in the preceding chapter, so that here we need note only that the dogs' induced activity was disrupted at the beginning of the experiments. However, after a short "training period," the animals differentiated the loudspeaker from its usual position, so that it could be placed on any square of the floor without markedly affecting their behavior. On some experimental days, the loudspeaker was placed on a table or hung from the wall over the floor or a table; the animals pawed it all the same. If the loudspeaker was placed on a table, in order to actively manipulate it and receive reinforcement the animal had to execute a more complicated motor act than previously, when the loudspeaker was on the floor. He now had to first jump onto the table and then paw the loudspeaker; all three dogs did this (Fig. 11). The active motor act was even more complex when the loud-

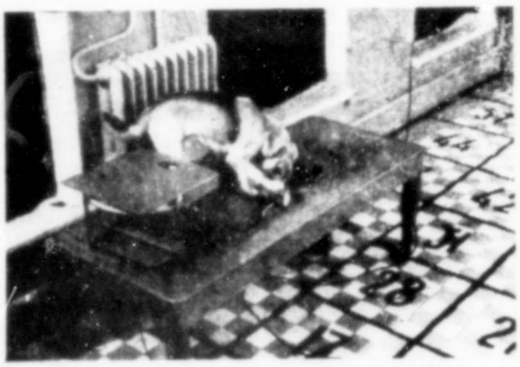

Fig. 11. Dzhek paws loudspeaker 1 on table 2.

speaker was hung on the wall over a table or the floor. In order to begin striking the loudspeaker and thus receive reinforcement, the animal had to first go to the loudspeaker, stand on his hind legs, and strike it from this position. The dogs successfully coped with this task and varied their movements in accordance with its complexity. If the loudspeaker was close to the floor, at a height of about 50 cm, the animals did not stand on their hind legs; if the loudspeaker was at a height of about 100 cm, the dogs stood on their hind legs, pawed at it with one or both of their front paws, and sometimes struck it with their noses (Fig. 12). In one case, the loudspeaker was hung so high that

Fig. 12. Dzhek strikes loudspeaker 1, which is suspended on wall, with his nose.

Dzhek had difficulty reaching it with his paw. He then began to jump and down on his hind legs, resting his front legs against the wall, and struck the loudspeaker with his nose. These data indicate that active motor reactions change with the situation. If the experimental conditions become more complicated, a more complex type of voluntary activity appears. However, no matter how complicated voluntary actions may be, they are formed on the basis of simple, well-mastered movements.

Thus, the experimental data of G.A. Shichko show that dogs can not only readily and actively reproduce voluntary reactions, but can also spontaneously employ new, more complex motor acts based on simple, well-mastered movements to meet the requirements of the experimental situation.

CONCLUSION

The problem of voluntary and involuntary is a scientific problem of great ideological significance and a struggle between materialism and idealism has long been waged about it. Idealists separate the voluntary from the involuntary and erect an impassable barrier between them, regarding the former as the product of the activity of a supernatural principle and the latter as the result of the functioning of the body. An incorrect interpretation of the voluntary served as the basis for the fantastic notion of freedom of will, which the idealists needed to defend an old religious function, the soul, to support the independence of behavior from the external world, and to refute the materialistic concept of psychic activity. One Russian idealist, N.Ya. Grot (1889), stated that the concept of freedom of will contained the idea of the will as an internal agent dependent only on itself. Another idealist, A.A. Vvedenskiy (1901), frankly declared that a belief in free will leads to recognition of the soul as an independent principle and of its immortality. He opposed the materialistic Sechenovian concept of psychic activity and asserted that materialism could not be proved scientifically and was itself merely a belief.

Many Russian scientists (I.M. Sechenov, S.S. Korsakov, A.A. Tokarskiy, and others) supported criticism of the idealistic concept of freedom of will and demonstrated that it was scientifically indefensible. In opposing the idealists, I.M. Sechenov (1878 and 1900) asserted that voluntary movements are free of the intervention of the will as an impersonal agent and suggested that the meaningless notion of the will be replaced by a scientific concept. He stated that a newborn infant exhibits only involuntary movements and that voluntary movements appear during the course of development and are learned under the influence of environmental conditions.

The idealists, ascribing the voluntary to the supernatural soul, which occurs only in man, were forced to deny that voluntary movements can occur in animals. Many idealists, including the dualist R. Descartes, affirmed this incorrect view.

Popular trends in modern bourgeois science (Freudianism, gestaltism, and behaviorism) give distorted and oversimplified interpretations of behavior, ascribing exaggeratedly great importance to inherent mechanisms and denigrating the role of the environment in the formation of psychic activity. Thus, for example, behaviorism attempts to reduce the entire complex diversity of higher nervous activity in animals and man to the primitive "stimulus-reaction" scheme. From this standpoint, animals and men are animated automatons and there is no qualitative difference between them. Behaviorism hoped to become the laboratory of society (D.B. Watson, 1927), but its defective principles led it into a blind alley.

Dialectical materialism, recognizing the reality of the voluntary and involuntary, believes that the difference them is relative rather than absolute and struggles both against artificial separation of the voluntary from the involuntary and against unscientific fusion of the two.

Acknowledgment of the voluntary does not in any way mean recognition of the reality of reactions independent of the environment. No matter what form a reaction takes, it cannot be effected spontaneously, without the participation of external factors, since, as M.V. Lomonosov correctly stated: "No movement can be effected naturally in a body if the latter is not set in motion by some other body."*

Voluntary and involuntary reactions are not rigidly delimited or separated from one another by an impassable barrier; quite the contrary, they are closely related and one can acquire the properties of the other under definite conditions. This has been quite well confirmed by the experimental data presented above.

One of the special features of involuntary reactions is the fact that they represent a regular response on the part of the organism to definite factors. For example, a shaking reaction regularly appears when the upper surface of the body is irritated and a sneezing reaction develops when the nasal mucosa is irritated. However, as the investigations of V.K. Fedorov and L.S. Gorshkova, R. Floru, and V.V. Yakovleva showed, these involuntary reactions can be made voluntary. It was found that, when accidental or purposely evoked shaking or sneezing was systematically reinforced, the animal later began to actively repeat these actions. Active repetition of a reaction is the principal indication that it is voluntary, so that there can scarcely be any doubt that voluntary execution of involuntary reactions occurred in the experiments conducted by the aforementioned researchers. This also indicates that the difference between voluntary and involuntary is relative rather than absolute.

Shaking can be used as an example to illustrate the general characteristics of the mechanism by which involuntary reactions are converted to voluntary reactions, leaving out numerous details. When accidental or intentionally evoked shaking was conjoined with food, a temporary association developed between the corresponding cortical points. Since, as I.P. Pavlov repeatedly noted, when there is a pathway between a kinesthetic and an alimentary cell excitation can move in both directions "...from the kinesthetic cell to the gustatory, or alimentary cell (during formation of the pathway) and from the alimentary cell to the kinesthetic cell (during alimentary excitation),"* it can be assumed that, when alimentary excitability was increased, the cortical projection of the shaking act was excited and the animals consequently went through the appropriate movements.

The shaking reflex is naturally closely associated with the activity of both the cortex and the lower-lying cerebral elements, but the decisive role in repetition of this reflex is played by the cortex, which is the material substrate of individually acquired reactions in higher animals.

Our experimental data enable us to surmise that the excitability of the neural structures governing active repetition of the voluntary components of the shaking reflex is higher than that of the structures governing the involuntary components of this reflex. The validity of this hypothesis is supported by the fact that the dogs readily and frequently effected the voluntary components of shaking but were frequently unable to carry out its involuntary components. Moreover, as V.V. Yakovleva's experiments showed, preliminarily moistening the skin led to a substantial increase in the number of times that active shaking was completed. It must be added that shaking was facilitated when the animal wore a leash on its neck, when it rolled on the mat, etc. All this increased the excitability of the cortical projection of the shaking reflex, thus facilitating active repetition.

The dogs did not repeat the different involuntary reactions with equal ease. They carried out scratching comparatively easily, but had substantially greater difficulty in executing sneezing and particularly shaking. This indicates that the excitability level varies in the cortical projections of different involuntary reactions.

The experiments of V.K. Fedorov and L.S. Gorshkova force us to assume that the active repetition of an unconditioned reflex and the conditioned-reflex repetition of the same reaction in response to a conditioned stimulus are phenomena that differ somewhat from one another. Active repetition of shaking and sneezing develops comparatively slowly, is rarely displayed in complete form, and is subsequently extinguished. Nevertheless, conditioned shaking and sneezing reflexes are induced rather easily, are rapidly fixed, and persist stably.

Active repetition of shaking and sneezing imposes a severe load on the nervous system, as is indicated by the numerous and often unsuccessful attempts to execute these acts. Conditioned shaking and sneezing reflexes are readily displayed in response to an appropriate conditioned stimulus and do not cause any noticeable strain on the animal's nervous system.

All this is due to the fact that, like an unconditioned reflex, a conditioned reflex is an involuntary reaction regularly displayed in response to a positive conditioned stimulus. Active execution of an unconditioned reflex is a voluntary reaction independently repeated by the animal. The activating focus of this repetition develops "centrally" (I.P. Pavlov), in the alimentary center. The formation of this focus of excitation and the associated active repetition of the involuntary act are naturally governed both by the internal state of the body (e.g., hunger) and by the environment. However, no environmental stimulus can of itself induce active shaking in a dog. In the case of a conditioned reflex, an involuntary reaction is displayed in response to a stimulus systematically reinforced by an unconditioned stimulus.

All this indicates that the active execution of an involuntary reaction is not identical to the execution of a conditioned reflex in response to a definite stimulus. However, the difference between voluntary and conditioned-reflex repetition of an unconditioned reflex is relative. They have much in common, principally the fact that they are based on temporal associations.

Investigations conducted by I.A. Alekseyeva, V.K. Fedorov, and G.A. Shichko showed that alimentary reinforcement of motor reactions usually regarded as voluntary (licking a lamp, pressing a rubber bulb, or pawing a loudspeaker) caused the animals to begin actively repeating these reactions. As was noted above, the experiments of V.K. Fedorov and L.S. Gorshkova, V.V. Yakovleva, and R. Floru showed the same to be true of involuntary reactions (shaking, sneezing, and scratching). Thus, there is an area of overlap between voluntary and involuntary reactions during their active repetition; this is strong confirmation that there is no absolute difference between them. This is also supported by the fact that an involuntary reaction can be made voluntary, as was described above, and a voluntary reaction can be made involuntary, as can readily be seen from the following data. The trips to the feeder during the intersignal pauses were obviously a voluntary reaction. However, when the animal made the same trip in response to the action of a conditioned stimulus, it was an involuntary motor reaction. The dog's moving toward the metronome and remaining near it that occurred in the first part of I.A. Alekseyeva's investigation was a voluntary reaction, while the movement in response to the electric bulb during the second part of the investigation was an involuntary reaction. The active pressing on a lever or pedal in L.G. Voronin's experiments was a voluntary movement but, after induction of a conditioned reflex involving pressing the pedal only in response to the conditioned stimulus, this movement acquired the character of an involuntary reaction. Finally, actively raising a paw, as in I.S. Rozental''s experiments (1936), was a voluntary reaction, but raising the same paw in response to a painful stimulus was an involuntary reaction. Many such examples could be cited, but the above well illustrate that a voluntary movement can be effected by an involuntary mechanism and that there are no fundamental differences between voluntary and involuntary reactions. "The only differences lie in the greater lability of the nervous mechanisms responsible for voluntary acts, in the ease with which conditioned associations can be formed and repeated, and in the permanent fixation of the latter, especially in young animals."*

There are nonfundamental relative differences between the performance of voluntary movements and the active execution of involuntary reactions. "In the first case, the animal immediately and consistently executes definite movements as soon as a conditioned pathway has been formed. Alimentary excitation is rapidly directed to the cortical motor region, where the requisite motor act is formed, then being executed. The existence of a conditioned pathway and the presence of alimentary excitation are inadequate for repetition of a motor reaction in the latter case; special conditions, under which this reaction can be formed and executed by the animal's nervous system, are required. This is apparently a result of the fact that the cortical motor region contains neither a structure that can be termed a center of involuntary reactions, such as the shaking reflex, nor the facilities for integrating all the constituents necessary for execution of the act of shaking."**

G.A. Shichko's investigation indicates that, during adaptation to the environment, more complicated motor acts can be formed on the basis of simple, well-mastered voluntary movements. This is a strong refutation of the artificial "stimulus-reaction" scheme propounded by the behaviorists.

The active repetition of such reactions as shaking, scratching, pressing a bulb, pawing a loudspeaker, and so forth is a component of the animal's complex behavior and is directed at obtaining food, so that these reactions must be regarded as food-seeking motor acts. They differ from natural food-seeking acts (stretching out a paw for food, etc.) in the fact that they lead to food only under experimental conditions, so that they have an artificial character. Under real, nonexperimental conditions, they bear no relationship to the procurement of food. The motor acts considered above can consequently be termed artificial food-seeking reactions.

An animal's behavior consists of voluntary and involuntary reactions. Thus, in I.A. Alekseyeva's experiments, going to the bulb and licking it are voluntary reactions, while going to the metronome in response to the electric light, going to the feeder in response to the metronome, eating the food, and the alimentary reflexes are all involuntary reactions. In G.A. Shichko's investigations, going to the loudspeaker and pawing it are voluntary movements, while going to the feeder in response to the metronome, eating, and the associated unconditioned reflexes (salivation, swallowing, etc.) are involuntary reactions.

All this shows that there is no absolute difference between voluntary and involuntary reactions; using the conditioned-reflex method, it is possible to strictly govern and control voluntary and involuntary reactions and to make the animal active, enabling him to spontaneously execute involuntary and voluntary acts.

Both our investigations and those conducted at other laboratories have demonstrated that considering animals as animated automatons, denying that their behavior contains voluntary movements, or ascribing exaggerated importance to such movements does not correspond to the true situation. Animals are not automatons; however, their voluntary activity does not differ so greatly from their involuntary activity that we would be justified in setting it up as something independent and designating this "something" by a special term.

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FOOTNOTES

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109** Pavlovskiye sredy [Pavlovian Media]. Moscow-Leningrad, 1949, Vol. 2, page 131.

109*** I.P. Pavlov. Polnoye sobraniye sochineniy [Complete Collected Works]. Moscow-Leningrad, 1951, Vol. 3, Book 2, page 315.

110* Pavlovskiye sredy. Moscow-Leningrad, 1949, Vol. 2, pages 180-181.

110** I.P. Pavlov. Polnoye sobraniye sochineniy. Moscow-Leningrad, 1951, 2nd Edition, Vol. 3, Book 2, page 316.

110*** Ibid., page 317.

110**** L.G. Voronin. Sravnitel'naya fiziologiya vysshey nervnoy deyatel'nosti [Comparative Physiology of Higher Nervous

Activity]. Izd-vo Moskovskogo un-ta., 1957, page 38.

111 The studies of V.K. Fedorov and L.S. Gorshkova are an exception.

112 P.S. Kupalov. In Collection entitled: "Ob"yedinennaya sessiya, posvyashchennaya desyatiletiyu so dnya smerti I.P. Pavlova" [Joint Session Dedicated to the Terth Anniversary of the Death of I.P. Pavlov], Moscow, 1948, page 73.

117 I.P. Pavlov. Polnoye sobraniye sochineniy. Moscow-Leningrad, 1951, Vol. 3, Book 2, page 317.

132 M.V. Lomonosov. Izbrannyye filosofskiye proizvedeniya [Selected Philosophical Works]. Gospolitizdat, 1950, page 100.

133 I.P. Pavlov. Polnoye sobraniye sochineniy. Moscow-Leningrad, 1951, Vol. 3, Book 2, page 316.

135* P.S. Kupalov. Ucheniye o reflekse i reflektornoy deyatel'nosti i perspektivy yego razvitiya [Theory of Reflexes and Reflex Activity, and Prospects for its Development]. Moscow, 1962, page 37.

135** P.S. Kupalov. In Collection entitled: "Ob"yedinennaya sessiya, posvyashchennaya desyatiletiyu so dnya smerti I.P. Pavlova." Moscow, 1948, page 75.

Chapter 4

EFFECT OF CERTAIN PHARMACOLOGICAL SUBSTANCES ON SITUATION AND SECRETORY ALIMENTARY CONDITIONED REFLEXES

Pharmacological investigations carried out under the direction of I.P. Pavlov have opened wide prospects for pharmacologists and have made it possible to study by means of conditioned reflexes the action mechanisms of various substances on the cerebral hemispheres. "Chemical substances," wrote I.P. Pavlov, "represent the most delicate analytical methods of physiology..., with the aid of chemical agents one can divide and isolate substances which can not be divided by any instruments."*

I.P. Pavlov attached great importance to pharmacological research in the field of higher neural activity, not only because it enabled the experimenter to expand the knowledge concerning the action mechanism of various substances, but also made it possible to modify the course of neural processes, thus facilitating their study.

Pharmacological substances can change the course of conditioned reflex reactions as a result of various causes: impairment of entry of a conditioned or unconditioned signal into the cortical part of the analyzer; impairment of the locking function between the cortical analyzer zones; change in the tonic effect from subcortical formations, in particular – of the ascending system of the reticular formation; changes in the effector link of a conditioned reflex, etc. In employing pharmacological substances, we aimed not only to study the character of their action on the central nervous system but also to elicit, as much as possible, certain physiological mechanisms of realization of the motor conditioned reflex reactions.

The physiologists always paid special attention to substances which selectively acted on the central nervous system.

In the physiological department imeni I.P. Pavlov of the Institute of Experimental Medicine (IEM) investigations have been conducted on the action of certain substances which selectively influence the reflex control of physiological functions. With this in view, one employs the classic Pavlovian salivation method, as well as the method of situation conditioned reflexes.

In the present chapter a particular attention is devoted to the data obtained by the method of situation conditioned reflexes. These results will be, as much as possible, compared with the facts obtained with the secretion method.

We investigated substances from various pharmacological groups which exert a special effect on the central nervous system:

1) analgesic preparations of the opium group: dicodide, thecodine, lidol (demerol), promedole, morphine;

2) cholinolytic preparations – aminoalkyls, esters of substituted acetic and glycolic acids (amisyl, amedine, aprophene, diphacyl, lachesine, etc.), atropine and amino alcohols (cyclodol, etc.);

3) adrenergic substances (adrenalin and sympatholytin);

4) a tranquilizator of the central nervous system (aminazine).

EFFECT OF ANALGESIC PREPARATIONS OF THE OPIUM GROUP ON THE SITUATION AND SECRETORY CONDITIONED REFLEXES

Alkaloids contained within the composition of opium include codeine (methylmorphine), the effect of which on the cerebral cortex is considerably less pronounced, as compared with morphine (it induces no euphoria, but it exerts a selective depressing effect on the cough center).

Dicodide (dihydrocodeinen), suggested as codeine substitute, reduces the excitability of the cough center to a greater extent and possesses a strong analgesic action. Thecodine (dihydrooxycodeine), manufactured in our country possesses an even greater analgesic action. It is used in the practice of reducing labor pain.

Synthetic preparations, lidol (dolantin or demerol) and promedole, are of considerable practical interest, because they are better tolerated by patients (induce no vomiting or constipation), do not yield to morphine in their analgesic effect, and do not produce in man any phenomena of longing and addiction.

Investigation of the effect of morphine and its derivatives on the course of situation conditioned reflexes was carried out by O.N. Voyevodina (1954, 1956) on seven dogs. In four of them, by means of the method of situation conditioned reflexes, one produced positive and negative (differentiations and delay) motor conditioned reflexes to visual, sound, and object-spatial stimuli. In the dogs Chernyavka and Tsezar' a complex behavior pattern was elaborated, consisting of: 1) a run to the feeding trough, upon letting the dog into the experimental chamber; 2) approach of the dog to the lamp after the first feeding and after licking the lamp; 3) upon lighting the lamp – a run of the dog to the rug; 4) the dog stands on the rug for 3-5 seconds, its head turned in the direction of the metronome; 5) at the sound of metronome, the dog runs to the feeding trough and starts eating.

In dogs Reni and Alma a simpler activity was elaborated: following its run to the table and eating the first meal, the dog stands on the rug, and a conditioned stimulus is switched on; the animal responds to a positive stimulus by running to the table, jumping on it and receiving food reinforcement, and to a negative stimulus the dog responds by remaining on the rug.

On three dogs (Jenny, Inga, Nord) the tests were carried out according to the classic salivation method in a soundproof camera, where at the metronome's 152 strikes per minute, light, bell and buzzer, positive conditioned reflexes were formed, and at the metronome's 120 strikes per minute, a differentiation was elaborated.

The preparations were administered to the dogs intramuscularly in the form of 0.01-0.1%-solution, within 30 minutes prior to the experiments. The effect of analgesic substances on the higher nervous activity was studied in the following doses:

thecodine...... 0.1-0.25-0.05 mg/kg
licodide....... 0.005-0.012-0.025-0.05-0.075-0.1 mg/kg
lidol.......... 0.01-0.1-1.0-1.5 mg/kg
promedole...... 0.1-0.25-0.5 mg/kg
morphine....... 0.05-0.1-0.15-0.25 mg/kg

Following administration of thecodine (0.25-0.5 mg/kg) and lidol (1-1.5 mg/kg), the synthetic activity of the cerebral cortex became impaired. This was fairly clearly elicided under conditions of free movement of the animal in the experimental chamber: one of the first components of motor conditioned reflex activity in the dogs dropped out – the animals did not approach the lamp and did not lick it, or they did not take their position on the rug; in the intervals between the conditioned stimuli the dogs just walked in the room. In all dogs, one observed a 1-2 second delay of the latent period of motor conditioned reactions. The animals ceased to react to the conditioned stimuli by 3-5 combinations sooner than usually. For instance, whereas in norm the animals made 12-13 runs to the table, following administration of lidol or thecodine, during the 7th-8th employment of the stimulus, the dogs turned toward the door and tried to get out of the experimental chamber.

In the same doses, thecodine (0.25-0.5 mg/kg) impaired the conditioned reflex activity elaborated according to the salivation method, this impairment lasting for a period of 3 days following a single administration of the preparation. Within 30 minutes after the injection, one observed an increase of latent periods, decrease of the level of conditioned positive reflexes on the average of 50%, maintenance of differentiation, and a diminution of the unconditioned salivation by 8-10%. On the day following injection, the level of positive conditioned reflexes remained reduced, and the differentiation reflex disappeared. During subsequent days the conditioned and unconditioned reflexes regained their initial level.

Data, analogous to the afore-mentioned ones, have been obtained in tests with lidol at a 1.5 mg/kg dose. When the administered lidol dose was reduced 5-10-fold, the changes in higher nervous activity showed a different pattern: the level of positive conditioned reflexes rose by 25-40%, whereas unconditioned salivation changed little, and the differentiations were retained. On the average (based on three experiments), following injection of lidol in a 0.01 mg/kg dose, the conditioned reflexes rose under the effect of weak, as well as strong, stimuli: those of a metronome – by 23%, light – by 17%, bell – by 40%. This fact indicates that lidol in small doses increases the excitability of cortical cells and intensifies their functional capacity.

Dicodide, in doses of 0.005-0.012 mg/kg, had a stimulating effect on the higher nervous system of the animals, analogous to lidol in a 0.1 mg/kg dose.

Upon injection of dicodide in a dose of 0.025-0.05 mg/kg, one observed in all animals a considerable increase of the latent period of conditioned secretory activity, reduction of the level of positive conditioned reflexes for 3-5 days; one also noted the absence of a motor alimentary reaction to the action of conditioned stimuli, while the differentiation reactions were not impaired.

Changes in the value of secretory conditioned reflexes, depending on the dose of dicodide, differed in various dogs (Table 7).

TABLE 7

Changes in the Value (in %) of Salivary Conditioned Reflexes of Dogs Under the Effect of Various Doses of Dicodide

1 Кличка собаки	2 Увеличение			3 Снижение			
	4 дозы						
	0,005	0,012	0,025	0,012	0,025	0,05	0,1
5 Джении	43	21,3	--	—	54,8	64,4	72
6 Инга	24	—	—	27,3	44	51	67
7 Норд	65,5	55,8	52,7	—	—	43	52,7

1) Name of dog; 2) increase; 3) decrease; 4) doses; 5) Jenny; 6) Inga; 7) Nord.

The above table cites mean data based on 45 applications of positive stimuli, following injection of dicodide in above indicated doses.

Promedole in doses of 0.1 and 0.25 mg/kg, similarly to other derivatives of morphine, induced a marked decrease of the level of positive conditioned reflexes, without impairment of differentiation.

Promedole did not impair the course of the unconditioned secretory reflex and did not reduce its value. On the other hand, conditioned reflexes decreased during the day of injection, as well as during subsequent 4-8 days, depending on the dose of administered substance, whereas the differentiation reflexes remained intact.

In experiments staged within 30 minutes following administration of promedole in a 0.5 mg/kg dose, one observes in addition to above cited disturbances, a marked increase of the latent periods of conditioned secretion (over 10-fold); the rate of the course of the unconditioned reaction did not change. Hence, promedole in doses of 0.1-0.5 mg/kg contributed to the lowering of the level of positive conditioned reflexes. This reduction of the level of positive conditioned reflexes took place without impairing the "law of force." Besides, promedole, in above doses, had no effect on the course of the unconditioned secretory reflex; hence, it exerted a specific effect on the process of excitation of the cortex of the large cerebral hemispheres by apparently lowering the excitability of the cortex as a whole. This unique property of the preparation can be utilized for the characterization of the force of the excitation process of the cerebral cortex. The effect of promedole on the conditioned reflexes was also investigated by N.S. Safronov (1956), Suy-Bin (1956), G.I. Tsobkallo, N.S. Safronov and V.K. Fedorov (1955). These authors also showed that analgesic preparations reduce the excitability of the brain.

On the basis of cited investigations, one can conclude that all investigated analgesic substances (thecodine, dicodide, lidol, promodole) in doses, close to therapeutic ones, induce a reduction of the level of positive conditioned reflexes, without impairing differentiation and unconditioned salivation (Table 8).

TABLE 8

Doses of Analgesic Substances which Induce Impairments of Conditioned Reflex Activity in Dogs, Following Subcutaneous Administration

1 Название препарата	2 Терапевтические дозы	3 Дозы, в мг/кг		
		усиливающие возбудительный процесс 4	угнетающие условнорефлекторную деятельность 5	7 нарушающие ситуационные условные рефлексы
		6 (слюнная методика)		
8 Текодин	0,1	—	0,1	0,25
9 Дикодид	0,05	0,005	0,01	—
10 Лидол	1,0	0,01	1,0	1,5
11 Промедол	0,15	—	0,1	—
12 Морфий	0,1	—	—	0,15

1) Name of preparation; 2) therapeutic doses; 3) doses in mg/kg; 4) increase the stimulating process; 5) inhibit conditioned reflex activity; 6) (salivation method); 7) impair the situation conditioned reflexes; 8) thecodine; 9) dicodide; 10) lidol; 11) promedole; 12) morphine.

Under conditions of free movement of the animal in the experimental chamber, lidol and thecodine in therapeutic doses did not impair the elaborated conditioned reflex motor reactions, but they did slow up the rate of their course and, hence, affected the mobility of neural processes by rendering them more inert.

In order to obtain the effect of an increase of excitability of the cerebral cortex, one should employ lidol and dicodide in 5-10 fold smaller quantities than the therapeutic dose. Under the effect of lidol (0.01 mg/kg) and dicodide (0.005-0.01 mg/kg) in these doses, one observed a shortening of the latent periods of conditioned secretory reactions and a rise in the level of positive conditioned reflexes (to a larger extent it was observed on the conditioned reflexes which were physically stronger, than the weak ones). No impairment of differentiation was observed under these conditions. This fact indicates that, in small doses, lidol and dicodide intensify the excitability of cortical cells.

Following a single administration of these preparations in doses exceeding the therapeutic doses 2-5-fold, disturbances of conditioned reflex activity were observed for 3 days. These disturbances were characterized by the absence of an alimentary motor reaction to conditioned reflexes, longer latent periods, lower level of positive conditioned reflexes of the type of a narcotic phase, and disappearance of the differentiation reaction. These disturbances were caused by a marked reduction of excitability of the cerebral cortex and, in particular, by a reduction of the cortical presence of the unconditioned secretory reflex; as a result, one observed a considerable lowering of the level of positive conditioned reflexes and a decrease of unconditioned secretion (mainly during the first 30 seconds from the start of feeding).

When experiments were conducted according to the method of situation conditioned reflexes, thecodine and lidol in doses exceeding therapeutic doses impaired the successive chain of conditioned reflex reactions. For instance, under the effect of thecodine (0.25-0.5 mg/kg), the dogs in the majority of cases performed stereotype movements; they ran to the lamp and then returned to the rug; less frequently, one observed the absence of the first component of the complex chain of conditioned reactions: the dogs did not approach the lamp and did not lick it; sometimes, all of the links of the complex sequence of the chain were absent (the dogs did not lick the lamp, did not go to the rug, but jumped on the table without the sounding of the metronome signal.

Since the investigated substances are morphine derivatives, it seemed of interest to compare their action with that of morphine proper. As per the data of O.N. Voyevodina, the injection of morphine in doses of 0.05-0.15 mg/kg resulted in an extension of the latent period of motor reactions, without impairing the course of previously elaborated conditioned reflex activity. Upon increase of the dose to 0.25 mg/kg one observed in the dogs an increased salivation, vomiting, refusal of food. Analogous data on the effect of morphine on conditioned reflexes were previously obtained also by other researchers (I.V. Zavadskiy, 1908; S.I. Potekhin, 1911; V.A. Krylov, 1926; V.P. Petropavlovskiy, 1930; I.I. Zborovskaya, 1939, et al.).

According to the data of S.I. Potekhin, morphine in the dose of 0.0005-0.0025 grams caused a considerable reduction of the value of secretory conditioned reflexes, while the natural conditioned reflexes reverted to the initial level within 30 minutes, and the artificial ones – within 60 minutes.

The authors attributed the drop in the value of conditioned reflexes to the interaction of neural centers, basing their conclusions on the general principles of neural physiology, that excitation of one center (emetic center, under the effect of morphine) inhibits the activity of another neural center (alimentary).

As shown by the experimental investigations of O.N. Voyevodina, the changes of higher nervous activity under the effect of morphine derivatives have certain characteristic features. For instance, under the effect of lidol, thecodine and other preparations, no refusal of food has been noted in all experiments, and there was no vomiting, whereas a single administration of these preparations has led to disturbances of conditioned reflex activity for 2 to 8 days. These disturbances are apparently caused, at first, by the reduction of excitability of cortical hemispheres – the cortical component of the unconditioned alimentary reflex, in particular – and then also of the subcortical formations (inhibition of unconditioned reactions).

Thus, the investigated analgesic substances exert a triphasic effect, depending on the employed preparation dose:

1) in 0.005-0.01 mg/kg doses, lidol and dicodide lead to an intensification of the stimulation process in the cerebral cortex;

2) in medium doses (close to therapeutic ones), all investigated preparations cause a weakening of the stimulation process, without impairment of differentiations or changes in unconditioned reactions. Under conditions of free movements of the animals, the preparations in these doses do not disturb the structure of elaborated consecutive conditioned motor reactions, but only cause a delay in their course;

3) in large doses, exceeding therapeutic ones, a sharp reduction was observed in the excitability of the cerebral cortex for 5-8 days, a weakening of differentiation inhibition, and impairment of unconditioned reactions (salivation and complex motor acts). When experiments were carried out according to the method of situation conditioned reflexes, an impairment was noted in the consecutive chain of complex conditioned-reflex motor reactions of the animals.

Various causes may be responsible for disturbances of conditioned reflex activity, regardless of the sites in the reflex arch which were subjected to the action of the pharmacological substance. According to the data of A.V. Val'dman (1960, 1961) and L.N. Sinitsyna (1961), analgesic substances do not disturb the conduction of afferent impulses along specific pathways to the corresponding projection zones of the cortex. Hence, the disturbances of the entry of afferent signals to cortical zones of the analyzers cannot be the cause of changes in situation conditioned reflexes under the effect of analgesics. On the other hand, all analgesics inhibited the reaction of EEG desynchronization, induced by activation of the reticular formation with various types of afferent stimuli: sound, light, pain, and interoceptive stimuli (L.V. Val'dman, 1961). Hence, inhibition of conditioned reflexes, induced by analgesics, can be caused by the direct action on the subcortical cerebral structures, with the result that the tonic influences of the ascending system of reticular formation are reduced, and this leads to the lowering of the general excitability level in the cerebral cortex. The intensification of excitation process following administration of small doses of analgesics may also be connected with the increase of tonic influences of the reticular formation on the cerebral cortex. This mediating action in our opinion differs from the direct effect of the substance on the cerebral cortex in that the locking function of the cortex is preserved, as well as the differentiation of stimuli and the voluntary activity of the animals. Large analgesic doses disturb these functions and, hence, exert their effect on the cerebral cortex. In cases where the unconditioned motor reactions are impaired (under the effect of large doses), changes may occur in the effector link of motor conditioned reflexes, since the inhibiting effect of analgesics on the polysynaptic reflexes is a well established fact (Wikler, 1950) as well as their effect on the motor reactions, induced by stimulation of the motor zone of the cortex (A.V. Val'dman, 1958).

EFFECT OF CHOLINOLYTIC SUBSTANCES ON SITUATION AND SECRETORY CONDITIONED REFLEXES

The range of practical use of atropine-like and cholinolytic substances, in general, is extremely wide, since they possess cholinolytic, ganglionblocking, spasmolytic, midriatic, local-anesthetic, antisecretory, and other properties. The property of atropine-like preparations of relaxing the smooth musculature and relieving the spasms of smooth-muscle organs accounts for their use in most diverse pathological conditions: bronchial asthma, spastic colitis, coronary spasms, gastric ulcer, cholelithiasis, urinary calculi and other diseases.

No less important is the field of practical use of these substances connected with their unique effect on the central nervous system. Cholinolytic preparations have been used since long ago for the treatment of Parkinson's syndrome and convulsive states. Most recently these preparations found their use as tranquilizers. The central action of cholinolytics is used also in surgery for the enhancement of the effect of analgesics.

Hence, in characterizing the pharmacological activity of cholinolytic substances in general, of great importance is the elicitation of the selectivity of action of a given preparation on the central nervous system.

Some cholinolytic preparations exert a special effect on the peripheral cholinoreceptors (salivary glands, intestinal muscles, gastric musculature, etc.); others – possess a predominant effect on the central nervous system. These differences in the action of these substances are utilized by clinicians in the selection of a preparation which acts in the desired direction.

The central activity of cholinolytic preparations was previously judged on the basis of their property of checking convulsions, tremor, cataleptic state, as well as other serious disturbances of the function of the cerebral cortex caused by cholinomimetic substances. Presently available data on the effect of certain cholinolytics on conditioned reflex activity have been obtained mainly on small laboratory animals: mice, rats, rabbits (N. Ya. Lukomskaya, 1957; N.V. Savateyev, 1957; A.T. Selivanova, 1958; P.P. Denisenko, 1961). On dogs one studied only the effect of the following preparations: pentaphene (Ye.K. Rozhkova, 1957), tropacine (R.Yu. Il'yuchenok, 1957), diphacyl and diazyl (S.S. Krylov, 1956).

Our laboratory (experiments of A.T. Selivanova, 1961, 1962) investigated the effect on the central nervous system of dogs of 13 cholinolytic substances (amizyl, amedine, diphacyl, aprophene, atropine, lachesine, cyclodol, etc.). Among these preparations there were compounds with more pronounced action on the central cholinergic synapses – the so-called central cholinolytics (S.V. Anichkov, 1958, 1960) – and preparations which block the peripheral cholinoreceptors. Hence, it was of interest to elicit any disorders of higher neural activity, which might be induced by pharmacological substances which block various links of the reflex arch.

Studies were conducted on 14 dogs. In four dogs, one elaborated positive (to a gurgling sound, metronome 120 strokes per minute, light) and negative (metronome 60 strokes per minute) secretory conditioned reflexes. In 10 dogs, situation conditioned reflexes were elaborated.

Metronome, gurgling, buzzer and light were positive condittioned stimuli. The stimulator was turned on only when the dog stood on the rug after the animal had preliminarily completed the voluntary motor reaction – licked the bowl or scratched the rug. When the positive stimulator was turned on the dog was supposed to jump on table No. 2, where it received its food reinforcement (20 grams of cooked meat). The differentiation was elaborated to the sound or to the metronome (60 strokes per minute). When these were turned on, the dog remained on the rug. The solutions of tested preparations were injected subcutaneously. The intervals between repeated administrations of the preparations were no less than 10-20 days.

Experiments with the method of situation conditioned reflexes showed that amizyl exerted the strongest effect on the behavior of animals; in a dose of 0.5 mg/kg is markedly changed the animal's behavior. Within 5-15 minutes following injection of the preparation the dogs started to whine, became restless, refused food. They had dyspnea and muscular weakness (especially of the posterior extremeties), which lasted 4-5 hours. Their pupils were dilated; when walking they knocked against various objects in the room, tried to hide themselves in dark corners. In this state the dogs did not react to stimuli and did not perform voluntary reactions during the entire day of testing. Only one dog (out of five) responded four hours later to stimuli; its latent periods of motor reaction and running time were longer, the differentiation reactions were gone, and food was eaten twice slower than under normal conditions.

On the following day the latent periods remained protracted and the differentiation was still absent. Only on the third day the indicators of conditioned reflex activity reverted to their initial level (Fig. 13).

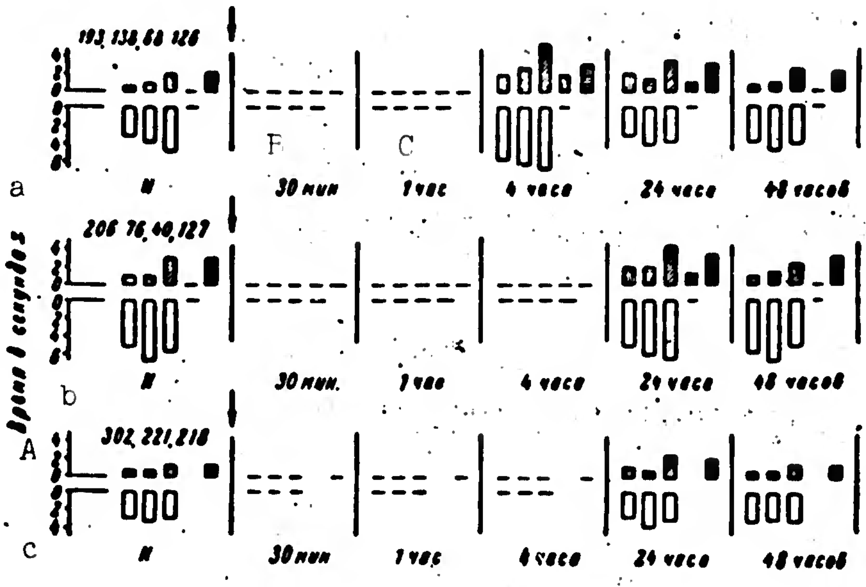


Fig. 13. Effect of amizyl in 0.5 mg/kg dose on situation conditioned reflexes of dogs. a) Dzhek 28/II 1952, weight 18.5 kg; b) Dozor 29.VII, 1953, weight 13.0 kg; c) Tobik 30/VI, 1953, weight 12.0 kg. Vertical stroke – latent period, to bell; horizontal stroke – latent period to the metronome; oblique stroke – latent period, to light; black column – latent period, to buzzer (differentiation); stroke within a square – running time to the feedtrough; white column – time consumed in eating the extra feed; indicator equals 0; *N* – norm; arrow – administration of amizyl. Time after injection of substance is marked below. Figures above columns of the latent periods in norm indicate the ordinal number of the application of a conditioned stimulus. A) Time, in seconds; B) 30 minutes; C) one hour.

Upon administration of amizyl in a dose of 0.1 mg/kg, the following disturbances of higher neural activity were noted: within 15-30 minutes there was complete inhibition of previously performed voluntary motor reactions, the latent periods increased up to the disappearance of conditioned reflexes to the metronome and light. The dogs were constantly walking about the room, did not remain on the rug. For 2-3 hours their work capacity was impaired; the animals made approximately half as many runs, as compared to norm.

On the following day the latent periods were protracted, especially to light, and following the use of differentiation one observed a successive inhibition. In dogs with an elaborated voluntary motor reaction one observed a reduction of activity: whereas prior to administration of the preparation 10 voluntary reactions were performed, there was none within 15-30 minutes after the injection, not more than four after 1-2 hours, and six on the following day. On the third day the higher nervous activity was normal (Fig. 14).

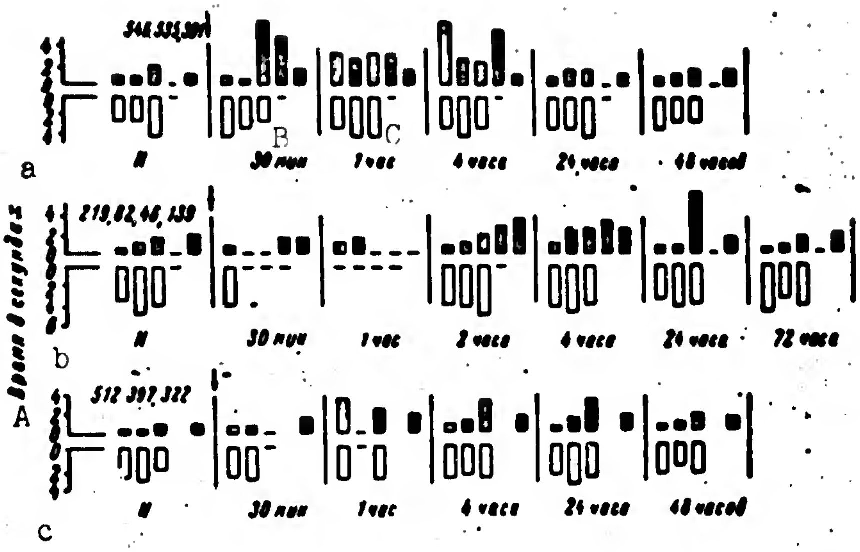


Fig. 14. Effect of amizyl in 0.1 mg/kg dose on the situation conditioned reflexes of dogs. a) Dzhek 20/IV, 1953, weight 20 kg; b) Dozor 7/VIII, 1953, weight 13.6 kg; c) Tobik 8/I, 1953, weight 12.6 kg. The symbols are the same as in Fig. 13. A) Time, in seconds; B) 30 minutes; C) one hour.

Upon injection of amizyl in a dose of 0.05 mg/kg, one observed for 1-2 hours a lack of differentiation and an increase of the latent period in the reflex to light. Within 4-24 hours the conditioned reflex activity reverted to norm. Amizyl in a dose of 0.01 mg/kg produced no substantial changes of conditioned reflexes in the majority of dogs; only voluntary reactions (licking of the bowl or scratching of the rug) were manifested in the animals at a lesser rate than usually. Amizyl in very small quantities (0.005 mg/kg) caused no disturbance of higher nervous activity in the majority of dogs, and in excitable animals a particular precision of work was noted: intersignal runs disappeared and the differentiation improved. One may assume that the slight attenuation of the stimulation process, caused by amizyl, leads to a balancing of the neural processes, whereas in the majority of experimental dogs, thanks to a marked predominance of the stimulation process, one usually observed frequent intersignal runs and incomplete differentiation (of 3 differentiations, one was lacking; upon turning-on of the negative stimulation, the animals got off the rug, but they did not jump on the table, etc.).

Thus, on the basis of conducted investigations we may conclude that amizyl in small doses (0.005 mg/kg), which still do not disturb the course of elaborated motor conditioned reflexes, induces a decrease in the amount and intensity of the voluntary motor food-seeking reactions. Under the effect of amizyl in large doses (0.05-0.1 mg/kg), the second link of complex synthetic motor activity becomes disrupted – the dog does not step on the rug, but walks about the room or lying down near the rug. At this time, the process of inner inhibition suffers – the differentiation is disrupted. With the increase of amizyl dose, a weakening takes place of the excitation process and a reduction of functional efficiency of the cortical cells (the latent periods increase, the conditioned motor reactions to weak stimuli disappear: first to light, then to the metronome and, finally, to all stimuli). The same effect was noted also following administration of other derivatives of glycolic acid – amedine, benzacine, phenylcyclohexylglycolic ester of diethylaminoethanol (preparation 1), but the doses are much higher. For instance, upon injection of amedine, in all dogs one observed disturbances of conditioned reflex activity only at a dose of one mg/kg. One noted an increase of latent periods and reflex time, as well as disruption of differentiation; on the following day the conditioned reflex activity reverted to the initial level. In dogs with a more complex motor activity pattern, more serious disturbances have taken place in response to alternating positive and negative stimuli (8+ and 8– stimulations in the experiment): dropping out of reflexes during 1-3 hours, consecutive inhibition and an ultraparadoxical phase (at a negative metronome signal the dogs jumped on the table; at a positive signal, there was no reaction at all). The higher nervous activity, became restored to norm only on the 3rd-4th day.

Amedine in a dose of one mg/kg, in addition to above-stated disturbances, caused an increase in the time required for the run of the animals; also, some conditioned motor reactions to a weak stimulus, such as light, disappeared (the animals remained on the rug or walked about in the room, instead of jumping on the table). No deviation from norm were observed on the following day. Analogous effect was produced by tiphen in doses of 0.5-1 mg/kg.

Aprophene, diphacyl, phenylcyclohexylacetic ester of diethyl-(or dimethyl)-aminoethanol (preparations 2 and 3) caused weak disturbances of higher nervous activity, as compared with the preparations of the previous group.

Upon administration of these preparations in doses of only 1-3 mg/kg, certain disturbances of conditioned reflex activity were observed: the latent periods became longer, differentiations were disrupted, and there was an increase in the length of time required for eating and return to the rug. Restoration of higher neural activity to the normal level would take place on the 2nd-3rd day, depending on the preparation, dose and individual characteristics of each animal (Fig. 15). Further increase of the amount of administered substance did not lead to a complete disappearance of the conditioned reflex activity, even at large doses. For instance, following injection of diphacyl in a dose of 10 mg/kg (exceeding the minimum active dose 10-fold), the dogs did not manifest even a partial disappearance of conditioned reflexes, whereas upon a 5-fold increase of the minimally-active dose of amizyl or amedine, atropine and other preparations, there developed in the cerebral cortex of the dogs a supraliminal protective inhibition with complete disappearance of the conditioned reaction for a period of 2-5 hours following injection.

Upon injection of lachexine and atropine in doses of 0.05-0.1 mg/kg, their peripheral effect on the salivary glands of the animals (dryness of mucosa) was manifested before the disturbances of conditioned reflex activity have made their appearance; in their character of action the disturbances resembled the effect of am-

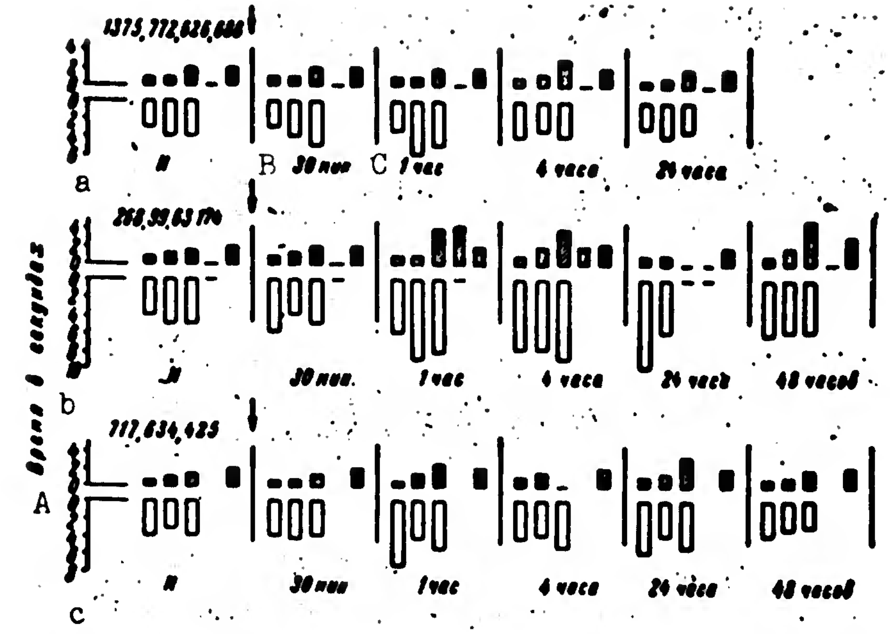


Fig. 15. Effect of diphacyl in a 1 mg/kg dose on situation conditioned reflexes of dogs. a) Dzhek 13/X, 1953, weight – 20.0 kg; b) Dozor 20/VIII, 1953, weight – 13.2 kg; c) Tobik 27/V, 1953, weight – 12.4 kg. The symbols are the same as in Fig. 13. A) Time, in seconds; B) 30 minutes; C) one hour.

izyl. The range of active doses was extremely narrow – from 0.1 to 0.5 mg/kg. Atropine and lachesine in doses of 0.5 mg/kg caused a complete disappearance of conditioned reflex motor activity and a rejection of food by the animals (Fig. 16).

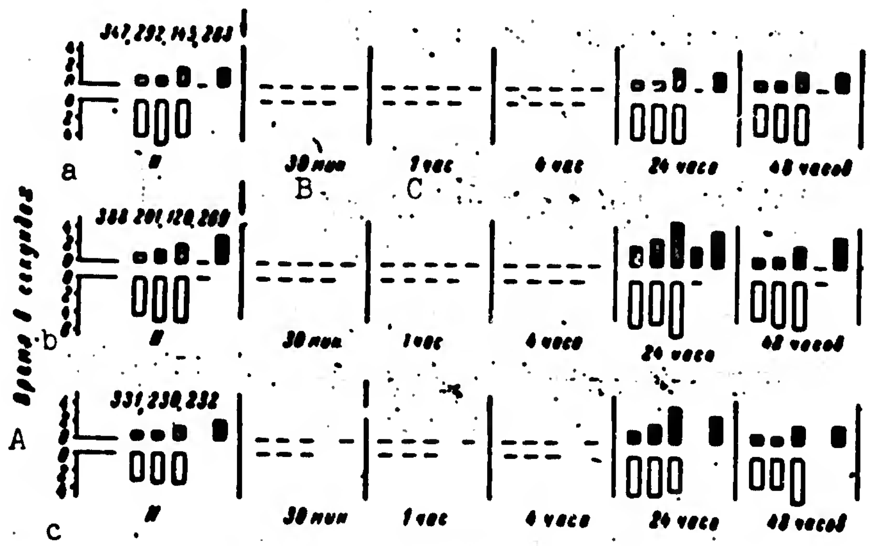


Fig. 16. Effect of atropine in a dose of 0.5 mg/kg on situation conditioned reflexes of dogs. a) Dzhek 12/V, 1952, weight – 10 kg; b) Dozor 30/XI, 1953, weight – 13 kg; c) Tobik 18/IX, 1952, weight – 12 kg. The symbols are the same as in Fig. 13. A) Time, in seconds; B) 30 minutes; C) one hour.

It should be noted that in dogs with a weak type of higher nervous activity and of a strongly imbalanced (unrestrained) nature, the impairment of conditioned reflex activity, following injection of cholinolytic substances, was observed at smaller doses and lasted longer than in dogs with a strong and balanced type of the nervous system and a satisfactory mobility of neural processes. As an example, we cite in Table 9 the doses of diphacyl and amizyl which induce minimal disturbances of higher nervous activity in dogs possessing various typological characteristics, determined according to the abbreviated standard of M.S. Kolesnikov and V.A. Troshikhin (1951).

TABLE 9

Changes of Higher Nervous Activity in Dogs Under the Effect of Various Pharmacological Substances

1 Кличка собаки	2 Тип высшей нервной деятельности	3 Доза (мг/кг), нарушающая высшую нервную деятельность		4 Длительность нарушений высшей нервной деятельности в часах	
		5 амизил	6 дифацил	амизил	дифацил
7 Джек	Сильный, уравновешенный, подвижный . . 12	0,1	2,0	24	24
8 Рыжий	То же . 13	0,1	1,0	24	4
9 Тобик	Сильный, неуравновешенный 14	0,05	0,5	48	24
10 Рекс	То же . 13	0,075	0,25	72	4
11 Жан	Слабый 15	0,01	0,1	72	24

1) Name of dog; 2) type of higher nervous activity; 3) dose (mg/kg) which impairs higher nervous activity; 4) duration of disturbances of higher nervous activity, in hours; 5) amizyl; 6) diphacyl; 7) Dzhek; 8) Ryzhiy; 9) Tobik; 10) Reks; 11) Zhan; 12) strong, well-balanced, lively; 13) the same; 14) strong, unbalanced; 15) weak.

Cyclodol, 1,1-diphenyl-3-(N-peperidyl)-propanol 1 (preparation 4) and 1-phenyl-1-(α-thienyl)-3-(N-piperidyl)-propanol 1 (preparation 5) induced disturbances of higher nervous activity in doses of 1-2 mg/kg. Preparation 5 exerted a weaker and transitory effect. Upon its administration in a 2 ml/kg dose, one observed for 30 minutes an increase of the latent periods, disruption of differentiations and a slowing up of consumption of the additional food portion.

Cyclodol exerted the strongest effect. In a dose of 1 mg/kg it induced within an hour after injection a complete inhibition of conditioned reflex motor activity, the animals rejecting their feed. In some dogs a marked dryness was observed and occasional vomiting. Within three hours the differentiations were still absent and an increase of latent periods to light was observed. The conditioned reflex activity became fully restored on the following day (Cf. Record of the experiment on 19/X 1956).

In experiments carried out according to the salivation method, the injection of amizyl in doses of 0.0005-0.005 mg/kg produced no change in the conditioned and unconditioned secretion during the day of injection. During the subsequent two days an increase was observed of conditioned salivation in response to all stimuli.

Following a twofold increase of the dose (0.01 mg/kg), the conditioned salivation decreased by 50%-70%, whereas unconditioned salivation showed no appreciable change. Only after a subsequent increase of the amount of injected substance (0.05 mg/kg), a reduction was observed of the amount of unconditioned salivation.

Aprophene (0.5-0.75 mg/kg), as well as amedine (0.01-0.05 mg/kg), caused a decrease of conditioned reflexes, without changing the total value of unconditioned salivation, although a reduction of the amount of unconditioned secretion was observed during the first 30 seconds, and its increase during the second 30 seconds after the start of eating – a fact indicating the reduction of excitability in the cortical zone of the unconditioned food reflex (P.S. Kupalov, 1955b) (Cf. record of experiment of 12/XII 1960).

Atropine and lachesine in doses (0.001-0.005 mg/kg and higher), within 30 minutes following injection, simultaneously reduced the conditioned as well as unconditioned salivation. On the following day an increase of secretion was observed (Cf. record of the experiment on 18/IV 1961).

Diphacyl affected the conditioned reflex activity of dogs in higher doses, as compared with other preparations. When diphacyl was administered in doses of 0.1-0.2-0.5 mg/kg, no changes in conditioned reflexes were observed; there was only a tendency toward unconditioned salivation. Upon injecting this preparation in doses of one mg/kg, and higher, the unconditioned salivation was inhibited first (record of experiment on 25/V 1961), and at higher doses – the conditioned and unconditioned salivation were inhibited.

Experiments conducted according to the method of situation conditioned reflexes established the fact that, upon administration of small doses of aminoalkyl esters of substituted glycolic acid (amizyl, amedine, preparations 1 and 2), there disappears, in the first place, the voluntary food-searching motor reaction, also the differentiation, as well as precision, of dog's position on the rug are impaired. Next, the latent periods increase and, finally, the motor reactions to conditioned stimuli disappear. Upon injection of large doses (0.1-0.15 mg/kg of amizyl, 0.75-1 mg/kg of preparation 1 and 2, 1-1.5 mg/kg of amedine, 0.5 mg/kg of lachesine, etc.), the partial or complete disappearance of conditioned reflexes is preceded by the emergence of phase states, more frequently in the form of the leveling, paradoxical, and ultraparadoxical phases. One observes an increased exhaustion of the central nervous system toward the end of each experiment (the dog performs 2-3-fold less runs than in norm). These changes of higher neural activity attest to the weakening of inhibitory as well as stimulating processes in the cerebral cortex, with subsequent reduction of work capacity and the development of protective inhibition.

Record of the Experiment on 19/X 1956 on the Dog Ryzhiy

1 Число применений условного раздражителя	2 Условные раздражители	3 Латентный период условного рефлекса (сек)	4 Время в секундах: 5 пробежки	6 съедания пищи	7 возвращения на коврик
598 8	Зуммер	0,5	2	3	10
504 9	Метроном	1	2	3	15
200 10	Свет	3	2	4	7
226 11	Звонок (диф.)	—	—	—	—
599 8	Зуммер	0,5	1	3	5
505 9	Метроном	0,5	2	3	6

Within 30 minutes following administration of cyclodol in a dose of 1 mg/kg:

600 8	Зуммер	0,5	2	4	3
506 9	Метроном	1	2	3	5
201 10	Свет	10	2	5	5
227 11	Звонок (диф.)	2	2	—	—
601 8	Зуммер	0,5	2	6	10
507 9	Метроном	0,5	2	4	7

Within an hour following administration:
The dog does not react, walks about the room; meat, thrown on the floor to the dog, is eaten slowly; the animal rubs snout with the paws (dryness of mucous membranes), vomiting.
Within three hours following administration of the preparation:

602 8	Зуммер	1	2	5	4
508 9	Метроном	1,5	2	4	5
202 10	Свет	10	2	6	8
228 11	Звонок (диф.)	2	2	—	—
603 8	Зуммер	1	2	6	10
509 9	Метроном	1,5	2	4	8

Within 24 hours following administration of the preparation.

604 8	Зуммер	0,5	1	3	5
510 9	Метроном	1	1,5	4	3
203 10	Свет	1,5	2	3	7
228 11	Звонок	—	—	—	—
605 8	Зуммер	1	1	3	7
511 9	Метроном	1	1,5	4	3

1) Number of applications of the conditioned stimulus; 2) conditioned stimuli; 3) latent period of the conditioned reflex (in seconds); 4) time, in seconds; 5) runs; 6) consuming food; 7) return to the rug; 8) buzzer; 9) metronome; 10) light; 11) bell (differentiation).

Record of the Experiment on 12/XII 1960 on the Dog Pisclya

Число применений условного раздражителя [1]	Условный раздражитель [2]	Период запаздывания слюнного условного рефлекса (сек) [3]	Величина условного рефлекса в делениях шкалы (1 дел.—0,1 мл) за 20 сек [4]	Величина безусловного слюнного рефлекса в делениях шкалы за [5]		
				первые 30 сек [6]	вторые 30 сек [7]	за 1 мин [8]
	[9] До введения препарата					
51	Метроном 120 . [10]	1	49	168	58	226
59	Бульканье . . . [11]	1	74	149	18	167
26	Свет . . . . . . [12]	1	64	161	35	196
15	Метроном 60 . . [10]	3	15	—	—	—
52	» 120 . . .	2	48	153	51	204
60	Бульканье . . . [11]	3	61	159	38	197
	Среднее арифметическое [13]		69	158	40	198

Within 20 minutes following injection of aprophene in a dose of 0.75 mg/kg

53	Метроном 120 . [10]	3	36	130	60	190
61	Бульканье . . . [11]	4	45	151	88	239
27	Свет . . . . . . [12]	3	33	137	70	207
16	Метроном 60 . [10]	3	17	—	—	—
54	» 120 . . .	4	29	130	77	207
62	Бульканье . . . [11]	3	47	144	69	21[illegible]
	Среднее арифметическое [13]		34	138	73	211

On the following day

55	Метроном 120 . [10]	1	49	171	81	252
63	Бульканье . . . [11]	2	70	155	46	201
28	Свет . . . . . . [12]	3	49	153	30	183
17	Метроном 60 . [10]	3	12	—	—	—
56	» 120 . . .	3	59	174	45	219
64	Бульканье . . . [11]	2	75	154	30	184
	Среднее арифметическое [13]		60	161	46	210

1) Number of applications of the conditioned stimulus; 2) conditioned stimulus; 3) delay period of the salivary conditioned reflex (seconds); 4) value of the conditioned reflex, in scale grades (one grade = 0.1 ml) during 20 seconds; 5) value of the unconditioned salivary reflex, in scale grades during; 6) the first 30 seconds; 7) second 30 seconds; 8) during one minute; 9) prior to administration of the preparation; 10) metronome 120; 11) gurgling sound; 12) light; 13) arithmetical mean.

Record of the Experiment on 18/IV 1961. Dog Chernysh

1 Число применений условного раздражителя	2 Условный раздражитель	3 Период запаздывания слюнного условного рефлекса (сек)	4 Величина условного рефлекса в делениях шкалы за 20 сек	5 Величина безусловного слюнного рефлекса в делениях шкалы (1 дел.=0,1 мл) за: 6 первые 30 сек	7 вторые 30 сек	8 1 мин
383	Бульканье . . 9 . .	2	17	121	103	124
328	Метроном 90 10 . .	6	20	123	83	206
156	» 40 . . .	5	3	—	—	—
329	» 90 . . .	3	9	112	92	204
27	Свет . . . . . 11 . .	10	2	108	85	193
384	Бульканье . . 9 . .	1	13	94	81	175
	Среднее арифметическое 12		12	111	89	200

Within 20 minutes following injection of lachesine in a dose of 0.01 mg/kg

385	Бульканье . . . 9 .	7	4	59	56	115
330	Метроном 90 10 .	2	10	63	53	116
157	» 40 . . .	2	6	—	—	—
331	» 90 . . .	9	3	86	75	161
28	Свет . . . . . 11 .	12	8	90	74	164
386	Бульканье . . . 9 .	12	3	91	78	169
	Среднее арифметическое 12		5	77	66	143

On the following day after administration of the preparation

387	Бульканье . . . 9 .	1	35	142	105	247
332	Метроном 90 10 .	2	39	127	83	210
158	» 40 . . .	2	11	—	—	—
333	» 90 . . .	6	17	127	101	228
29	Свет . . . . . 11 .	1	15	114	86	200
388	Бульканье . . . 9 .	1	23	125	83	208
	Среднее арифметическое 12		26	126	91	217

1) Number of applications of a conditioned stimulus; 2) conditioned stimulus; 3) delay period of the salivary conditioned reflex (seconds); 4) value of the conditioned reflex in scale grades during 20 seconds; 5) value of the unconditioned salivary reflex in scale grades (one grade = 0.1 ml) during; 6) the first 30 seconds; 7) second 30 seconds; 8) one minute; 9) gurgling; 10) metronome; 11) light; 12) arithmetical mean.

Record of the Experiment on 25/V 1961 on the Dog Dzhim

Число применений условного раздражителя [1]	Условный раздражитель [2]	Период запаздывания слюнного рефлекса (сек) [3]	Величина условного рефлекса в делениях шкалы за 20 сек [4]	Величина безусловного слюнного рефлекса в делениях шкалы (1 дел.—0,1 мл) за: [5]		
				[6] первые 30 сек	[7] вторые 30 сек	[8] 1 мин
253	Метроном . . . [9] . .	4	8	139	85	224
226	Бульканье . . . [10] . .	3	31	155	94	249
142	Свет . . . . . . [11] . .	4	15	141	102	243
132	Метроном 60 . . [9] . .	5	9	—	—	—
254	» 120	2	19	129	72	201
227	Бульканье . . . [10] . .	2	30	151	92	243
	Среднее арифметическое [12]		21			234
Within 30 minutes following injection of one mg/kg of diphacyl						
255	Метроном 120 . . [9] .	4	15	75	38	113
228	Бульканье . . . . [10] .	3	24	62	38	100
143	Свет . . . . [11] .	2	22	83	24	107
133	Метроном 60 . . [9] .	6	3	—	—	—
256	» 120	3	15	102	93	195
229	Бульканье . . . . [10] .	2	26	130	116	246
	Среднее арифметическое [12]		20			152
Within 24 hours following injection of the preparation						
257	Метроном 120 . . [9] .	10	12	138	97	235
230	Бульканье . . . . [10] .	3	43	141	97	238
144	Свет . . . . [11] .	3	34	139	58	197
134	Метроном 60 . . [9] .	3	12	—	—	—
258	» 120	3	35	131	90	221
231	Бульканье . . . . [10] .	3	41	120	90	210
	Среднее арифметическое [12]		33			220

1) Number of applications of a conditioned stimulus; 2) conditioned stimulus; 3) delay period of the salivary reflex (seconds); 4) value of the conditioned reflex, in scale grades for 20 seconds; 5) value of the unconditioned reflex in scale grades (one grade = 0.1 ml) during; 6) the first 30 seconds; 7) second 30 seconds; 8) one minute; 9) metronome; 10) gurgling; 11) light; 12) arithmetical mean.

Restoration of the normal course of conditioned reflex activity is observed toward the 2nd-5th day, depending on the substance, dose and nervous system of the animal.

Using the method of salivary conditioned reflexes, one may elicit among cholinolytics some preparations possessing a special effect on the central nervous system (central cholinolytics). These preparations may include amizyl, amedine and aprophene, because these substances exert in minimal quantities an effect on conditioned reflexes and on the cortical representation of the unconditioned reflex, which is expressed in the reduction of salivation during the first 15 seconds from the start of feeding, and in the impairment of differentiation. Also diphacyl can be included in the preparations of central action; in its action diphacyl differs from other preparations, in that it exerts an initial effect on subcortical formations (the unconditioned salivation is inhibited in doses which do not affect the innervation of the salivary gland and conditioned salivation).

These data have been obtained by S.S. Krylov (1953). Based on his data, the author advanced a hypothesis that the inhibiting effect of diphacyl on the salivary unconditioned reflex depends on its action on the subcortical centers, because, according to the data of T.V. Tomilina (1951), diphacyl in a dose of 5 mg/kg had no effect on the innervation of the salivary gland. Subsequently, we corroborated this hypothesis, when we injected diphacyl directly into subcortical formations (reticular formation of the mesencephalon) through cannulae implanted in the brain of animals in whom conditioned motor reflexes have been elaborated (A.T. Selivanova and N.N. Lazuko, 1961, 1963).

In employing the method of salivary conditioned reflexes, it is impossible to elicit the character of action on the central nervous system of substances such as atropine and lachesine, which inhibit salivation through their peripheral action on the salivary glands. Therefore, the central action of such atropine-like preparations is best to investigate by means of the motor method of situation-conditioned reflexes. Experiments based on this method showed that atropine and lachesine inhibited the alimentary motor conditioned reflexes when one used doses 50-100-fold larger than doses which reduced secretion, i.e., exerted peripheral action (Table 10).

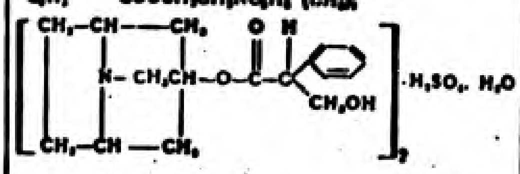
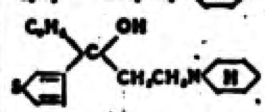
In employing the method of conditioned situation reflexes, were able to establish minimally-active doses for the higher nervous activity of the experimental animals, in regard to all investigated cholinolytic substances, including those affecting the salivary glands (Cf. Table 10).

In Table 10, a minimal acting dose is considered a minimal dose which in three dogs disrupted differentiation and increased the latent periods.

As shown in this table, the effect of cholinolytics on the cerebral cortex activity varies in its strength. This can be judged, according to the established doses which disturb the conditioned reflex activity. A comparison of investigated substances

TABLE 10

Minimal Doses of Preparations which Inhibit Salivary and Motor Alimentary Conditioned Reflexes in Dogs

[1] Название препарата	[2] Химическое строение	[3] Дозы (в мг/кг), нарушающие		
		[4] [illegible] условные рефлексы	[5] слюнные условные рефлексы	[6] слюнные безусловные рефлексы
[7] Амизил	$(C_6H_5)(C_6H_5)C(OH)COOCH_2CH_2N(C_2H_5)_2$	0.05—0.1	0.01	0.05
[8] Бензацин	$(C_6H_5)(C_6H_5)C(OH)COOCH_2CH_2N(CH_3)_2$	0.5	—	—
[9] Препарат 1	$(C_6H_5)(C_6H_{11})C(OH)COOCH_2CH_2N(C_2H_5)_2$	0.5	—	—
[10] Амедин	$(C_6H_5)(C_6H_{11})C(OH)COOCH_2CH_2N(CH_3)_2$	0.75	0.05	0.1
[11] Апрофен	$(C_6H_5)(C_6H_5)C(CH_3)COOCH_2CH_2N(C_2H_5)_2$	1.5	0.75	1.0
[12] Дифацил	$(C_6H_5)(C_6H_5)C(H)COOCH_2CH_2N(C_2H_5)_2$	1.5—2.0	1.5	1.0
[9] Препарат 2	$(C_6H_5)(C_6H_{11})C(H)COOCH_2CH_2N(C_2H_5)_2$	1.25	—	—
[9] Препарат 3	$(C_6H_5)(C_6H_{11})C(H)COOCH_2CH_2N(CH_3)_2$	1.5	—	—
[13] Тифен	$(C_6H_5)(C_6H_5)C(H)COSCH_2CH_2N(C_2H_5)_2$	0.5—1.0	—	—
[14] Лахезин	$(C_6H_5)(C_6H_5)C(OH)COOCH_2CH_2NC_2H_5(CH_3)_2$	0.1	0.001	0.001
[15] Атропин		0.1	0.005	0.005
[16] Циклодол		1.0	—	—
[9] Препарат 4		1.0	—	—
[9] Препарат 5		2.0	—	—

1) Name of preparation; 2) chemical structure; 3) doses (in mg/kg) which impair; 4) situation conditioned reflexes; 5) salivary conditioned reflexes; 6) salivary unconditioned reflexes; 7) amizyl; 8) benzacine; 9) preparation; 10) amedine; 11) aprophene; 12) diphacyl; 13) tiphen; 14) lachesine; 15) atropine; 16) cyclodol.

with each other, as to the strength of their central action, is of great importance in clinical studies, because it permits the selection of preparations possessing a good therapeutic effect and disturb only slightly the conditioned reflex activity of animals, or the psychic activity of humans. Of all our investigated preparations, the most promising from the point of view of clinical application, and taking into account minimal disturbances of higher nervous activity and sufficiently strong central cholinolytic action (according to the data of S.V. Anichkov, 1958, 1962; P.P. Denisenko, 1960; S.G. Kuznetsov and S.N. Golikov, 1960, S.S. Liberman, 1956; M.D. Mashkovskiy and S.S. Liberman, 1950, 1957, et al.), are, in our opinion, the following preparations: amedine – from the investigated derivatives of glycolic acid; diphacyl and aprophene – from acetic acid derivatives; preparation 5 – from the group of amino alcohols.

As regards the further synthesis of new compounds, of interest to chemists-synthesists and pharmacologists in the comparison of the strength of central action of these preparations (i.e., of doses which affect the conditioned reflex activity) with their chemical structure.

In Soviet and foreign literature these comparisons are widely carried out, but not in regard to the strength of the direct effect of the substance proper, elicited by the method of conditioned reflexes, but on the basis of other tests which indirectly establish the strength of central action of these preparations – elimination by cholinolytic preparations of convulsions or tremor induced by cholinomimetic substances: nicotine, arecoline, etc. (S.V. Anichkov and M.L. Belen'kiy, 1953; Z.I. Vedeneyeva, 1956; S. N. Golikov, 1956; P.P. Denisenko, 1960; S.S. Liberman, 1956; Yu.G. Fedorchuk, 1958; Lands and Luduena, 1956).

In comparing the effect of minimal doses of cholinolytic preparations on the higher nervous activity of dogs, one can see (Cf. Table 10) that the intensity of central action increases:

1) upon substitution of hydrogen in an acetic acid molecule with hydroxyl (to compare preparations amizyl and diphacyl, preparations 1 and 2, amedin and preparation 3), or with the methyl group (aprophene);

2) upon substitution of methyl radicals in the nitrogen of amino ester with the ethyl radicals (compare benzacine and amizyl, amedine and preparation 1, preparation 3 and 2);

3) upon substitution of the oxygen bridge with sulfur (tiphen).

The central effect of aminoalkyl esters decreases, when one phenyl in the molecule of diphenylacetic and diphenylglycolic acids is replaced with a cyclohexyl.

Upon switching to quaternary ammonium bases, the peripheral action increases, while the central action is weakened (compare lachesine with amizyl).

The effect of amino alcohols on the higher nervous activity as compared with amino esters, derivatives of glycolic acid, is much less pronounced (cyclodol, preparations 4 and 5 as compared with amizyl, benzacine, preparation 1, amedine) and approaches the effect of acetic acid derivatives.

Under seemingly most negligible changes of the chemical structure of a preparation, the strength as well as the localization and the character of action of the compound undergoes a change. For instance, when a hydroxyl in the molecule of glycolic acid is replaced with hydrogen, the preparation acquires new pharmacological properties, and there is a change in the localization of its initial effect on the brain. Diphacyl in small doses affects mainly the subcortical formations (A.T. Selivanova and N.N. Lazuko, 1961, 1963; S.S. Krylov, 1956), whereas amizyl initially affects the cerebral cortex. In aprophene (hydrogen is replaced with a methyl group), the effect on the cortex and subcortical formations is manifested at almost identical doses; although as to intensity of action this preparation is closer to diphacyl, and it corresponds more to amizyl in its character of action.

EFFECT OF ADRENERGIC SUBSTANCES (ADRENALINE AND SYMPATHOLYTIN) ON SITUATION AND SECRETORY CONDITIONED REFLEXES

Investigation of the effect of sympatholytin – a substance which blocks the adrenoreactive systems – was carried out by V.V. Yakovleva and O.N. Voyevodina by the method of situation conditioned reflexes and the salivation method. Sympatholytin was administered per os in doses of 10-15 mg/kg, or intravenously in doses of 5-6 mg/kg. The tests were made within 30 minutes and 3 hours after administration of the preparation.

Immediately following administration of sympatholytin, salivation takes place, which lasts 20 to 30 minutes.

In view of the fact the sympatholytin blocks the sympathetic innervation of submaxillary and parotid glands, the effect is manifested of a predominant action of n. vagus.

Sympatholytin, introduced per os or intravenously, stimulated the emetic center (vomiting was observed in experimental dogs). Following administration of sympatholytin the animals appeared sluggish and sometimes refused to eat.

Intravenous injection of the preparation sometimes caused pulse acceleration and dyspnea.

When the experiments were carried out under conditions of free behavior of the animal, the conditioned reflexes and differentiations were impaired. An ultraparadoxical phase was observed: in response to a negative stimulus the animals ran and jumped on the table, and they did not run in response to a positive stimulus. The conditioned reflexes were often absent not only in response to weak but also to strong stimuli, and the dogs tried to escape from the experimental premises.

Following administration of sympatholytin, one observed for several hours a slowing up of the movements of the animals. On the 2nd-3rd day the conditioned reflex activity reverted to norm.

In experiments conducted according to the secretory method, the conditioned reflexes in dogs showed a marked decrease within three hours following intravenous administration of sympatholytin, the weak stimuli exerting a greater effect than the strong ones. Differentiations were disrupted. On the following day the values of conditioned reflexes increased, but the correlations as to strength remained impaired; the differentiations were still further impaired. On the 2nd-3rd day, the value of all conditioned reflexes dropped; they rose again during the next few days. These fluctuations of conditioned reflex activity in the direction of a sharp rise alternating with a drop were observed for 6-7 days, following which the entire conditioned reflex activity was restored to normal levels.

Hence, with the use of various investigation methods, analogous results have been obtained: sympatholytin in the investigated doses impaired the conditioned reflex activity of dogs for a period of 3-7 days. Besides, one observed a slowing up of movements, vomiting, sluggishness, and the tendency of animals to escape from the experimental premises.

Effect of adrenaline (a substance stimulating the adrenoreactive systems) was investigated by V.D. Volkova (1961) on dogs with elaborated situation conditioned reflexes.

Injection of adrenaline in doses of 0.005-0.15 mg/kg caused a shortening of the latent periods of conditioned reflexes and an increase in the rate of the movement of animals; the formed stereotype of conditioned reflexes was not disturbed. Some of the dogs were rather restless in their behavior, drank often, shook and scratched themselves.

Injection of 0.025 mg/kg of adrenaline did not appreciably affect the conditioned reflex activity, but the general anxiety of the animals showed a marked increase: they would sit down, or get up and start walking about the room; their runs to the door became quite frequent, as well as the scratching and shaking movements. In view of the general agitated state of the animals we had to at times discontinue the tests.

Injection of 0.05 mg/kg of adrenaline caused an increase in the latent periods of conditioned motor reflexes, and the rate of motor reactions decreased; in half of the cases the differentiations were absent. The movements of animals became sluggish, uncertain, and phenomena of a general motor agitation showed an increase. After the first 4-6 combinations the animals often showed a tendency to go to the door and lie down; they whimpered, showed no reaction to the stimuli or to the knocking of the food receptacle. Within 3-4 hours after adrenaline injection the changes in higher nervous activity were more clearly manifested than an hour after injection, and the excitability to food stimulation decreased. On the following day, the dogs often manifested an increased motor activity, and on the 2nd-3rd day the conditioned reflex activity did not differ from norm.

Hence, adrenaline in small doses (0.005-0.15 mg/kg) causes an increase in the excitability of cortical cells, and in large doses – a decrease. However, the effect of adrenaline, as well as sympatholytin, even in small doses is manifested simultaneously also on unconditioned reflexes: shaking, alimentary and vomiting reflex. These facts are fully in accord with literary data because, in the opinion of many authors, the subcortical formations (of the reticular formation of the brain stem include adrenoreactive systems on which the adrenergic substances exert their effect.

EFFECT OF AMINAZINE ON SITUATION CONDITIONED REFLEXES

Effect of Aminazine on Situation Conditioned Reflexes in Intact Dogs

In connection with the wide clinical use of tranquilizers, in particular aminazine, for the treatment of nervous diseases, of considerable theoretical interest has been the study of its effect on the higher nervous activity of animals. In the I.P. Pavlov Physiological Department, the effect of aminazine was investigated on the normal and functionally altered higher nervous activity of dogs. We shall dwell in more detail on the results of the aminazine effect on the complex conditioned reflex activity, elaborated according to the method of situation reflexes.

The experiments were conducted by V.D. Volkova (1960), M.M. Khananashvili (1960) and O.N. Voyevodina (1961). The following behavior pattern has been developed in each dog: return to a definite place in the room (to the rug) following regular food reinforcement, standing on the rug until the stimulator was turned on; response to the positive stimulator – running to the corresponding table; upon turning on of the inhibition stimulator – the dog remains standing on the rug. In addition, in 7 dogs the differentiation of conditioned stimuli was elaborated, which differed as to the location of food reinforcement (from various troughs), i.e., based on spatial differentiation of the reinforcement spot of conditioned stimuli.

Aminazine was injected subcutaneously once, against a background of conditioned reflexes and stable differentiations. The following doses were employed: 0.1, 0.25, 0.5, 0.75, 1.0, 1.5, 2.0 and 2.25 mg/kg. Upon injection of aminazine in a dose of 0.1-0.5 mg/kg, the behavior of animals did not change and the formed conditioned motor reactions remained unaltered, or these changes were negligible and of transitory nature. When the aminazine dose was raised to 1-2 mg/kg, a decrease was observed of the general motor activity of the animals, a 3-4-fold increase of the latent periods of conditioned motor reactions, and an increase of the running time and of the duration of feeding time, up to 30-60 seconds (in norm – 10-20 seconds). Having finished eating the animals remained on the table a few minutes, whereas under normal conditions their reaction was to return to the rug at once. In norm, after a positive conditioned stimulus was turned on, the dog would go to the rug along the shortest way, whereas following injection of 1 mg/kg of aminazine, the initial movement of the dog was often not directed toward the feeding trough but to the source of the conditioned stimulus, and only then – toward the trough. The disturbances of higher nervous activity of the animals gradually increased. Whereas at the start of the experiment, within 30-50 minutes following administration of aminazine, the signal value of conditioned stimuli was preserved and the animals ran to the feeding trough, during the second half of the experiment the conditioned reflexes to weak stimuli were completely absent, and after 2-4 hours they could not be obtained also in response to the action of stimuli of medium strength.

The tested aminazine doses, in all cases where the conditioned reflex activity remained intact, did not impair the differentiation of conditioned reflexes; neither was there always observed a consecutive inhibition, following the use of an inhibition stimulus. Only in the experiments of O.N. Voyevodina (1961) was a disappearance of differentiations (3 out of 8) observed in those dogs which experimentally received a large number (8) of negative stimuli.

On the 2nd-4th day following aminazine administration in doses of 1-2 mg/kg, the general motor activity of the animals reverted to norm, but disturbances of conditioned reflex activity in some animals (Smirnyy and Belyy) were observed for a more prolonged period of time (1-2 weeks).

On the basis of presented data, the following conclusion can be made: aminazine induces, first of all, a reduction of the general motor activity of the animals. Their movements become sluggish, uncertain, inaccurate and retarded; a weakening of the tonus of skeletal musculature is noted and the process of mastication and swallowing of food is markedly slowed up.

Under the effect of small doses (0.1-0.5 to 1 mg/kg) the structure of the conditioned reflex is preserved, but the entire activity proceeds at a lower functional level. With the increase of the aninazine dose (1.5-2.0 mg/kg), a disturbance is observed of the very structure of the conditioned reflex which in norm consists of a consecutive chain of complex motor reactions. The impairment of the conditioned reflex structure starts with an intensification of the first alimentary reaction; it is manifested in the fact that the initial movement of the animal in response to the conditioned stimulation is not in the direction of the place of reinforcement – the feeding trough – but to the source of conditioned stimulation. Subsequently, the concluding act of the conditioned reflex – the run to the feeding trough – also disappears completely.

The mechanism of reduction of motor activity and weakening of skeletal musculature in the animals has been insufficiently clarified, judging by the available literary data. Some authors (Behrend, 1952; Kopera; Armitage, 1954) are of the opinion that aminazine, in large doses, exerts a direct paralyzing effect on skeletal musculature; other authors think that aminazine increases the effect of curariform substances, but they do not indicate whether this action is of peripheral or central nature. M.D. Mashkovskiy and V.A. Medvedev (1959) carried out special studies on cats and rabbits, in order to ascertain as to what extent is the aminazine-induced muscular weakening connected with its curariform effect on the neuromuscular synapses. It turned out that even in large doses (up to 10 mg/kg), upon intravenous administration, aminazine exerted no characteristic curariform effect (no direct inhibiting effect of aminazine on the skeletal musculature was observed). On the basis of these observations, the authors assume that the weakening of skeletal musculature is connected with the effect of aminazine on the higher sections of the nervous system.

After the effect of aminazine on the higher nervous activity of normal animals has been established, a change in the initial functional state of the cortex was noted.

Despite the available experimental investigations and numerous clinical data, the question still remains debatable in regard to the action mechanism of aminazine on the nervous system. In this connection, the aim of our investigations included, the study of the effect of aminazine on situation conditioned reflexes in dogs with pathologically altered state of the central nervous system which took place following the effect of ionizing radiation on the animal, as well as in dogs which have been subjected to certain brain operations (removal of frontal lobes, removal of the cerebellum, or separation of the optic and motor analyzers.

Effect of Aminazine on Situation Conditioned Reflexes in Dogs Exposed to the Action of Ionizing Radiation

Observation were conducted on 4 dogs, in whom prior to irradiation a complex stereotype has been elaborated of motor conditioned reflex activity to various stimuli. For instance, in the dogs Tolstyak, Sharik and Soltan, the conditioned reflex activity consisted of the following: following first run to the table and eating the reinforcement food portion, the dog stepped on the rug; when the positive conditioned stimulus was turned on (metronome), the dog started to run and jumped on table 1, and when the differentiation metronome was turned on the dog remained on the rug. The positive and inhibition conditioned stimuli differed from one another merely in their spatial localization in the experimental room.

Prior to irradiation, a stable conditioned reflex activity was elaborated in the dogs. However, under the effect of total irradiations in doses of 12-28 *r* (daily irradiation — 1 *r*) changes of higher nervous activity developed in the animals; these changes are described in detail in Chapter 5.

Here we shall only mention that all dogs exposed to small Roentgen doses (12-15-19-28 *r*) never manifested a refusal of food or fatigue during the experiments. However, the process of inner inhibition was impaired for a period of 56-87 days.

Upon administration of aminazine, following irradiation of the dogs, there have been observed, during the compensation stage of disturbances of higher nervous activity, substantial and prolonged disturbances of situation conditioned reflexes, analogous to those observed for 2-4 months following irradiation. For example, under the effect of a single injection of aminazine in doses of 0.5-1 mg/kg, the dogs did not at once go to the rug after their meal; the animals manifested circus movements, which as a rule are characteristic of irradiated animals, the differentiations were impaired for 6-12 days and the latent period of the conditioned reflex increased by 0.8-2 seconds.

Within 6-12 days following a single administration of aminazine, the conditioned reflex activity of the dog reverted to its normal level. Only in the dog Pal'ma, after aminazine administration, the conditioned reflex activity was impaired for 46 days following a single injection of this preparation, mainly as the result of disruption of differentiations.

O.N. Voyevodina also investigated dogs previously subjected to a total X-ray irradiation with large doses (100-300 r). After the level of conditioned reflex activity in these dogs had reverted to norm (within 5 years), the irradiated animals were subcutaneously injected aminazine in doses: 1.0-0.25 mg/kg; 0.5-0.75 mg/kg; 1.0-1.5 mg/kg; 2 mg/kg; 2.5 mg/kg.

The most characteristic feature of disturbances observed under these conditions was the emergence of persistent circus movements. The greater the aminazine dose, the more pronounced were the circus movements, manifested in various tempi; at a gallop, trot, or at a walking pace which changed to a rapid short-step run.

As a result of the appearance of circus movements, the correct orientation of the animals in the experimental chamber became disturbed. Besides, complete cessation of conditioned reflex motor activity was noted on the 2nd-4th day following aminazine injection in a dose of 1-2 mg/kg, and in some dogs – even upon administration of smaller doses (0.2-0.5 mg/kg).

In these cases, the animals performed during the entire experiment circular movements, which became particularly intensified upon inclusion of differentiation conditioned stimuli. Under the effect of positive conditioned reflexes the dogs sometimes made erroneous runs to the tables.

It should be pointed out that in healthy animals the injections of aminazine in a dose of 0.25 mg/kg induced no changes in the situation conditioned reflexes.

Hence, the conducted experiments showed that in irradiated dogs, even within 1-5 years following irradiation, the injection of aminazine causes disturbances of conditioned reflex activity. These disturbances are analogous to those originating directly following irradiations, i.e., under the effect of aminazine a picture is formed of an acute period of disturbances of higher nervous activity caused by exposure to X-ray radiation. Under the effect of aminazine, longer disturbances (6-12 days) of conditioned reflex motor activity are taking place than in healthy animals (2-4 days), and they are observed also at smaller doses. It is characteristic that, whereas in healthy animals an aminazine injection almost never induced a weakening of the processes of inner inhibition (the differentiation and delayed response), in irradiated animals aminazine injection, as a rule, caused the disruption of differentiation and of the inactive phase of the delayed reflex.

Hence, the tests carried out on irradiated animals show that under the effect of aminazine a disturbance takes place of the compensatory mechanisms of cortical activity.

Effect of Aminazine, Chloral Hydrate and Nembutal on Situation Reflexes of Dogs Following Extirpation of Frontal Lobes

V.I. Syrenskiy (1961) investigated the effect of aminazine, chloral hydrate and nembutal on situation conditioned reflexes of dogs with extirpated frontal lobes.

Following lobectomy in dogs, together with other disorders there is often observed a pathological increase of motor activity. Some authors are inclined to connect this disorder with the damage to the motor zone of the cerebral cortex (Yu.S. Konorskiy, 1957, et al.); others (Ward, 1948; Turner, 1954) connect it with the damage of subcortical formations. V.I. Syrenskiy (1960) also observed this fact, which prompted the author to attempt an analysis of this phenomenon with the use of the method of situation conditioned reflexes and the administration of certain pharmacological substances.

There is a current opinion that chloral hydrate acts mainly on the cortex of the large hemispheres, nembutal — on the brain stem, and aminazine — on the reticular formation. One would therefore expect that the use of these substances might help in ascertaining, as to which parts of the brain are responsible for the origin of pathological motor activity, observed after a lobectomy.

Investigations were carried out on 3 dogs, in whom the following conditioned reflex activity has been elaborated. In the dog Chernyy, a positive differentiation of food receptacles 1 and 2 was elaborated, i.e., when a metronome of 60 strokes per minute was turned on, the dog jumped on table 1 where it received food from the receptable, and when the metronome sounded 240 strokes per minute, a run was elaborated to receptacle 2.

In the dogs Uragan and Charlie, a positive differentiation was elaborated of the food receptacles to a tone (1000 cps), and metronome 120 strokes per minute, and an inhibition conditioned reflex to a bell.

Following the development and reinforcement of situation conditioned reflexes, a bilateral removal of the pole of frontal lobes was performed. Following lobectomy, the pharmacological substances were used at intervals of 4-5 days, so as to prevent cumulation phenomena. Nembutal was given in a dose of 20 mg per kg weight of the animal, chloral hydrate in a dose of 170-200 mg per kg body weight, and aminazine was injected subcutaneously in a dose of one mg/kg. The experiment was conducted within 1, 24, 48 hours following administration of the medicinal substance. It should be noted that a positive effect from the use of these medicinal substances was observed at various periods. Chloral hydrate acted in the majority of cases as early as within an hour, nembutal – more frequently after 24 hours; aminazine, on the other hand, showed no constancy of action.

In all operated animals, following lobectomy, one observed a pathological rise of motor activity at various periods (on the 2nd, 5th and 7th day). Various manifestations of these motor reactions can be divided into two groups:

1) obsessive changes of position, not connected with conditioned reflex activity: run along the wall, clockwise and counterclockwise;

2) impairment of the normal course of the situation conditioned reflex, manifested in nonsignal runs and jumps on tables and in motor stereotypes. For instance, after standing on the rug the animals did not remain on it but started walking in the direction of the location of the conditioned sound stimulators; after approaching them, it turned around and returned to the rug. This shifting of positions was observed forseveral minutes.

The duration of pathological activity in the dogs varied in the dog Chernyy – 32 days, in Charlie – 43 days, in Urgan – 60 days.

The results of the use of pharmacological substances were as follows. In Uragan – experiment on 25/II 1959 – nembutal was used for the first time during the period when the entire activity of the animal in the experimental room consisted of a run along the walls and nonsignal runs to tables (record of experiment on 24/II 1959). In response to sound conditioned stimuli, an intensification was observed on the first food reaction (movement of the animal to the source of sound). Within 24 hours after the administration of nembutal (record of experiment of 26/II 1959) the running changed to a walking pace; the dog was not moving constantly any longer, but having made several circles or jumps on the tables it would stop (often near the rug), following which it would again start moving about the room.

Nembutal was administered to this dog for the second time, during the period when obsessive movements along the walls and nonsignal runs and jumping on the tables almost ceased.

During the pauses between conditioned signals the animal did not remain on the rug, but began moving in the direction of conditioned stimulators, and back. A positive conditioned reaction was noted to the tone and metronome, but differentiation of tables was impaired at this stage. Within 24 hours after administration of nembutal, the dog began to linger on the rug up to 5 seconds. Besides, having started to the location of sound stimulators, the

Excerpts from the Records of Experiments on Dog Uragan 24/II 1959 (Prior to the Use of Medicinal Substances)

1 Условный раздражитель	2 Латентный период условного рефлекса (сек)	3 Время побежки (сек)	4 Характер условной реакции	5 Время стояния на коврике (сек)	6 Примечание
[7] Метроном 120 (стол 2)	0,5	20,0	[8] Направился к раздражителю, остановился около него и побежал к правому столу (неправильно) направился к условному раздражителю, остановился и двинулся к столу 2	[13] От 0,5—0,8	[9] В паузе непрестанно находится в движении, перемещаясь от коврика к условному раздражителю и обратно и так раз за разом
Метроном 120 (стол 2)	0,4	12,0			
[10] Тон 1000 гц (стол 1)	0,3	14,0	[11] Направился к условному раздражителю, остановился и двинулся к столу 2		
[12] Звонок (тормоз)	0,4	12,0	[11] Направился к условному раздражителю, остановился и двинулся к столу 1		
[10] Тон 1000 гц (стол 1)	0,3	15,0	[11] Направился к условному раздражителю, остановился и двинулся к столу 1		
[7] Метроном 120 (стол 2)	0,5	13,0	[11] Направился к условному раздражителю, остановился и двинулся к столу 1		

(The following day after injection of nembutal, 26/II 1959

[7] Метроном 120 (стол 2)	0,5	8,0	[14] Направился к условному раздражителю и затем побежал к столу 2	От 0,8—2,0	
[10] Тон 1000 гц	0,4	5,0	[14] Направился к условному раздражителю и затем к столу 2		
[7] Метроном 120 (стол 2)	0,3	4,0	[15] Направился к условному раздражителю и сразу к столу 1		[17] Как и прежде, перемещается от коврика к условным раздражителям непрерывно, но уже не бегом, а шагом. В некоторых случаях задерживается на коврике более 1 мин
[12] Звонок (тормоз)	0,4	4,0	[14] Направился к условному раздражителю и затем к столу 2		
[12] Тон 1000 гц стол 1	0,4	5,0	[14] Направился к условному раздражителю и затем к столу 1		
[7] Метроном 120 (стол 2)	0,6	0,3	[16] Направился к условному раздражителю, не доходя до него, бежит к столу 2		

1) Conditioned stimulus; 2) latent period of the conditioned reflex (seconds); 3) duration of run (seconds); 4) character of conditioned reaction; 5) duration of remaining on the rug (seconds); 6) footnote; 7) metronome 120 (table 2); 8) started in the direction of the stimulator, stopped near it and ran to the right table (incorrectly), started toward the conditioned stimulator, stopped, and started toward table 2; 9) during the pause the animal is in constant motion, moving from rug to the conditioned stimulator and back, repeating it several times; 10) tone 1000 cps (table 1); 11) started for the conditioned stimulator, stopped, and started toward table 2; 12) bell (inhibitor); 13) from; 14) started for the conditioned stimulator, and then ran to table 2; 15) started walking toward the conditioned stimulus then at once to table 1; 16) started toward the conditioned stimulus, did not reach it, and ran to table 2; 17) just as before, moves from rug to the conditioned stimulators constantly, but not at a run, walking slowly. In some cases stops on rug over a minute.

Excerpt from the Record of 1/III 1959 on the Day of Chloral Hydrate Administration

[1] Метроном 120 (стол 2)	0,2	8,0	[2] Направился к условному раздражителю и затем к столу 1	[3] От 0,4—0,8	[4] Перемещается от коврика к условному раздражителю и обратно
[5] Тон 1000 гц (стол 1)	0,3	3,0	[6] Направился к условному раздражителю, а от него к столу 1		
[1] Метроном 120 (стол 2)	0,6	4,0	[2] Направился к условному раздражителю, а затем к столу 2		
[7] Звонок	0,6	8,0	[8] Бежит к столу 2		
[1] Метроном 120	0,5	10,0	[2] Направился к условному раздражителю, а затем к столу 1		
[4] Тон 1000 гц	0,4	5,0	[8] Бежит к столу 1		

1) Metronome 120 (table 2); 2) started toward the conditioned stimulator, and then to table 1; 3) from 0.4 to 0.8; 4) moves from rug to the conditioned stimulator, and back; 5) tone 1000 cps (table 1); 6) started toward the conditioned stimulators, and from there to table 1; 7) bell; 8) runs to table 2.

dog did not reach them and turned back. The differentiation of tables improved: whereas prior to administration of nembutal, the number of errors comprised 75%, after nembutal administration the errors dropped to 20%. The inhibition differentiation was impaired, nevertheless.

The use of chloral hydrate did not result in the restoration of conditioned reflex activity during the pauses between sound stimuli. The differentiation of tables improved slightly (the number of errors decreased from 75% to 50%). Differentiation inhibition remained impaired (Cf. record of the experiment on 1/III 1959).

Hence, both pharmacological substances contributed to the restoration of positive conditioned reflexes to sound stimuli. Restoration of inhibition reflexes proceeded less successfully. Besides, nembutal, as contrasted with chloral hydrate, possessed the property of interrupting and cutting off the pathological motor reactions.

Aminazine turned out to be close in its effect to nembutal, but it differs from it in the sense that in a number of instances it proved to be more effective.

We cite a record of an experiment (of 9/III 1959) carried out on the dog Uragan after a bilateral extirpation of frontal lobes, followed by administration of aminazine.

Excerpt from the Record of 9/III 1959. Dog Uragan (Aminazine Injected in a Dose of One mg/ /kg of Body Weight)

[1] Условный раздражитель	[2] Латентный период условного рефлекса (сек)	[3] Время пробежки (сек)	[4] Характер условной реакции	[5] Время стояния на коврике (сек)	[6] Примечание
[7] Метроном 120 (стол 2)	0,5	3,0	[8] Направляется к условному раздражителю, затем к столу 2	[9] От 1,0—2,0	
[11] Тон 1000 гц (стол 1)	0,4	2,0	[12] Направился к условному раздражителю, затем к столу 1 (правильно)		[10] Ходит по комнате от коврика к условному раздражителю и обратно. Вставая на коврик, задерживается на нем
[13] Звонок (тормоз)	—	—	[14] Ходит по комнате		
[11] Тон 1000 гц (стол 1)	0,4	2,4	[8] Направился к условному раздражителю, затем к столу 2		
[7] Метроном 120 (стол 2)	0,5	2,0	[8] Направился к условному раздражителю, затем к столу 2		
[11] Тон 1000 гц (стол 1)	0,3	2,2	[8] Направился к условному раздражителю, затем к столу 1		

1) Conditioned stimulus; 2) latent period of the conditioned reflex (seconds); 3) duration of a run (seconds); 4) character of the conditioned reaction; 5) duration of remaining on the rug (seconds); 6) footnote; 7) metronome 120 (table 2); 8) starts in the direction of the conditioned stimulator, then back to table 2; 9) from 1.0 to 2.0; 10) walks in the room from the rug to the con-

ditioned stimulator, and back. Standing on the rug, lingers on it for a while; 11) tone 1000 cps (table 1); 12) started toward the conditioned stimulator, and then – to table 2 (correctly); 13) bell (inhibition); 14) walks about the room.

The experiments showed that aminazine contributed to the normalization of pathological motor reactions in every case, nembutal – in 3 out of 4 cases, chloral hydrate – in none. All these substances contributed to a certain extent to the restoration of positive conditioned reflexes to sound stimuli; restoration of inhibition reflexes was observed only in 57% of cases.

Inasmuch as it has been established that soporific pharmacological substances contributed to the restoration of conditioned motor reflexes to sound stimuli, one may assume that the cortical and subcortical structures are involved in the pathological activity. In view of the fact that chloral hydrate, in contrast to nembutal and aminazine, is unable to interrupt the pathological motor reactions, the hyperactivity which originated following lobectomy is apparently realized at the expense of the stem part of the brain.

Effect of Aminazine on Situation Conditioned Reflexes of Dogs Following Extirpation of the New Cerebellum

Morphological and physiological investigations have now established definite anatomical and functional ties between the cerebellum and reticular formation. An opinion has been advanced that in the regulation of functions of the reticular formation a leading role belongs to the cerebellum, which through its inhibiting and stimulating mechanisms changes the function of reticular formation in the descending as well as ascending direction (Broadall, 1960; Morussi, 1957). In order to elicit the functional interrelations of the neocerebellum with the reticular formation, we studied the effect of small doses of aminazine on the complex situation conditioned reflexes, prior and after extirpation of the neocerebellum.

Experiments were carried out on 4 dogs: Bodryy, Dzhek, Tarzan and Shmel'ka. Spatial situation conditioned reflexes were elaborated in the experimental animals: to light (lamp of 200 watts) and sound stimuli, with a run to tables 1 and 2.

The effect of aminazine was studied, prior and after the operation. Aminazine was administered in doses of 0.25; 0.5; 1.0 mg/ /kg of body weight, in the form of 2.5% solution, subcutaneously, within 60 minutes prior to the experiment.

The disturbance of voluntary movements and situation conditioned reflexes, originating after extirpation of the neocerebellum, are described in detail in Chapter 6 "Certain Problems of Structural Organization of Situation Conditioned Reflexes."

As soon as the compensation of observed disturbances has been established, we started testing the aminazine effect in above indicated doses.

The experiments showed that a small dose of 0.25 mg/kg induced in dogs a marked decomposation of voluntary movements; in addition, there appeared ataxia, atony, rigidity of the muscles of anterior paws. The animals stumbled during their walk, often fell, and all their movements became retarded. The rate of realization of all motor reactions decreased.

It is to be remembered that in norm this dose of aminazine (0.25 mg/kg) did not cause any appreciable disturbances. It is of interest that the above dose has led to a marked decompensation of conditioned reflex activity. In dogs, on the 5th-12th day the conditioned reflex to light disappeared; it became restored later, but with a faulty motor reaction (a run was made not the feeding receptacle 1, but to feed 2). There was also observed an impairment of the positive differentiation of sound signals. The motor reaction to conditioned sound stimuli, which was elaborated as a run to the feeding receptacle 1, was realized by the dogs to the feeding trough 2, and vice versa. For instance, Dzhek and Tarzan responded to the light and sound signal, and Shmelek to the left metronome signal by running to trough 2 (instead of 1), and to the sound of a bell, or the left metronome Dzhek and Tarzan approached trough 1 (instead of 2). Besides, an intensification was observed of the first alimentary reaction to every positive signal and a disruption of differentiation. The graph (Fig. 17) shows the disruption of inhibition differentiation following administration of various doses of aminazine.

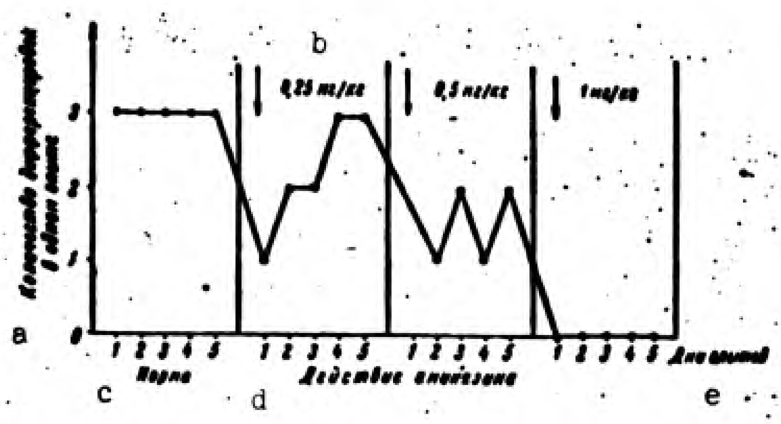


Fig. 17. Disruption of differentiations following administration of aminazine to the dog Tarzan. a) Number of differentiations in one experiment; b) 0.25 mg/kg; c) norm; d) effect of aminazine; e) days of experiments.

When inhibition signals were turned on, the animals began leaving the rug and jumping on the tables.

Large aminazine doses (0.5 and 1 mg/kg) caused a more pronounced manifestation of the above phenomena.

Hence, administration of aminazine in doses of 0.25; 0.5 and

1 mg/kg to dogs with an extirpated neocerebellum, again induce during the compensation stage of cortical activity marked disturbances of higher nervous activity, and lead to the appearance of certain symptoms, which are usually observed during an acute postoperative period. The changes in situation conditioned reflexes and motor reactions lasted no less than 10-12 days after each injection (in norm 3-5 days). With the increase of dose, the disturbances of higher nervous activity became more pronounced.

Effect of Aminazine on Situation Conditioned Reflexes of Dogs Following an Operation of Separation Cortical Analyzers

M.M. Khananashvili (1957, 1960) investigated the effect of aminazine on the complex conditioned reflex activity of animals following an operation of separation of cortical analyzers (Fig. 18). As a result of the operation, the associative ties between the cortical projection zones became disrupted, but their interaction was preserved via subcortical structures. Such animals may serve as a model for the study of the role of subcortical formations in the work of the cortex of the large hemispheres and, hence, also for the investigation of the mechanism of action of pharmacological substances on the higher nervous activity of the brain.

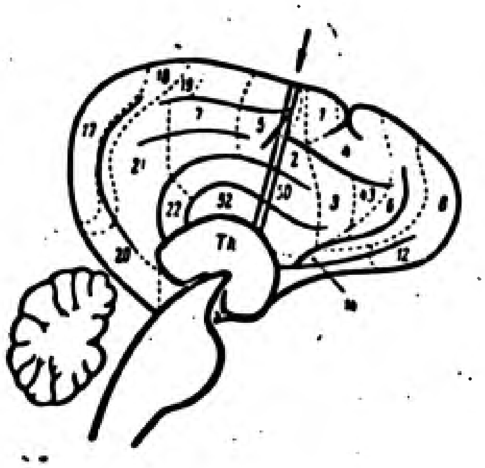


Fig. 18. Diagram of the operation of a complete transverse separation of the anterior and posterior zones of the cortex of the large hemispheres.

The author showed earlier that following the above indicated operation, the interaction of separated analyzers does not disappear, and that the complex motor conditioned reflexes to light stimuli are retained (M.M. Khananashvili, 1958).

The use of aminazine in a 0.5 mg/kg dose induce in the animals substantial changes in conditioned reflex activity, close in their nature to changes observed in normal animals after an injection of this preparation in a 1.0 mg/kg dose.

Experiments carried out on normal animals showed that aminazine in a dose of 1.0 mg/kg substantially impairs their conditioned reflex activity. At first, its effect is manifested in a lengthening of the latent period of conditioned reflexes, an increase in the time of running to the feeding trough and in a weakening of the orientation reactions during the intervals between conditioned stimuli. The observed phenomena point to the inertness of the excitation process, which is also attested by the fact that the animals remain for some time at the trough after they got through eating. The structure of the conditioned reflex remains intact under these conditions, and the entire conditioned reflex activity proceeds at a lower functional level.

With the increase of aminazine dose, an impairment is observed of the very structure of the conditioned reflex - a reflex representing a complex chain of consecutive motor reactions.

The impairment of the functional structure of the conditioned reflex starts with an intensification of the first alimentary reaction (when the initial movement of the animal is directed not straight to the location of the reinforcement - the feeding trough - but to the source of conditioned stimulation). Subsequently, there is a complete dropping out of the concluding act in the conditioned reflex chain: the animal does not go to the feed trough, but remains under the stand with the conditioned stimulator, or does not move at all from the spot where the animal is usually standing during the intervals between stimulations.

The neural mechanism of observed changes consists of a gradual decrease of excitability of the neural structures at the level of the cortex of the large hemispheres, since it can be considered as an established fact that the differentiation of visual stimuli (various figures) and the complex motor reaction elaborated in the animals are realized with the invariable participation of corresponding cortical analyzers. However, this concept of the mechanism of aminazine action does not yet answer the question, whether the changes of higher nervous activity are the result of the direct effect of a given preparation on the cortical cells, or of the reduction of cortical excitability produced by the initial inhibiting effect of aminazine on the subcortical activating system.

Analysis of the aminazine effect on the neural processes of the higher parts of the brain, carried out by P.S. Kupalov (1958) on the basis of experimental data which were obtained by his associates, boils down to the following. Under the effect of aminazine in small doses, the temporary associations, as such, are not impaired, as pointed out in the works of M.M. Khananashvili (1957), L.N. Gavrilova (1958), I.A. Lapina (1958), N.A. Kostenetskaya (1958), N.N. Kudryavtseva (1958), V.D. Volkova (1960), O.N. Voyevodina (1961) and N.P. Murav'yeva (1960). Aminazine affects neural process of the diffuse nature, and especially the processes which control the general functional state of the cerebral cortex; aminazine impairs the conditioned reflex control of the cortical tonus and leads to the reduction of the value of secretory conditions of the reflexes (N.A. Kostenetskaya, 1958; N.P. Murav'yeva, 1960; N. N. Kudryavtseva, 1958; G.N. Tsobkall and V.K. Bolondinskiy, 1960).

In the case of unilateral conditioned reflexes, the use of aminazine reduces irradiation of the excitation process (I.A. Lapina, 1958). Hence, there is reason to assume that aminazine acts on the diffuse, activating mechanism, in which the most important role belongs to the reticular system. This fact has been corroborated by electrophysiological investigations of many authors (A.I. Shumilina, 1956; V.G. Agafonov, 1956; A.V. Val'dman et al., 1960; P.K. Anokhin, 1958b; R.Yu. Il'yuchenok and M.D. Mashkovskiy, 1961; F.B. Bredli, 1962).

In our investigations the animals with separated cortical analyzers proved to be more sensitive to aminazine, than normal dogs.

It was established previously by M.M. Khananashvili that the interaction of cortical analyzers, following disruption of the associative connections between them, can be accomplished via subcortical pathways and subcortical nuclei. This mechanism of cerebral activity, being subordinated in normal animals, assumes the leading role after the disruption of the intracortical mechanism of neural integration.

The use of these animals for the investigation of the effect of aminazine on higher nervous activity makes it possible to elicit the different sensitivity to this preparation of cortical and subcortical mechanisms of integration of neural processes, and to form an idea concerning the greater sensitivity of subcortical formation to this preparation. At the same time, the available facts permit the assumption that aminazine acts directly also on the cerebral cortex (D.A. Biryukov, 1958; L.N. Gavrilova, 1958; N.A. Kostendtskaya, 1958; A.A. Antonova, 1958; K.V. Stroykova, 1959; V.D. Volkova, 1960; N.P. Murav'yeva, 1960; G.N. Tsobkallo and V.K. Bolondinskiy, 1960; Malmejac and Plane, 1955 et al.

Disturbances of cortical functions under the effect of aminazine are most clearly elicited in dogs with a weakened nervous system. Experiments conducted on animals which underwent a brain operation or were subjected to the action of X-ray, showed that an injection of aminazine leads to a marked decomposition of higher nervous activity; the animals manifest disorders usually observed during the acute phase following intervention – surgical or irradiation. These disorders, as well as the inhibition of motor reactions were caused by small doses of aminazine (0.1-0.2 mg/kg), which had no such effect on normal animals.

In favor of the "cortical" effect of aminazine one may cite the work of B.S. Bamdas and coauthors (1956) who detected reversible changes in cortical cells following administration of aminazine; also the works of I.A. Fedorov and S.E. Shiol' (1956) which established the fact that a greater accumulation of aminazine takes place in the cortex than in other parts of the brain. There are literary data pointing to the effect of aminazine on the spinal cord, with approximately the same doses (1-2 mg/kg) which act on the subcortical and formations and cerebral cortex of the animals (S. Ya. Arbuzov, P.K. D'yachenko, Yu.I. Shanin, 1955). Hence, aminazine affects various parts of the central nervous system; however, disturbances elicited with the method of situation conditioned reflexes attest to the fact that aminazine exerts a greater effect on subcortical formations (reticular formation) of the brain stem.

CONCLUSION

In comparing the above described disturbances of conditioned reflex motor activity under the effect of various pharmacological preparations, certain general rules can be noted in the effect of these substances on situation conditioned reflexes, without dwelling on the peculiarities cited in the course of description of the experimental data.

In the majority of cases, upon administration to dogs of minimal doses of substances possessing an inhibiting cortical effect (amizyl, amedine, aprophene, etc.), changes are observed of motor conditioned reflexes which develop in a definite consecutive order.

1. The voluntary food-searching motor reactions undergo a change, or disappear entirely.

2. The active inner inhibition weakens; the differentiation of conditioned sound or visual stimuli, which are identical in intensity but are located in different places, is impaired and so is also the differentiation of tables in regard to the site of food reinforcement, etc.

3. One of the first trigger components of the complex motor reaction drops out (the dog does not occupy the initial location in the experimental room – does not stand on the rug or on a definite square).

4. The latent periods of conditioned reflexes are lengthened, up to a complete disappearance of the response motor reaction to the effect of the stimulator. In the first place, the motor reaction drops out to weak conditioned stimuli, or to stimuli connected with the differentiated object ("associated pair").

5. At the height of intoxication, there originate as a rule phenomena of diffuse cortical inhibition with phase states (equalizing, paradoxical and ultraparadoxical).

Preparations which belong to various groups (analgesic, adrenergic, etc.) but exert mainly an effect on the subcortical formations in minimally active doses, do not change the voluntary motor reactions, have no effect on the differential inhibition and do not impair the structure of the conditioned reflex, although the entire conditioned reflex activity proceeds at a lower functional level. Simultaneously with a reduction of the cortical tonus, there is a clearly manifested disturbance of unconditioned reflex activity (the general motor activity, shaking-off reflex, alimentary reflex, etc.). With an increase of the administered dose, there appear disturbances connected with the effect of the preparation on the cerebral cortex: the dogs do not carry out the previously elaborated voluntary motor reactions, often do not take up their position on the rug, there is a weakening of differentiation inhibition, etc.

Certain substances which block the peripheral effector link of the conditioned reflex arch, cause disturbances in the behavior of animals only when administered in very large doses. For instance, the cholinolytic preparation – lachesine – exerts a peripheral effect on the salivary glands, by inhibiting unconditioned salivation in the dose of 0.001-0.005 mg/kg, and impairing the situation conditioned reflexes in doses 100-fold larger (0.1-0.5 mg/kg). Hence, central disorders originate only, upon complete elimination of the effector link (injection of lachesine causes a marked dryness of mucous membranes and an impairment of vision); these disorders have certain unique characteristics which differ from the above described in that the conditioned reflexes, as such, remain intact: the dog moves toward the table in response to a signal, but does not jump on the table; if the feeding trough is taken off the table, the dog takes the meat out of the trough and throws it on the floor, but does not eat it. When these peripheral symptoms are eliminated with the use of small quantities of a cholinomimetic substance (pilocarpine of carbocholine) which causes no change in the conditioned activity of the dogs, the higher nervous activity is immediately restored to norm (A.T. Selivanova, 1958). This fact once more attests to the fact that the changes in situation conditioned reflexes, following administration of these substances, depends on their peripheral action.

It should be pointed out that, other conditions being equal, stronger and more prolonged behavior disturbances are observed in dogs with a weak type of nervous system, than in animals of a strong type.

Manu-script Page No.	[Footnote]
138	I.P. Pavlov. Polnoye sobraniye sochineniy [I.P. Pavlov. Complete Works], 1951, Vol. 2, p. 318.

Chapter 5

EFFECT OF VARIOUS DOSES OF ROENTGEN RAYS ON THE COURSE OF SITUATION CONDITIONED REFLEXES FOLLOWING SINGLE AND REPEATED TOTAL IRRADIATIONS

In connection with the wide use of isotopes in atomic energy and industry, agriculture and medical practice, the physiologists are facing an important task of the thorough investigation of the effect of ionizing radiation on the living organism, and in particular on the higher parts of the central nervous system of man and animals.

In current investigations devoted to the effect of ionizing radiation on the activity of higher sections of the brain, the functional state of the latter was investigated by means of various methods: the classic method of secretory conditioned reflexes of I.P. Pavlov, the method of motor conditioned reflexes (on small animals – rabbits, rats, mice, birds), the method of electroencephalography, and by various zoopsychological methods. As a result of conducted studies, it has been established that the occurring changes of higher nervous activity depended: on the total irradiation dose, on the irradiation method, on the functional state of the cerebral cortex and on the type of higher nervous activity (M.I. Nemenov, 1928, 1929, 1932, 1938, 1944, 1950; R. Lyman, P.S. Kupalov and R. Scholz, 1933; P.S. Kupalov, 1959; P.S. Kupalov and A.M. Ushakova, 1931; M.I. Nemenov and V.V. Yakovleva, 1940; Ye.I. Bakin, 1946; P.I. Lomonos, 1953, 1955, 1956, 1957; N.N. Livshits, 1953, 1954, 1955, 196d; M.N. Livanov, 1944, 1956, 1957, 1962; M.N. Livanov et al., 1935, 1958, 1959; L.I. Kotlyarevskiy, L.S. Gorsheleva and L.Ye. Khozak, 1956, 1958; P.D. Gorizontov, 1954, 1955, 1959; Yu.G. Grigor'yev, 1954, 1956, 1958; L.A. Orbeli, 1955, 1956; A.V. Lebedinskiy, 1955, 1957; A.V. Lebedinskiy et al., 1958, 1959, 1960; F.P. Mayorov et al., 1949; N.Ya. Lipatova et al., 1957; M.N. Pobedinskiy, 1954; I.A. Piontkovskiy et al., 1957; L.Ye Khozak, 1958; D.A. Biryukov, 1957; Yu.G. Grigor'yev, 1958; V. Ye. Miklashevskiy, 1959a and b; R.S. Zlatin, 1959; Di Mascio et al., 1956; Leary and Ruch, 1954, 1955, and many others.

Despite the fact that there is a large number of works devoted to the study of the effect of ionizing radiation on cerebral activity, there still remains the little investigated problem concerning the effect of this type of energy on the most complex forms of the behavior of animals.

Starting in 1955 and continuing at the present time, investigations are conducted in the Physiological Department im. I.P. Pavlov (Institute of Experimental Medicine, AMS USSR) by O.N. Voyevodina and I.V. Malyukova, devoted to the study of the effect of various X-ray doses on situation conditioned reflexes of dogs.

In the present work we are citing investigation data of experiments conducted on 14 dogs. In all dogs, prior to irradiation, one elaborated and reinforced various complex positive and inhibiting motor conditioned reflexes, with a run to one or two tables. In addition, prior to irradiation, one tested in all animals the mobility of their nervous processes, by substituting the stereotype of a positive stimulus the differentiation stimulus, and conversely – an inhibition stimulus with a positive one, and one also tested the force of an inhibition process by lengthening the action time of the differentiation stimulus 6-12-fold (in norm 5 seconds). Prior to irradiation, these tests did not disturb the normal course of conditioned reflex motor activity. Neither were any changes observed in the course of conditioned reflex activity in dogs, when control tests were conducted with simulated irradiation, i.e., when the dogs were brought into the X-ray room, placed in a wooden box, and the noise of an X-ray apparatus was switched on (O.N. Voyevodina, 1956, 1960).

Following the afore-mentioned experiments, every dog was subjected to total X-ray irradiation under the following conditions: with two RUM-3 apparatus by means of crossed fields, at the voltage of 180 kv, 15 ma current, with one or two filters 0.5 mm Cu, or 0.5 mm Cu + 1 mm Al, at 80 to 100 cm focal distance. Irradiation conditions are shown in Table 11, indicating that various dogs received different X-ray doses which, however, did not exceed 300 r at a single irradiation. Repeated irradiations were carried out during the period when following a previous irradiation the conditioned reflex activity became fully restored. In order to ascertain the cumulative or compensatory functions of the cerebral cortex, repeated irradiations were carried out at various intervals, following the initial X-ray irradiation.

Prior and after irradiation, the leucocyte count in the peripheral blood was regularly performed and the changes in body weight of the animals were constantly checked.

TABLE 11

Conditions of X-ray Irradiation of Dogs

[1] Клички собак	[2] Разовая доза (в р)	[3] Суммарная доза (в р)	[4] Ритм облучения
[5] Ядинка	10	320	[6] За восемь месяцев
[7] Пальма	300	300	[8] Однократно
[9] Рэни	100	300	[10] Через 3 мес. и 20 дней после первого облучения и через 6 мес. и 21 день после второго облучения
[11] Бой	100	100	[8] Однократно
[12] Джек	10	100	[13] Три раза в неделю
[14] Барсик	10	70	» » »
[15] Черный	10	70	» » »
[16] Ядинка	10	40	[17] Ежедневно (через 5 лет после первого облучения в дозе 320 р)
[18] Альма	10	30	[19] Ежедневно
[20] Толстяк	8	8	[8] Однократно
[21] Шарик	1	28	[22] Ежедневно (через год после облучения в дозе 8 р)
[7] Пальма	1	19	[2] Ежедневно (через 5 лет после облучения в дозе 300 р)
[24a] Аккорд	1	15	[1] Ежедневно
[20] Толстяк	1	15	[2] Ежедневно (через год после облучения в дозе 8 р)
[23] Джой	1	12	[19] Ежедневно
[24] Солтан	1	12	[22] Ежедневно (через год после облучения в дозе 8 р)
[24a] Аккорд	1	12	[25] Ежедневно (через 37 дней после облучения в дозе 15 р)
[21] Шарик	1	8	[1] Ежедневно
[24] Солтан	1	8	»
[23] Джой	1	7	[25] Ежедневно (через 47 дней после облучения в дозе 12 р)

1) Dog's name; 2) single dose (in r); 3) summary dose (in r); 4) irradiation rhythm; 5) Yadinka; 6) during eight months; 7) Pal'ma; 8) once; 9) Reni; 10) within 3 months and 20 days after the first irradiation, and within 6 months and 21 days after the second irradiation; 11) Boy; 12) Dzhek; 13) thrice a week; 14) Barsik; 15) Chernyy; 16) Yadinka; 17) daily (within 5 years following first irradiation with a dose of 320 r); 18) Al'ma; 19) daily; 20) Tolstyak; 21) Sharik; 22) daily (within a year following irradiation with a dose of 8 r); 23) Joy; 24) Soltan; 24a) Akkord; 25) daily (within 37 days following irradiation with a dose of 15 r).

EFFECT OF SINGLE AND REPEATED TOTAL IRRADIATIONS OF DOGS WITH DOSES OF 300r-100r ON THE COURSE OF SITUATION CONDITIONED REFLEXES

On the basis of experiments conducted by O.N. Voyevodina with single total irradiation of dogs in 300-100 *r* doses, the following has been ascertained. In all animals, in experiments carried out within 30 minutes following irradiation, one observed an impairment of previously elaborated conditioned reflex motor activity: after eating the first feed, the dogs began a disoriented run about the room, jumped repeatedly on tables, and did not once stand on the rug during the entire experiment. Blood samples obtained from the animals within 3-5 minutes after the experiments (or within 43-45 minutes after irradiation) showed an increased amount of leucocytes (Tables 12, 13, 14) in the peripheral blood.

On subsequent days the behavior of the dogs underwent a change, depending on irradiation dose. For instance, in the dog Pal'ma (300 *r*), of a weak type of higher nervous activity, as early as on the second day following irradiation one observed an inhibition and rigidity of motor reactions. Following the first reinforced feedings (on tables 1 and 2), the dog walked slowly in the experimental room, but did not stand on the rug. When the positive conditioned stimuli were turned on, the dog showed no orientation reaction (the turn of the head in the direction of the conditioned stimulator) or a conditioned motor reflex.

In experiments on the 6th and 9th days after irradiation, the conditioned reflex in Pal'ma was observed only in response to the first application of the conditioned stimulator. In these experiments, circus motor reactions appeared for the first time: following the first food reinforcement, the dog jumped off the table and started to perform circular movements in the middle of the room, walking around the rug or the water bowl. During the experiment the dog manifested an increased thirst.

During the next 20 experimental days the dog carried out only the first conditioned reflex reaction, whereas in response to subsequent positive stimuli it remained standing or started to walk to the table which did not correspond to the signal value of the conditioned stimulus (i.e., a faulty differentiation of the tables was observed), or the dog came near the door of the experimental room, lay down, and did not react to conditioned stimulation signals.

A particularly marked disturbance of synthetic activity of the cerebral cortex was manifested in Pal'ma on the 21st day following irradiation, when the number of leucocytes in the peripheral blood dropped 74.9%, and the body weight of the animal decreased by 4.5%, i.e., when the radiation sickness reached its maximum development. On that day the dog refused even the first food reinforcements, and during the entire experiment did not react to the signals of positive conditioned stimuli; when the differentiation stimulator was turned on, the dog jumped on the table instead of remaining on the rug, i.e., ultraparadoxical associations originated in the animal in the process of conditioned reflex motor activity. This state of higher nervous activity was

TABLE 12

Number of Leucocytes in the Peripheral Blood and the Weight of Dog Pal'ma, Prior and After Total Single Irradiation with a 300 *r* Dose

1 № опыта	2 Дата 1955 г.	3 Вес (в кг)	4 Количество лейкоцитов в 1 мм³ крови из краевой вены уха
61	5/IV	11,05	10 250
63	7/IV	10,95	10 450
64	16/IV	11,0	11 000
65	24/IV	10,95	12 250
66	25/IV	11,0	11 750
67	26/IV	11,5	12 600

27 April 1955 the dog was subjected to total irradiation with a 300 *r* dose

68	27/IV	11,25	17 750
69	28/IV	11,0	14 550
70	29/IV	11,15	8 100
71	30/IV	11,05	9 350
72	3/V	10,15	6 900
73	4/V	10,0	6 500
74	6/V	10,0	6 850
75	7/V	10,35	6 000
76	10/V	10,5	6 200
77	12/V	10,65	4 350
78	14/V	10,5	3 600
79	16/V	10,5	2 950
80	1/VI	10,75	7 000
82	4/VI	10,8	6 000
83	7/VI	11,0	6 600
84	9/VI	11,2	6 100
85	11/VI	11,3	7 950
86	13/VI	11,2	5 900
87	17/VI	11,3	5 950
88	20/VI	11,25	6 100
89	24/VI	11,4	7 250
90	27/VI	11,6	7 700
91	30/VI	11,2	6 300
92	4/VII	11,5	6 300
93	6/VII	11,4	6 500
94	11/VII	11,5	6 750
95	14/VII	11,85	8 550
96	21/VII	11,2	6 300
97	25/VII	11,35	6 750
98	27/VII	12,7	7 600

Following the summer rest

99	3/IX	11,9	7 900
102	6/IX	11,85	8 050
104	10/IX	12,0	8 250
105	13/IX	11,6	7 000
107	17/IX	12,0	6 050
108	19/IX	11,95	6 650
109	20/IX	12,1	7 000
112	23/IX	12,1	7 250
114	26/IX	12,0	7 000
115	28/IX	12,1	7 650
116	4/X	12,0	7 500
117	7/X	12,0	5 850
120	18/X	11,9	6 500
123	19/X	12,0	7 250
127	29/X	12,0	8 800
130	4/XI	11,5	6 050
132	12/XI	11,0	7 050
136	19/XI	11,1	8 300

1) Experiment No.; 2) date, year 1955; 3) weight (in kg); 4) number of leucocytes in one mm^3 of blood from a marginal aural vein.

TABLE 13

Number of Leucocytes in the Peripheral Blood and the Weight of Dog Reni, Prior and After Total Irradiation with a 100 *r* Dose

1 № опыта	2 Дата 1955 г.	3 Вес (в кг)	Количество лейкоцитов в 1 мм³ крови из краевой вены уха 4
631	9/IV	14,55	14 850
632	12/IV	14,65	12 250
633	14/IV	14,7	10 550
634	16/IV	14,9	15 750
635	23/IV	15,0	15 850
636	25/IV	14,75	15 850
637	26/IV	14,85	13 450
639	4/V	15,150	15 600
640	1/VI	16,5	14 200
641	2/VI	16,4	14 050
642	3/VI	16,5	14 050
644	6/VI	16,4	13 800

7 June the dog was subjected to total irradiation with a 100 *r* dose

645	7/VI	16,35	17 750
646	8/VI	16,0	12 650
647	9/VI	15,4	6 700
648	11/VI	15,2	9 150
649	13/VI	14,8	6 900
650	17/VI	15,3	7 050
651	20/VI	15,2	6 900
652	24/VI	15,11	7 850
653	27/VI	14,6	8 750
654	30/VI	14,8	7 250
655	4/VII	14,5	9 300
656	5/VII	14,6	9 500
660	25/VII	14,3	9 250
663	29/VII	14,5	9 300

Following a summer rest

665	3/IX	15,1	12 300
668	5/IX	15,2	12 350
671	10/IX	15,3	12 000
672	13/IX	15,5	10 600
676	16/IX	15,1	9 750
678	20/IX	15,0	9 900
680	22/IX	14,95	9 900
681	23/IX	15,1	10 050
682	24/IX	15,0	10 150
683	26/IX	14,9	10 900

27 September the dog was subjected to a second total irradiation with a 100 *r* dose

684	27/IX	14,85	11 100
685	28/IX	15,0	8 250
686	29/IX	15,0	6 800

687	30/IX	14,95	11 050
689	4/X	15,1	9 750
691	7/X	15,1	7 200
695	13/X	15,0	8 050
698	19/X	15,1	7 000
703	29/X	15,1	9 000
706	4/XI	14,9	6 750
708	12/XI	15,1	9 500
712	19/XI	14,95	10 000
716	1/XII	15,1	9 350
717	6/XII	14,8	7 500
718	15/XII	15,0	7 950
721	25/XII	13,85	7 550
723	27/XII	15,0	8 000

The year 1956

727	9/I	14,0	10 000
731	19/I	15,0	9 750
733	23/I	14,35	8 850
735	26/I	14,4	13 000
737	7/II	14,6	12 550
739	13/II	14,25	9 150
744	22/II	14,2	9 250
752	12/III	14,5	10 250
754	14/III	14,6	10 800

16 March the dog was subjected to the third total irradiation with a 100 r dose

755	16/III	14,5	10 750
756	17/III	14,3	9 200
757	19/III	14,3	7 500
760	22/III	14,6	7 150
766	29/III	14,5	7 150
767	30/III	14,6	7 900
772	5/IV	14,75	7 250
777	13/IV	15,0	9 500
781	19/IV	15,5	9 000
785	5/V	15,4	9 750
786	8/V	15,2	10 800
787	14/V	15,0	9 900
789	17/V	15,0	10 400
796	26/V	15,2	10 750
807	25/VI	15,5	12 300
813	5/VII	15,5	12 250
814	7/VII	15,65	11 570
815	10/VII	15,7	10 150

The year 1957

822	5/II	15,7	9 250
823	8/II	15,4	7 750
824	12/II	15,2	7 250
...	...	...	...
829	11/III	15,3	8 150
840	22/III	15,2	8 750
845	30/III	15,3	10 250
853	9/IV	15,3	9 150
877	7/V	15,5	9 050
880	10/V	15,4	9 750
894	8/VI	15,5	9 050
896	11/VI	15,3	10 500
900	17/VI	15,4	10 050
921	15/VII	15,35	8 050
930	12/IX	15,05	7 750
932	13/IX	15,0	7 750
933	15/IX	15,0	10 750

*The delayed reflex became restored on the 91st day following irradiation.

1) Experiment No.; 2) date; 3) weight (in kg); 4) number of leucocytes in 1 mm^3 from a marginal aural vein.

TABLE 14

Number of Leucocytes in the Peripheral Blood and the Weight of Dog Boy Prior and After Total Irradiation with a 100 *r* Dose

1 № опыта	2 Дата 1956 г.	3 Вес (в кг)	4 Количество лейкоцитов в 1 мм³ крови из краевой вены уха
88	21/III	24,5	10 500
89	23/III	24,7	11 500
93	28/III	24,5	11 750
97	3/IV	24,6	12 000
118	20/IV	24,5	12 400
119	23/IV	24,6	11 250
24 April the dog was subjected to irradiation with a 100 *r* dose			
120	24/IV	24,4	16 750
121	25/IV	24,6	13 180
122	26/IV	24,5	9 200
124	28/IV	23,65	9 100
125	3/V	23,5	6 900
127	5/V	23,3	8 450
128	8/V	22,8	6 250
129	14/V	24,5	5 950
130	15/V	24,0	7 500
131	17/V	23,8	7 150
133	19/V	23,9	9 250
136	24/V	24,0	9 750
138	28/V	24,0	10 750
141	1/VI	24,4	11 000
142	4/VI	24,5	11 750
144	12/VI	24,5	9 750
145	14/VI	24,5	10 500
147	18/VI	24,4	10 050
148	19/VI	24,5	11 750
149	26/VI	24,4	10 150
150	29/VI	24,6	11 250
151	5/VII	25,0	12 250

1) Experiment No.; 2) date, 1956; 3) weight (in kg); 4) number of leucocytes in one mm^3 of blood from a marginal aural vein.

observed during the first seven months. During the following 5 months, one observed only in some tests a normal conditioned reflex activity of the animal; in the rest, the latent period of conditioned reflexes was always longer, and a disturbance was often observed of a positive differentiation of the tables. Thus, in the dog Pal'ma, which was subjected to a total single irradiation with a 300 *r* dose during a 12 month period, one observed following irradiation distinct changes in higher nervous activity in the form of partial or complete disappearance of conditioned motor reflexes, disruption of inhibition differentiations, impairment of positive differentiation of tables, the development of phasic states in the cerebral cortex and the decrease in the general work capacity of the animal (O.N. Voyevodina, 1956).

In contrast to Pal'ma, the dog Reni, also of a weak type of higher neural activity, was subjected to X-ray irradiation with a 100 *r* dose only. Within 30 minutes following irradiation, the dog manifested experimentally certain changes in the course of situation conditioned reflexes, which were similar to those observed in the dog Pal'ma. On the 5th and 14th day following irradiation, the spatial conditioned reflex became disturbed in Reni (the dog di not take up its position on the rug).

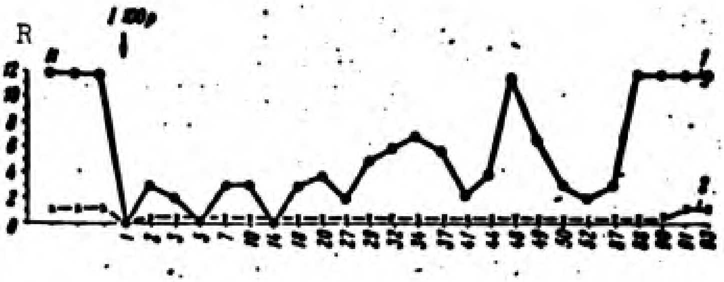


Fig. 19. Impairment of conditioned reflex activity of the dog Reni (R) subjected to a single total irradiation with a 100 *r* dose. On the abscissa axis the numbers indicate days up to (*N*), during (arrow-100 *r*) and after irradiation; on the ordinate axis: 1) the number of retained positive; 2) inhibition stimuli employed in the experiment.

In subsequent experiments, as shown clearly in Fig. 19, the conditioned reflex activity of Reni was considerably more disturbed: the conditioned reflexes to positive stimuli became impaired, and a regular disruption was observed of the delayed-response conditioned reflex, formed on the light stimulus, which was retarded by 120 seconds. In analogy with the dog Pal'ma, there were also observed in Reni, following irradiation, an increased thirst, easy fatigue and the appearance of circus movements in the intervals between the switching on of the conditioned stimuli.

A comparison of the results obtained on Pal'ma and Reni shows that there was no complete parallelism either in the extent of changes of conditioned reflex activity, or of body weight, or of the amount of leucocytes in the blood. For instance, during the first day following irradiation, the conditioned reflex activity in Reni was completely disrupted, whereas the leucocyte count was higher than in norm (Table 13), and on the 3rd day a maximal reduction of the number of leucocytes was observed (by 51.4%) as well as of the body weight of the animals (6.09%), whereas a restoration of conditioned reflex activity to the first two stimuli was already in progress.

Despite the fact that in Reni after 3 months, and in Pal'ma after 12 months, following irradiation, a complete restoration of conditioned reflex motor activity was observed, their leucocyte count still remained at a considerably reduced level (3000-4000 below norm).

In the third dog, Boy, of the well balanced type of higher nervous activity, and similarly exposed to a single 100 *r* irradiation, one observed shorter (during one month) disruptions of conditioned reflex motor activity, than in Reni. It was characteristic in regard to Boy that on the 1st, 2nd, 4th, 5th, 12th, 15th and 24th day following irradiation, a complete disappearance was noted of the elaborated conditioned reflex motor activity (Fig. 20). Following the initial food reinforcements on both tables, the dog did not take up its position on the rug, but kept on moving in a haphazard manner about the room, jumped repeatedly on the tables, approached the door, tried to open it and lay down near the door, where it remained until the end of the experiment. The dog did not run to the tables in response to the turning-on of positive conditioned stimuli. Only in certain instances, when the differentiation stimulus was turned on, did the dog run and jump on the table, i.e., an ultraparadoxical phase was observed in the activity of the motor analyzer. In Boy, in contrast to the other two dogs (Pal'ma and Reni), the disruption of differential inhibition was observed only until the 27th day (following irradiation), as well as increased thirst and circus movements which became particularly intense in response to a differentiation signal. The latent period of conditioned reflexes to stimuli, employed after the disrupted differentiation, was 5-10-fold longer.

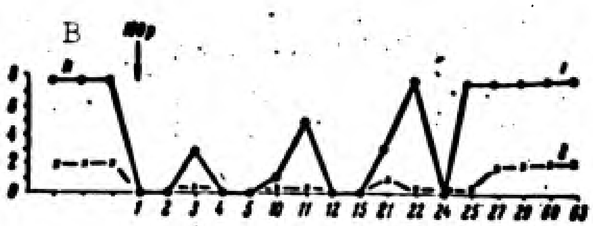


Fig. 20. Impairment of conditioned reflex motor activity in the dog Boy (B) following total single irradiation with a 100 *r* dose. The symbols are the same as in Fig. 19.

Thus, on the basis of experimental data concerning the effect of total single irradiation of dogs with 100-300 *r* doses of X-rays, it can be concluded that, as early as within 30 minutes following irradiation, one observed in all animals spatial disturbances of temporary associations (the dogs do not step on the rug) and uncoordinated movements in the experimental room.

Subsequently, for a period of 1 to 3 months, as a dose of 100 *r*, and up to 12 months at a dose of 300 *r*, there was a weakening of the excitation process, attested by the lenghtening of the period of conditioned motor reflexes, impaired differentiation of the two tables and lower performance efficiency of the animals. There was also disturbance of the process of inner inhibition, which was manifested in the disruption of differentiations and of the inactive phase of the delayed reflex, in the appearance of consecutive inhibition and in intersignal motor reactions of the animals. The impairment of differentiation of the two tables indicates a weakening of concentration of the excitation process.

The restoration of conditioned reflexes to positive stimuli took place 2-3 days earlier than the restoration of differentiation and retardation of the inhibition process.

The fact of reduction of the number of leucocytes in the peripheral blood and easy fatigability of experimental animals is in accord with the observations on humans. As per literary data, also in humans a drop in leucocyte count and easy fatigability sets in following irradiation (G.L. Gempel'man, Kh. Lisko, I. Gofman, 1954; R.J. Hasterlick and L.D. Marinelli, 1956 et al.).

It should be underlined that no complete parallelism was observed in our experiments between the gravity of developed disturbances of higher nervous activity and changes in the blood indexes - the reduction of the amount of leucocyte - as well as between the irradiation dose and the periods of restoration of conditioned reflex motor activity of the animals. For example, in the dogs Reni and Boy, exposed to the same dose (100 r), the restoration of conditioned reflex activity occurred at different periods: in Reni within 3 months, in Boy within a month. The difference in the restoration period of conditioned reflex activity in these dogs apparently depends not only on the type of their higher neural activity (M.I. Nemenov, 1928; P.S. Kupalov et al., 1931; P.I. Lomonos, 1953; N.N. Livshits, 1955a; A.A. Grafov, 1958; I.A. Piontkovskiy, 1958; L.I. Kotlyarevskiy et al., 1956, 1958; L.S. Gorsheleva, 1958; N.G. Ivanova, 1958 et al.) but also on the complexity of conditioned reflex motor activity of the animal which has been elaborated prior to irradiation. In Reni a stereotype delayed response reflex and differentiation were elaborated, and in Boy - only differentiations.

Our investigations further demonstrated that the degree of disturbance of higher nervous activity in dogs depends also on the dose of irradiation. For instance, in Pal'ma and Boy, at an identical stereotype of elaborated conditioned reflex motor activity, the restoration of conditioned reflex motor activity took place at different periods, depending on the irradiation dose: in Pal'ma - within 12 months, in Boy - within a month following irradiation.

The next task of our investigation was the study of the effect of multiple total irradiation on the higher nervous activity of animals. Experiments were carried out on Reni. Following complete restoration of its conditioned reflex activity the dog was again irradiated with a 100 r dose.

As a result of the repeated irradiation (the total dose amounted to 200 r), the dog manifested the same disturbances of higher nervous activity as during the first irradiation; however, these disturbances lasted a longer period of time than after the first irradiation (Fig. 21).

In the experiment conducted within 30 minutes following the second irradiation, one observed in Reni an impairment of the delayed conditioned reflex, which has been elaborated to the light of an electric lamp of 250 w, with a lag of 120 seconds: on the 15th second of the action of the light stimulus, the dog walked off the rug and ran to the table, jumped on it, and remained standing there for 10 seconds. In response to the positive stimulus, employed after the disturbed delayed reflex, one observed an increase of the latent period of the conditioned motor reflex up to three seconds (in norm – 1 second) and a 5-10-fold increase of

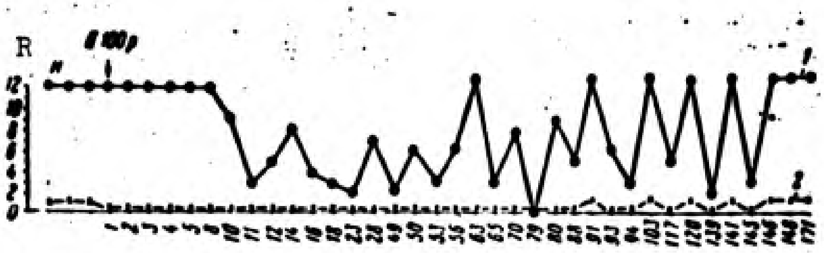


Fig. 21. Changes of conditioned reflex motor activity in the dog Reni (R) which has been exposed to a second irradiation with a 100 *r* dose (total dose of the two irradiations – 200 *r*). The symbols are the same as in Fig. 19.

time required for the return of the dog to the rug. The spatial conditioned reflex of standing on the rug became impaired. During the first week these disturbances showed a gradual increase. Similarly to the first irradiation, the dog manifested circus movement and an increased thirst (the dog drank water up to 6 times during the experiment, instead of 1-2 times prior to irradiation).

Starting on the 10th day following irradiation, and up to the 145th day, Reni manifested disturbances in the course of positive conditioned reflexes: lenghthening of the latent period of conditioned reflexes and of the time required for the return of the dog to the rug. Symptoms of easy fatigability of the animal were noted (during certain experiments only two instead of 12 conditioned reflexes could be employed), following which the dog did not take up its standing position on the rug, but lay down near the door. In some test an ultraparadoxical reaction was noted.

Following the second irradiation with a 100 *r* dose the conditioned reflex motor reaction of the dog Reni was restored only on the 146th day, as can be seen in Fig. 21, i.e., 58 days later than after the first irradiation. During 145 days following the second irradiation, the course of the elaborated conditioned reflex motor activity was of a cyclic nature: days of normal conditioned reflex activity alternated with days the motor conditioned reflexes were disturbed. Following the second irradiation, the delayed reflex also remained disturbed for a longer period of time than after the first irradiation.

It is of interest to point out that the number of leucocytes in the blood after the second irradiation decreased to a lesser degree than after the first irradiation (Cf. Table 13). During the first day following the second irradiation, there was no such markedly manifested leucocytosis (11,100), as on the first day following the first irradiation (17,750). Hence, also in this case we could not elicit any direct parallelism between the indexes of changes in conditioned reflex motor activity and the reduction of the number of leucocytes in the peripheral blood.

Fig. 22. Changes in conditioned reflex motor activity in the dog Reni (R) following third irradiation with a 100 *r* dose (total dose 300 *r*). The symbols are the same as in Fig. 19.

Within 6 months and 21 days after the second irradiation, against a background of completely restored conditioned reflex activity, the dog Reni was exposed to a third irradiation with a 100 *r* dose (total dose of all three irradiations – 300 *r*).

Following the third irradiation, the number of leucocytes on that day was 10,750; it subsequently decreased at approximately the same rate as after the first two irradiations. As regards changes of conditioned reflex motor activity, they lasted 452 days after the third irradiation, i.e., over 15 months. Figure 22 clearly shows the changes in conditioned motor reflexes in Reni after the third irradiation.

Hence, following the third irradiation the dog Reni manifested still more prolonged disturbances in the course of conditioned reflex motor activity than after the second and first irradiation. Similarly to the first two irradiations, one observed a sharp reduction of the functional efficiency of the cerebral cortex, which was expressed in the cyclic character of the course of conditioned reflex motor activity, in the emergence of an ultraparadoxical phase, in the impairment of the process of inner inhibition and in the weakening of the excitation process. However, also after the third irradiation, the prolonged disturbances in the course of the basic neural process of the cerebral cortex did not proceed parallel with the reduction in the amount of leucocytes in the peripheral blood. This is in accord with the findings of N.N. Livshits (1955b), who observed disturbances of the secretory alimentary conditioned reflexes without marked changes of the blood, following repeated X-ray irradiations of dogs.

In comparing the result of three irradiations of the dog Reni with a 100 *r* dose (total dose 300 *r*) with the results of a single exposure to an X-ray dose of 300 *r* (the dog Pal'ma), it can be seen that in the first case there are observed more prolonged disturbances of higher nervous activity than in the second case.

EFFECT OF A SINGLE AND REPEATED TOTAL IRRADIATION OF DOGS IN 10 *r*-1 *r* DOSES ON THE COURSE OF SITUATION CONDITIONED REFLEXES

A number of investigators, who studied the effect of small doses of ionizing radiation on the human organism, point to the fact that during the development of the initial stages of chronic radiation sickness one observes, in the first place, changes in the activity of the nervous system (M.Ya. Bel'govskiy, 1951; Ch. Berens, 1951; Ye.G. Zhuk, 1957; A.L. Morozov, E.A. Drogichina, M. A. Kazakevich, N.I. Ivanov and S.F. Belova, 1957; E.Ya. Grayevskiy and N.I. Shapiro, 1958; I.S. Glazunov and P.M. Kireyev, 1958; M.A. Kazakevich, 1957, A.V. Kozlova, 1954; A.V. Lebedinskiy, 1957; M.N. Pobedinskiy, 1954; B.N. Rapoport, 1958 et al.).

The early complaints of individuals who have had contact with ionizing radiation for a number of years are: easy fatigability, headache, vertigo, poor sleep, reduced work capacity, and deterioration of memory. The initial clinical symptoms are characterized by an increased excitability of the peripheral and central nervous system, manifested in a heightened susceptibility to external stimuli. There is also observed an increased lability of the autonomous nervous system, its disfunction and asthenia. In regard to the cardiovascular system, one observes bradycardia, lability of arterial pressure in the form of hypotonia or hypertonia, tendency to angiospasms and angioneuroses. Later, disturbances of the hemopoietic function appear in the form of a reduced content of erythrocytes and neutrophiles, and a relative lymphocytosis with eosinopenia and monocytopenia.

Investigations on animals also point to changes in the structure and function of the nervous system, as early as within the initial stages of their irradiation with small doses. For instance, M.A. Aleksandrovskaya (1958a and b) showed that, under the effect of irradiation of white rats with 50-150 *r* doses, there appear in the layers III and IV of the cerebral cortex phenomena of turbid cellular edema, granularity of the cellular protoplasm, peripheral tigrolysis, vacuolization of individual cells and their pyknosis. In the diencephalon and nuclei of the cerebrocranial nerves, the cellular vacuolization is still more clearly manifested; even a cellular cytolysis is observed. The amount of RNA in the cells of layers III and IV of the cerebral cortex increases, following irradiation with a 50 *r* dose, and it decreases sharply when a total dose of 150 *r* is used.

A.G. Khanin (1958) subjected dogs to total irradiation with a 15 *r* dose and induced in them the development of a chronic form of radiation disease. On the basis of his morphological studies he established the fact that the first stage of the development of radiation sickness is characterized by reactive changes of the interneuronal synapses, and in the second stage some of the intact synapses are involved in the radiation affliction, while a partial restoration of interneuronal begins to take place. The third and fourth stage of radiation sickness was accompanied by degenerative necrobiotic irreversible synaptic changes. The studies carried out by Yu.M. Olenov (1950), N.I. Artyukhina (1959a and b) and A.L. Shabadash (1957) also point to structural changes in the central nervous system following irradiation of animals with small doses of ionizing radiation.

Of particular interest is the study of functional disturbances of cerebral cortex activity following exposure of the organism to small doses of ionizing radiation.

M.N. Livanov (1956, 1962) investigated changes in the bioelectric activity of the cerebral cortex in persons subjected (for therapeutic purposes) to the action of X-rays in a dose of 25 *r*. It was found that, whereas prior to irradiation the initial background of activity was low, the bioelectric activity of the cerebral cortex rose following irradiation and conversely, when prior to irradiation the initial background activity was high, the bioelectric activity decreased after irradiation. The authors thinks that ionizing radiation exerts a direct, as well as reflex effect on the activity of the nervous system.

A number of authors, who used the method of motor reflexes of L.I. Kotlyarevskiy and the method of secretory conditioned reflexes of I.P. Pavlov, demonstrated the effect of small doses of ionizing radiation on the conditioned reflex activity of various animals. L.I. Kotlyarevskiy, L.S. Gorsheleva and L.Ye. Khozak (1956), L.S. Gorsheleva (1958), and L.Ye. Khozak (1958) noted the disturbances of differentiations in rats irradiated with small X-ray doses (0.5 *r*, 5 *r*). L.G. Samoylova (1959a and b), employing an irradiation dose of 0.05 *r* or 0.1 *r* in rats during daily or alternating days of irradiation, observed (at a total dose of 3-4 *r*) a disturbance of differentiations and phasic phenomena.

Other authors (O.F. Makarchenko and R.S. Zlanin, 1959), employing the classic method of I.P. Pavlov, observed a change in conditioned reflex activity of dogs irradiated with a 0.05 *r* dose (daily irradiation). As early as within 1-2 months from the start of irradiation, a change in differentiations was observed. Analogous data ere obtained by Ye.S. Meyzerov (1958) on dogs. Ye.M. Kobakova and V.A. Troshikhin (1958), in irradiating dogs daily with gamma-rays of radioactive cobalt, in a considerably larger dose (2-2.5 *r*), obtained opposite data.

They found no changes of conditioned salivary reflexes, whatsoever, during the first two years of irradiations (at a total dose of 1200 *r*); only toward the end of the third year of irradiation, when total doses reached 1825 *r*, a disturbance was observed of conditioned reflex activity in the form of cyclic movements, and an imbalance of basic neural process with a slight weakening of the inhibition process.

In contrast with the data of Ye.M. Kobakova and V.A. Troshikhin, other authors (Kh.Kh. Yarullin, 1958; N.N. Livshits, 1953 et al.) showed that, upon irradiation of dogs with 10-15 *r* doses, one observes at a total dose of 30-45-75 *r* or 135-195 *r*, disturbances of conditioned salivary reflexes in the form of disruption of differentiation, the development of phasic states, reduction in the value of reflexes, etc.

Authors who conducted experiments with the use of zoopsychological methods do not point to any worsening of "memorization" or a change in behavior reactions in the irradiation of animals with fractional doses of X-rays, raised up to fatal dose. For instance, Moon et al. (1955), Harlow and Moon et al. (1956) subjected monkeys to total X-ray irradiation with a 100 *r* dose every 35 days (up to a fatal exit), at a total dose of 300-1200 *r*, observed only reduction of the appetite, a drop in weight and diminished motor activity.

On the basis of cited experimental data, obtained with the use of various methods, it can be seen that the problem of the effect on the organism of small doses of ionizing radiation requires further study.

The task of our investigation included a systematic and prolonged observation of changes in situation conditioned reflexes of dogs following their irradiation with X-rays in small doses equalling 10-1 r.

Situation and Salivary Conditioned Reflex Changes Under the Effect of Repeated Irradiations with a 10 r Dose

This series of tests was conducted on 5 dogs: on 4 (Al'ma, Barsik, Dzhek and Chernyy) — with the method of situation conditioned reflexes, and on 1 (Yadinka) — with the salivary method.

In the dog Yadinka a system was elaborated of salivary conditioned reflexes to strong and weak stimuli (O.P. Yaroslavtseva, 1958). Six positive conditioned stimuli and one differentiation, at 5-minute intervals, were used in the experiment. The conditioned stimuli were applied for 30 seconds and were then reinforced with food (20 grams of a sugar-meat powder moistened with water at the ratio of 1:1). The conditioned and unconditioned salivation was recorded on a scale, each grade of which equalled 0.01 ml.

In the dogs Barsik, Dzhek and Chernyy monotype conditioned motor reflexes were elaborated. Eleven conditioned stimulations were employed; of these, 8 positive (to a metronome 120) and 3 differentiations (to metronome 60).

In the dog Al'ma a more complex stereotype of conditioned reflex activity was developed to a system consisting of 12 stimulations: of these, 9 positive, 2 differentiations and 1 delayed. The only difference was the location of the differentiation metronome 60 and the positive metronome 120. The delayed reflex was elaborated to the light of a 250 w bulb, at a delay of 140 seconds. The intervals between the turning-on of the conditioned reflexes varied from 5 to 120 seconds.

Prior to irradiation, the conditioned reflex motor activity of the animals proceeded as follows: the dog entered the experimental room, ran to table 1, jumped on it and ate the first food reinforcement. Usually, after eating, the dog remained on the table not longer than 1-2 seconds, it then jumped off the table and returned to the rug (within 2-3 seconds). The dog remained standing on the rug until the positive conditioned signal was turned on, at the sound of which a positive conditioned reflex — a run to the food table — was manifested in all animals. The latent period of the conditioned reflex in all dogs did not exceed 0.5-1 second. Under the effect of differentiation stimulation, the dogs usually remained standing on the rug. This type of activity was constant and stable in every dog. It did not become impaired when control tests with simulated irradiation were carried out, as well as during a 6-12-fold prolongation of the action time of differentiation stimuli. These tests also had no effect on the number of leucocytes (O.N. Voyevodina, 1956, 1961; O.P. Yarslavtseva, 1958).

Prior to irradiation of the dog Al'ma (experiments of O.N. Voyevodina) investigations have been carried out for a period over 4 years and 1022 experiments were staged; on the dogs Barsik, Dzhek and Chernyy (experiments of I.V. Malyukova) the conditioned reflex activity was elaborated during a 4-month period; on the dog Yadinka over 1000 experiments were carried out; the dog was irradiated 32 times with a 10 r dose of each irradiation (total dose 320 r); within 5 years following the last irradiation, conducted by O.P. Yaroslavskiy (1958), Yadinka was again subjected to irradiation (experiments of O.N. Voyevodina).

The irradiations with a 10 r dose were conducted in two variants: the dogs Al'ma and Yadinka were irradiated daily, and the other three dogs were irradiated thrice in seven days (i.e., every other day); the dose of a single irradiation in the case of each dog was 10 r. Table 11 (page   ) cited the conditions and total general dose of irradiations of these dogs.

In experiments on Al'ma and Yadinka, following repeated daily irradiations with a 10 r dose, the following changes in the course of conditioned reflex activity were observed: within 30 minutes following first irradiation, the dog Al'ma showed no disturbance of positive conditioned reflex activity and differentiation inhibition; however, the inactive phase of the delayed reflex became impaired. In response to a turned-on light delayed stimulus, the dog remained on the rug not 140 seconds, as usual, but only 30 seconds; after 30 seconds the dog stepped off the rug, ran to the table and jumped on it. It then jumped off the table, but did not return to the rug at once; instead, for 60 seconds (as against 2-3 seconds in norm) it walked about the room, drank some water, approached the door, and only then went back to the rug and stayed on it until the next positive conditioned signal was turned on. At the same time, no change was observed in the latent period of conditioned positive reflexes. Hence, following the first irradiation of Al'ma with a 10 r dose, a definite disturbance was observed in the course of the delayed reflex, while the behavior of the dog during the intervals between the action of conditioned stimuli showed only an insignificant change. Our observed fact of impairment of the delayed conditioned motor reflex under the effect of a single irradiation of the dog with a 10 r dose has been experimentally corroborated by G.M. Ayrapetyants (1958).

After the second irradiation with a 10 r dose (total dose 20 r), the conditioned reflex motor activity of the dog Al'ma was disturbed to a greater extent than after the first irradiation. The disturbances were manifested not only in the impairment of the inactive phase of the delayed reflex but also in the disruption of differentiations. When differentiation signals were turned on, the dog ran to the table at once, jumped on it, approached the feeding trough, but having found no food would jump off the table and return to the rug within 45-60 seconds.

Following the third irradiation (total dose 30 r), within 30 minutes a serious disturbance of conditioned reflex activity was observed experimentally in Al'ma: as early as within three applications of the positive stimuli, i.e., prior to the use of the delayed stimulus, the dog jumped off the table, bypassed the rug and turned toward the door; it tried to open it, then lay near it and remained there for 20 minutes. Similarly to the first few days, the dog showed no changes in the latent period of the conditioned reflex. The fact should be particularly stressed that the conditioned reflex activity of the dog ceased prior to the use of the delayed reflex. As mentioned above, it is precisely the impairment of the delayed reflex which was noted after the first irradiation with a 10 r dose. Of interest is also the fact that at the time of above stated disturbances of higher nervous activity which have taken place after the third irradiation, the number of leucocytes in the dog's blood remained within normal limits (Table 15). Subsequent experiments with this dog were carried out without additional X-ray irradiation. It was found that, even after cessation of irradiation, the impairment of conditioned reflex activity in Al'ma kept increasing for 1¼ months. For instance, on 2nd, 8th, 20th, 27th, 30th, 40th and 42nd days following irradiation, the positive conditioned reflexes of the dog were entirely absent, but its first run to the table was preserved. Upon entering the room, the dog ran to the table, jumped on it and ate the first food reinforcement, following which it jumped off the table, walked for 2-10 minutes about the room performing circus movements, drank water often and in large quantities, and then either approached the door and lay on the floor (over 20 minutes), or went under the table where it usually obtained food before and did not return to the rug any more. In some experiments ultraparadoxical phenomena were observed, which consisted of the fact that the dog reacted with a positive reflex neither to the sound of the positive metronome, nor to the knocking of the feeding trough; however, when the differentiation metronome was turned on, the dog would get up, run to the table and jump on it.

At the same time, starting on the 6th day and up to the 189th day following irradiation, one observed in the dog a 2-10-fold prolongation of the latent period of the conditioned motor reflex. In addition, from the first day and up to the 189th day following irradiation, there was a constant disturbance of the delayed reflex and of differentiation inhibition, as well as a decrease of positive conditioned reflex motor activity. For example, in experiments on the 3rd, 4th, 6th, 9th, 24th, 26th, 33rd, 54th, 78th, 126th and 189th days, only 2-6 conditioned stimuli (instead of 12) could be successfully employed. During the rest of the time, as seen in Fig. 23, the conditioned reflex positive activity proceeded in a wave-like manner; at times it approached the normal level, at other times it would again show a marked worsening.

Subsequently, on the 191st day following irradiation, the following disturbances of Al'ma's behavior pattern were noted: a 10-20-40-fold increase of time required for the dog to return to the rug after feeding, also circus movements in a circle in the center of the room or around the rug were observed. Often, these circus movements increased with the impairment of differentiation. Also other reactions were noted: the dog turned with its tail to the differentiation stimulator (when it was turned on), or it began tugging at the rug with its forepaws, or tried to move it to another spot; sometimes autonomous reactions were observed: dysp-

TABLE 15

Number of Leucocytes in the Peripheral Blood in Dog Al'ma, Prior and After Irradiation

1) № опыта	2) Дата 1956 г.	3) Количество лейкоцитов в 1 мм³ крови из краевой вены уха
1000	3/III	14 100
1004	13/III	13 400
1011	22/III	13 800
1022	12/IV	13 700
14/IV the dog was subjected to the first irradiation with a 10 r dose		
1023	14/IV	14 250
15/IV the dog was subjected to second irradiation with a 10 r dose		
1024	15/IV	14 500
16/IV the dog was subjected to third irradiation with a 10 r dose (total dose for 3 days – 30 r)		
1025	16/IV	15 250
Irradiation discontinued		
1026	17/IV	15 500
1027	18/IV	15 750
1029	21/IV	14 250
1030	4/V	14 500
1039	10/V	13 250
1041	13/V	14 000
1042	16/V	14 250
1047	26/V	16 500
1049	28/V	14 750
1056	9/VI	14 250
1057	12/VI	14 250
1059	1/VII	14 250
1065	16/VII	13 500
1070	19/VIII	14 000
1073	4/IX	13 500
1076	8/X	14 200
1078	17/X	14 000
1080	21/X	14 000

1) No. of experiment; 2) date; 3) number of leucocytes in one mm³ of blood from the marginal aural vein.

nea, urination, etc.

A complete restoration of conditioned reflex activity in Al'ma, following the third irradiation, has taken place on the 192nd day only.

During the entire period of impairment of situation conditioned reflex, resulting from a triple irradiation with a total dose of 30 r, no changes of the number of leucocytes in the peripheral blood were observed in Al'ma (Cf. Table 15).

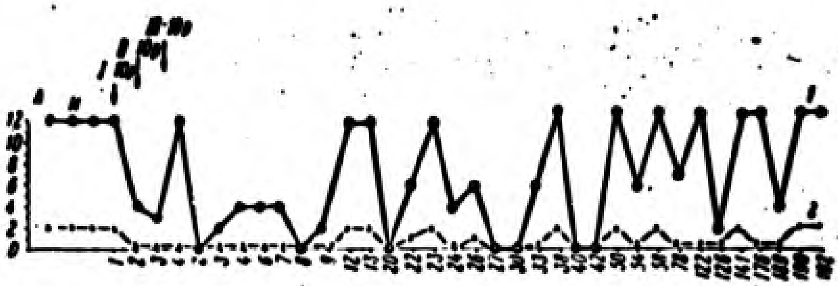


Fig. 23. Changes of conditioned reflex motor activity in the dog Al'ma (A) following a triple exposure to irradiation with a total dose of 30 r (10 r – 3 days). Arrows with figures I-II-III – irradiation days. The other symbols are the same as in Fig. 19.

In the dog Yadinka, under the effect of repeated irradiations conducted within 5 years following the initial irradiations, there have been also prolonged disturbances observed in the course of secretory alimentary conditioned reflexes. For instance, after two irradiations, when the total dose reached 20 r, there was a rise observed in the level of positive conditioned reflexes (Table 16). There seemed to be also an improvement in the inhibition process: the secretion response to the differentiation stimulus (M-60) was less than the one observed prior to the daily repeated irradiations. However, during the following experiments, when the total irradiation dose in the dog Yadinka reached 40 r, a considerable reduction was observed of the level of positive conditioned reflexes not only to weak but also to strong stimuli. There was also an increased secretion to the differentiation stimulus – a fact attesting to the weakening not only of the excitation process but also of the process of inhibition of the cerebral cortex. At the same time, there was no decrease in the value of the unconditioned secretory reflex.

During subsequent experiments, the dog Yadinka was not exposed to additional X-ray irradiation. However, during a period of 5 months a cyclic course was observed, as well as phasic states (equalizing, paradoxical and ultraparadoxical phases), during which conditioned salivation proceeded sometimes at a low level, at other times – at a high level. It is of interest that after the first irradiations, carried out on this dog by O.P. Yaroslavtseva (1958), these phenomena were not observed. In experiments conducted by O.N. Voyevodina on the 5th, 8th, 14th, 21st, 34th and 81st days after the irradiations have been discontinued, a marked impairment of differentiation was observed. The secretion of saliva in response to the differentiation metronome (M-60) reached 75-80 points on the scale, whereas prior to irradiation it varied from 0 to 15 points. As a result of repeated irradiations, during some experimental days the secretion to strong positive stimuli (bell and metronome) was lower than the secretion value in response to a differentiation stimulus. Under these conditions, a marked irradiation of the inhibition process along the cerebral cortex was taking place. In experiments with responses not only to weak but also to strong conditioned stimuli, employed prior and after the differentiation stimulus, the conditioned secretion was

TABLE 16

The Value of Conditioned Secretory Reflexes in the Dog Yadinka Prior, During and After Irradiation

1 Условные раздражители	Величина условных секреторных рефлексов в делениях шкалы за 30 сек 2															
	3 до облучения	4 общее облучение 40 р по 10 р четыре дня подряд				5 после прекращения облучения										
		6 1-й день	2-й день	3-й день	4-й день	5-й день	8-й день	14-й день	21-й день	31-й день	47-й день	48-й день	101-й день	106-й день	137-й день	151-й день
7 Звонок	50	65	100	45	25	0	12	30	28	10	26	13	9	13	32	40
М-120	60	75	80	54	30	35	60	65	85	30	94	48	83	50	60	75
8 Свет	31	35	35	27	15	3	21	32	50	21	15	9	25	30	30	27
М-60	0—15	4	11	8	19	38	70	70	75	52	19	12	80	10	27	0
8 Свет	41	49	45	12	0	2	20	30	43	20	8	0	12	0	19	24
М-120	62	60	90	75	38	32	40	50	75	30	20	13	3	45	43	55
7 Звонок	58	80	75	32	30	34	35	41	55	20	15	12	0	15	25	50

Annotation: M-120 – positive metronome; M-60 – differentiation, light – an electric bulb of 40 w.

1) Conditioned stimuli; 2) value of conditioned secretory reflexes, in points on the scale, during 30 seconds; 3) prior to irradiation; 4) total irradiation 40 *r*, at 10 *r*, four consecutive days; 5) following the discontinuance of irradiation; 6) first day; 7) bell; 8) light.

entirely absent, or appeared after a considerable delay – within 5-25 seconds, instead of 2-4 seconds in norm).

There was also observed an explosive course of conditioned secretion to a positive metronome, employed prior, as well as after, the differentiation stimulus – a fact indicating the weakening of the force, mobility and stability of the process of inner inhibition of the cerebral cortex (P.S. Kupalov, N.A. Kostenetskaya, 1951).

A complete restoration of conditioned reflex activity, following repeated irradiation, has taken place in the dog Yadinka on the 151st day. There was no appreciable reduction of the number of leucocytes, following repeated irradiations, although the conditioned reflex activity of the dog was impaired to a greater extent and for a longer period of time than after the initial irradiations carried out by O.P. Yaroslavtseva (1958).

Experiments of I.V. Malyukova (1959) on the dogs Barsik, Dzhek and Chernyy which were exposed to irradiation with a 10 *r* dose for 7-10 days (a total dose of 70-100 *r*), also established that changes of conditioned reflex activity precede the changes in the blood.

All three dogs (Barsik, Dzhek and Chernyy), following first irradiation with a 10 r dose manifested a disturbance of differentiation and an abundance of intersignal motor reactions, i.e., the dogs performed runs and jumps on the table, without the signals of conditioned stimuli. There was also a rise of general motor activity; the animals often jumped on the table on which they never previously received any food. Besides, soon after the first irradiation, there appeared circus movements, and the time of return to the rug was lenghtened by 60 to 90 seconds.

Subsequent irradiation of the dogs was accompanied by more pronounced changes in the course of situation conditioned reflexes, than after the first irradiation. For instance, in the dogs Barsik and Chernyy after 5 irradiations, the experiment was accompanied by motor excitation, which changed on the following day by motor inhibition, whereas in Dzhek a stronger motor excitation was noted than in Barsik and Chernyy during the experiments conducted from the first to the sixth irradiation.

All subsequent irradiations of these dogs (6th and 7th in Barsik, and from the 6th to 10th in Chernyy and Dzhek) were accompanied by a depressive state.

Hence, as a result of repeated irradiations conducted on alternate days (at a single dose of 10 r and total doses of 70-100 r), all animals showed a rise in the general motor activity, stereotype circus movements, and impaired differentiations. The dogs Dzhek and Chernyy refused to react to stimuli after the 5th-6th irradiation. In the middle of the experiment (after 6-8 tests), the dogs got off the rug and walked to the door, tried to open it, barked, whimpered, but did not return to the rug. Refusal of performing its conditioned tasks was also observed in Al'ma which received only a total of 30 r, but the irradiation was daily in this case and its stereotype of conditioned reflex activity was more complex than in other dogs (the stereotype was described earlier).

For 4-7 months, following irradiation, the dogs Barsik, Dzhek and Chernyy manifested a disturbance of differentiations in 50-100% of cases, while the positive conditioned reflexes remained intact. At the same time a change in the number of leucocytes in the peripheral blood was observed. For instance, after 3-5 irradiations, the dogs showed an increase in the number of leucocytes by 2000-3000 over the normal level. Subsequent irradiations resulted in a decrease of the number of leucocytes by 2000-2500 below norm. On the 14th day, following cessation of irradiation, the leucocyte level reverted to norm (Table 17), whereas the conditioned reflex motor activity of all three dogs remained impaired for 4-7 months.

Thus, experiments with irradiations performed on the three dogs with a single 10 r dose, thrice within 7 days (total dose 70-100 r), indicate a disturbance of higher nervous activity of the animals following irradiation. The changes of conditioned reflex activity are observed as early as within 30 minutes following the first irradiation, whereas changes in the leucocyte level in the direction of a decrease takes place only after 3-5 irradiations.

TABLE 17

Number of Leucocytes in the Peripheral Blood, Prior, During and After Irradiation of the Dogs Barsik and Chernyy with a Total Dose of 70 *r*, and the Dog Dzhek – with 100 *r*.

1 Клички собак	2 Норма	3 Количество лейкоцитов в 1 $мм^3$ крови из краевой вены уха					
		4 в период облучения					
		I	III	V	VII	IX	X-е
5 Барсик	12 000—13 000	13 500	15 500	11 000	10 000	—	—
6 Черный	12 000—13 000	13 000	14 000	15 000	11 000	—	—
7 Джек	13 000—14 000	14 000	16 000	13 800	12 500	12 000	11 500

Continued

1 Клички собак	2 Норма	3 Количество лейкоцитов в 1 $мм^3$ крови из краевой вены уха			
		8 после прекращения облучения через месяцы			
		1-й	2-й	3-й	4-й
5 Барсик	12 000—13 000	12 000	12 400	12 200	12 000
6 Черный	12 000—13 000	12 200	12 500	12 100	12 500
7 Джек	13 000—14 000	13 500	13 500	13 400	14 000

1) Names of dogs; 2) norm; 3) number of leucocytes in 1 mm^3 of blood from the marginal aural vein; 4) during the irradiation period; 5) Barsik; 6) Chernyy; 7) Dzhek; 8) several months after discontinuance of irradiation.

Subsequently, a disturbance of conditioned reflex activity was observed in the dogs Barsik, Dzhek and Chernyy for 4-7 months following irradiation. In Dzhek there was a complete restoration noted of conditioned reflex motor activity within 10 days, in Barsik – within 19 days and in Chernyy – within 16 days, but subsequently this activity became impaired again. A cyclic pattern was detected in the course of conditioned situation reflexes. Only once or twice per month, for a period of 1-2 experimental days, a complete restoration of conditioned reflex motor activity to normal levels was recorded; during the rest of the time the dogs manifested a partial or complete disruption of differentiations, circus movements, a retarded return to the rug, occasional intersignal motor reactions and increased thirst. The conditioned reflex motor activity to positive conditioned stimuli was fully preserved.

Table 18 shows that in the dog Dzhek, following irradiation with a total dose of 100 *r*, the differentiation inhibition was restored two months later than in the dogs Barsik and Chernyy, which received under the same irradiation conditions only 70 *r*.

On the basis of data obtained on 5 dogs, it can be concluded that following repeated irradiations there are observed prolonged and considerable disturbances of situation, as well as secretory

TABLE 18

Impairment of Differentiation Inhibition

1 Кличка собаки	2 Количество сохранившихся дифференцировок									
	3 в норме	4 В период облучения								
		I	II	III	IV	V	VI	VII	VIII	X
5 Барсик	3	1	0	1	0	0	0	0	—	—
6 Джек	3	0	0	0	0	0	0	0	0	0
7 Черный	3	0	0	0	0	0	0	0	—	—

Continued

1 Кличка собаки	2 Количество сохранившихся дифференцировок									
	3 в норме	8 После прекращения облучения								
		9 дни			10 месяцы					
		10-й	16-й	19-й	2-й	3-й	4-й	5-й	6-й	7-й
5 Барсик	3	0	0	3	1	2	3	3	3	3
6 Джек	3	3	0	0	0	0	0	0	2	3
7 Черный	3	0	3	0	0	0	0	0	3	3

1) Name of dog; 2) number of retained differentiations; 3) in norm; 4) during the irradiation period; 5) Barsik; 6) Dzhek; 7) Chernyy; 8) after discontinuance of irradiation; 9) days; 10) months.

salivary conditioned reflexes. These disturbances are characterized, first of all, by disruption of the delayed reflex and differentiations, followed by the development of phasic states and easy fatigue.

Hence, repeated irradiations of dogs with 10 r doses lead to a weakening of the tonus and performance efficiency of the cerebral cortex and to an impairment of the normal correlation of the processes of excitation and inhibition, with a predominant impairment of inner inhibition.

All disturbances of the course of conditioned reflex motor and secretory activity of the dogs take place much earlier than changes in the amount of leucocytes in the peripheral blood.

Together with the disturbance of conditioned situation reflexes during the irradiation period, as well as following cessation of irradiation, an increased motor activity was noted in the dogs during the period of 4-6-7 months – circus movements which often increased under the effect of differentiation stimuli, negative reactions made their appearance, and increased thirst was observed.

Changes in Conditioned Situation Reflexes Following Single and Repeated Irradiations of Dogs with 1 *r* Dose

This series of experiments was carried out by O.N. Voyevodina on six dogs (Akkord, Dzhoy, Pal'ma, Soltan, Tolstyak, Sharik).

In the dogs Soltan, Tolstyak and Sharik, prior to irradiation, a monotype conditioned reflex motor activity was developed and reinforced. Conditioned reflexes were formed to rhythmic alternation of the positive metronome, located to the right, and of the differentiation metronome located to the left of the dog, the dog standing on the rug (square 46).

In the dogs Akkord and Dzhoy an additional conditioned reflex was formed to the light of a bulb of 150 w, and a differentiation to the light of 40 w bulb.

The conditioned stimuli (8 positive and 6-7 differentiated) were used in a definite sequence. In the dog Pal'ma, conditioned reflex activity was elaborated at a food reinforcement on two tables. At the sound of a metronome, the animal ran to table 1; at the sound of a bell – to table 2. Eight positive and three differentiation conditioned stimuli were used in the experiment.

In all dogs, prior to irradiation, the conditioned reflex activity was stable.

Prior to irradiation, the dogs were tested for the mobility of their cortical neural processes (a differentiation stimulus replaced the positive stimulus in the system of rhythmic stimuli, and vice versa), and for the strength of the inhibition process – by prolonging the action of the differentiation stimulus from 5 seconds to 30-60 seconds. During these tests, no disturbances were ever observed in the course of conditioned situation reflexes. Neither has "simulated" irradiation affected the course of conditioned reflex activity (O.N. Voyevodina, 1960, 1961).

Prior to irradiation, the following number of experiments were carried out on the dogs: on Sharik – 176, on Tolstyak – 141, on Soltan – 72, on Akkord – 374, on Dzhoy – 308 and on Pal'ma – 1119. The dogs were then subjected to total irradiation with Roentgen rays. The irradiation conditions are cited in Table 11 (p.).

As a result of conducted experiments (daily irradiation with 1 *r* dose), for a period of 7 days, no deviations from norm were observed in Sharik and Soltan in the course of formed conditioned reflexes, with the exception of a slight shortening (by 0.2-0.4 seconds) of the latent period of the conditioned reflex. The dogs manifested excessive thirst (they drank water from a bowl 4 times, instead of 1-2 times prior to irradiation).

After the 8th irradiation, there appeared symptoms of disturbed higher neural activity: the dogs did not return to the rug immediately; instead, they walked about the room, jumped on tables without any discernible reason, ran to the door. In the intervals, between the turning-on of the conditioned stimuli, they performed circus movements in their walk about the room. In Soltan, at this irradiation dose (8 *r*), a disturbance of differentiation inhibition was observed. Subsequently, in some experiments one observed an impairment of 3 differentiations out of 7 (Fig. 24).

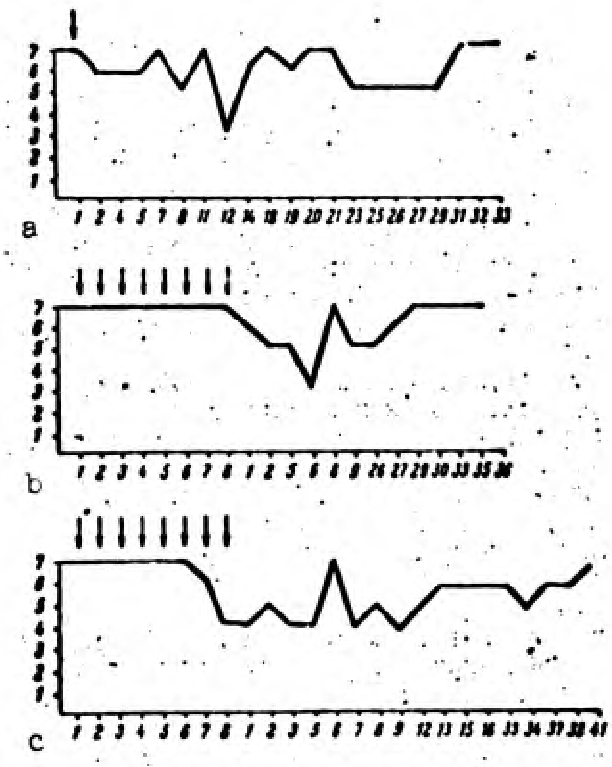


Fig. 24. Changes in differentiation following total irradiation of dogs. On the abscissa axis – days of experiments following irradiation; on the ordinate axis – the number of differentiation stimuli, employed in the experiment; a – dog Tolstyak; b – Sharik; c – Soltan. Each arrow corresponds to irradiation with an 8 *r* dose (a) and 1 *r* dose (b and c).

The dog Sharik (8 *r* irradiation dose), at the sound of differentiation metronome, remained on the rug, or turned around 180° and sometimes rotated around its axis. Analogous changes of behavior were observed also in the dog Tolstyak; in the latter, one out of 7 differentiations employed in the experiment was impaired. In view of the fact that, following irradiation of the dogs (Soltan, Sharik and Tolstyak) with a 8 *r* dose, deviations were observed in the pattern of conditioned situation reflexes, further irradiations were discontinued. It was found that despite the cessation of irradiations, further worsening of conditioned reflex activity was taking place, manifested mainly in a larger number of disruptions of differentiations and in the impairment of spatial orientation of the dogs under experimental conditions (the dogs did not take up their position on the rug).

For a period of 29-40 days following cessation of irradiation, together with aforementioned changes, one observed in the dogs an intensification of the orientation reaction to the action of the positive metronome; the dogs turned their head in the direction of the stimulator, and only after 3-5 seconds (instead of 0.5 seconds) ran and jumped on the table, or they approached first the wall where the metronome was standing on the shelf, remained with their head raised (up to 10 seconds), then ran to the table, jumped on it, and ate. The increase of orientation reaction in the dogs was noted only during the period when a disruption of differentiation inhibition was observed.

During the disruption of differentiation inhibition (in Tolstyak – for 31 days following irradiation, in Sharik for 28, and in Soltan for 38), a consecutive inhibition was taking place, as a rule, and it manifested itself in the lengthening of the latent period of the conditioned motor reflex – three-fold and over, as compared with norm. During this period there was also observed an increase in the motor reaction. For instance, when at the sound of the differentiation metronome the dogs did not get off the rug, they turned away at 180° from the table with food, sometimes shifted from one paw to another on the rug, or performed pendulum-like head movements, and sometimes they would even spin around on the rug.

Upon a 6-fold prolongation time of the effect of the differentiation metronome (from 5 to 30 seconds), the dogs would get off the rug after 8-10 seconds and jump on the table – a fact indicating a weakening of the inhibition process. When positive metronome was substituted with a differentiation metronome, the dogs would also get off the rug and jump on the table.

Hence, following irradiation with a total dose of 8 *r*, all investigated dogs manifested a lasting disturbance of the process of inner inhibition and a disturbance of the course of conditioned situation reflexes.

As seen in Tables 19, 20 and 21, the number of leucocytes in the peripheral blood showed no change during this period.

Analogous disturbances of the elaborated conditioned reflex motor activity, without a change in the amount of leucocytes, were obtained on the dogs Akkord and Dzhoy. The difference consisted of the fact that the disturbances in the dog Akkord (15 *r*) and Dzhoy (12 *r*) took place at higher total irradiation doses. In addition, one observed in these dogs an earlier disturbance of differentiation inhibition which had been elaborated in response to a light stimulus. Figure 25 shows that, following 8th irradiation (total dose 8 *r*) in Dzhoy and the 11th irradiation (total dose 11 *r*) in Akkord, there was observed a disruption of 1 out of 3 differentiations to a light stimulus. Upon further irradiation of these dogs, a disruption of two differentiations to a light stimulus has taken place. However, when the total irradiation dose reached 12 *r* in Dzhoy and 15 *r* in Akkord, one observed in both dogs also a disturbance of differentiation to the sound stimulus. Analysis of the data (Cf. Fig. 25) shows that, following cessation of irradiation in the dog Akkord for 26 days and in Dzhoy for 35 days, the disturbances of differentiations employed in the experiment continued to develop. In Dzhoy on the 10th, 13th and 21st days following cessation of irradiation, only 1 out of 6 differentiations remained intact in the experiment. During the period of

TABLE 19

Number of Leucocytes in the Peripheral Blood of the Dog Sharik, Prior, During and After Irradiation with an 8 *r* Dose

1 № опыта	2 Дата 1959 г.	3 Количество лейкоцитов в 1 мм³ крови из краевой вены уха	
159	16/IV	12 250	
165	24/IV	9 500	
170	8/V	10 750	
169	6/V	11 750	
173	15/V	10 250	
174	16/V	9 750	
175	18/V	10 500	

19/V the dog was irradiated for the first time with an 1 *r* dose

			4
176	19/V	11 250	
176	21/V	9 500	(III облуч. — 3 р)
180	23/V	10 750	(V облуч. — 5 р)
182	26/V	9 750	(VII облуч. — 7 р)
183	27/V	11 750	(VIII облуч. — 8 р)

Irradiation discontinued

185	29/V	11 750
187	2/VI	10 250
189	5/VI	10 250
191	23/V	9 250
193	27/VI	10 000
195	2/VII	11 750
197	11/VII	11 050
198	16/VII	10 500

After the summer rest

200	28/VIII	9 750
206	4/IX	10 250
207	5/IX	9 250
211	10/IX	10 000
214	14/IX	9 750
221	24/IX	10 250
226	30/IX	10 250
231	6/X	10 500
236	12/X	9 750
241	20/X	9 500
247	29/X	10 250
252	5/XI	9 750
255	12/XI	10 250
262	24/XI	10 750
267	1/XII	10 250
270	7/XII	10 000

1) No. of experiment; 2) date, 1959; 3) number of leucocytes in 1 mm³ of blood from the marginal aural vein; 4) irradiation.

TABLE 20

Number of Leucocytes in the Peripheral Blood of the Dog Soltan, Prior, During and After Irradiation with an 8 r Dose

1 № опыта	2 Дата 1959 г.	3 Количество лейкоцитов в 1 мм³ крови из краевой вены уха
16	29/I	9 250
20	5/II	10 000
26	20/II	10 250
36	6/III	11 250
40	12/III	10 250
49	31/III	11 000
54	9/IV	9 750
63	21/IV	10 000
69	6/V	11 250
72	11/V	10 250
12/V the dog irradiated for the first time with a 1 r dose		
73	12/V	11 250
75	14/V	4 11 750 (III облуч. в дозе 1 p)
80	20/V	5 12 750 (VIII облуч. в дозе 1 p) (суммарная доза 8 p)
Irradiation discontinued		
81	21/V	12 000
82	22/V	10 750
84	25/V	11 750
86	27/V	11 250
91	4/VI	10 000
95	26/VI	10 500
98	2/VII	11 000
100	11/VII	9 600
101	16/VII	13 450
103	28/VIII	10 000
After the summer rest		
109	4/IX	9 750
115	11/IX	10 750
122	21/IX	9 750
128	29/IX	12 600
139	15/X	10 500
149	29/X	10 250
154	5/XI	9 250
159	17/XI	12 400
162	21/XI	9 750
164	24/XI	9 500
173	8/XII	10 250

1) No. of experiment; 2) date, 1959; 3) number of leucocytes in 1 mm^3 of blood from the marginal aural vein; 4) (III irradiations with a 1 r dose); 5) (VIII irradiations with a 1 r dose) (total dose 8 r).

TABLE 21

Number of Leucocytes in the Peripheral Blood of the Dog Tolstyak, Prior, During and After a Single Irradiation with an 8 *r* Dose

1 № опыта	2 Дата 1959 г.	3 Количество лейкоцитов в 1 мм³ крови из краевой вены уха
86	2/VIII	10 750
95	28/VIII	10 750
107	12/IX	10 000
108	14/IX	10 500
115	24/IX	9 500
117	26/IX	9 000
120	30/IX	10 750
122	2/X	9 750
125	6/X	9 750
133	17/X	9 250
136	22/X	9 000
141	29/X	9 750

30/X the dog was subjected to a single irradiation with an 8 *r* dose

142	30/X	10 500
144	2/XI	10 600
145	3/XI	10 150
148	9/XI	9 750
150	12/XI	10 500
152	17/XI	8 650
155	21/XI	10 250
157	24/XI	10 050
160	28/XI	9 750
163	3/XII	10 000

1) No. of experiment; 2) date, 1959; 3) number of leucocytes in 1 mm³ of blood from the marginal aural vein.

impaired differentiation inhibition, following irradiation, one observed a consecutive inhibition. In response to a positive stimulus, employed after a disrupted differentiation, one observed an extension of the latent period of the conditioned motor reflex 1½ to 2-fold greater than the normal period; the dogs manifested circus movements, excessive thirst and lenghtening of the time required for the turn to the rug.

It can be assumed that the earlier disturbance of the process of inner inhibition, elaborated in the dogs Akkord and Dzhoy to a light stimulus, as compared with the differentiation inhibition elaborated to a sound stimulus (metronome), has taken place on account of the lesser physical force of the sound stimulus. The fact of earlier disturbance of the differentiation inhibition, elaborated in response to a light stimulus, was elicited also in dogs which received no X-ray irradiation, but were subjected to various surgical interventions on the cerebral cortex in experiments, which were carried out also according to the method of situation conditioned reflexes (M.M. Khananashvili, V.I. Syrenskiy).

Hence, it can be seen from above presented data that under

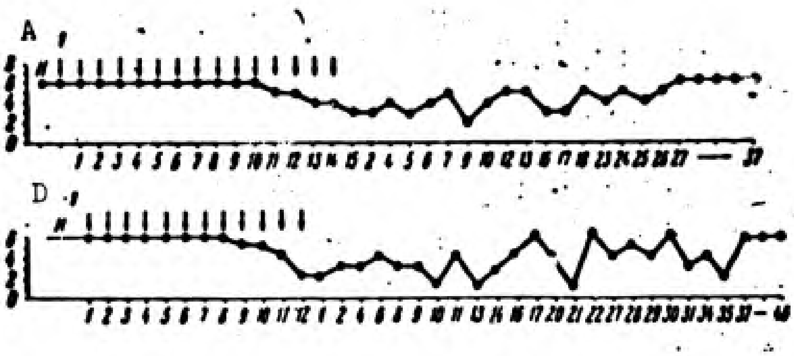


Fig. 25. Change in the differentiations in the dogs Akkord (A-1) and Dzhoy (D-1) irradiated with a dose of 15-12 *r* (1 *r* for 12 or 15 days). On the abscissa axis – days of the experiment, prior, during and after irradiation; on the ordinate axis – the number of differentiation stimuli employed in the experiment. Each arrow corresponds to an irradiation with a 1 *r* dose.

the effect of small doses (1 *r*) of X-rays, there take place in dogs, possessing a complex background of conditioned reflex motor activity, considerable and protracted disturbances of the process of conditioned reflex activity, but that the number of leucocytes in the peripheral blood undergoes no change.

In view of the fact that, as pointed out above, the literature offers contradictory data concerning the ability of the cerebral cortex of summarizing the harmful effect of radiation, or adapting itself to repeated irradiations, we carried out experiments with repeated irradiation of dogs (in 1 *r* doses), at various time intervals following the initial irradiation. The repeated irradiations were always carried out after the complete restoration of conditioned reflex activity of the dogs.

This series of experiments was conducted on 6 dogs (Akkord, Dzhoy, Pal'ma, Soltan, Tolstyak and Sharik). Pal'ma was subjected to a repeated irradiation within 5 years following the first irradiation; Sharik, Tolstyak, Soltan – within a year, and Akkord and Dzhoy – within 37-46 days. The dogs were irradiated daily, except off-days, with a single irradiation dose of 1 *r* (Cf. Table 11, p. 180). The repeated irradiations continued until the dogs have manifested changes of conditioned reflex motor activity, analogous to those observed after the first irradiations with small doses.

The results of conducted experiments with repeated irradiations of dogs (at a daily irradiation dose of 1 *r*) showed that, when the dogs are irradiated within 1-5 years from the time of the first irradiation, the disturbances of higher nervous activity would set in after larger doses (12-15-19-28 *r*) than the 8 *r* doses employed during the initial irradiation. It has been also demonstrated (Cf. Table 22 and Fig. 26) that under the effect of repeated irradiations, the process of inner inhibition became disturbed to a greater extent and that it required longer periods for its restoration than after the initial irradiation in small doses. Upon comparing Fig. 24 and 25 with Fig. 26, it can be seen that,

TABLE 22

Restoration Rate of Differentiation Inhibition in Dogs which were Exposed to Initial and Repeated Irradiations

1 Кличка собаки	2 Суммарная доза при общем облучении (в р)		5 Восстановление дифференцировочного торможения, выраженное в днях, прошедших после:	
	3 первичном	4 вторичном	6 первого облучения	7 второго облучения
8 Аккорд	15	12	27	30
9 Джой	12	7	37	37
10 Пальма	300	19	365	88
11 Солтан	8	12	40	56
12 Толстяк	8	15	31	116
13 Шарик	8	28	29	78

1) Name of dog; 2) summary dose upon total irradiation (in r); 3) initial; 4) repeated; 5) restoration of differentiation inhibition, expressed in days since; 6) the first irradiation; 7) second irradiation; 8) Akkord; 9) Dzhoy; 10) Pal'ma; 11) Soltan, 12) Tolstyak; 13) Sharik.

following a second irradiation and a cessation of irradiations, all investigated dogs manifested a larger number of impaired differentiations than after the first irradiation. The consecutive inhibition was also more pronounced after secondary irradiation, as compared with the initial one. For instance, in all dogs there was a marked lengthening (by 0.5-1.5 seconds) of the latent period of the conditioned reflex. In response to a positive stimulus which was employed after the differentiation has been found to be impaired, the latent period of the conditioned reflex proved to be always longer in every experiment. At the same time, one observed circus movements and excessive thirst. In a number of tests, the dogs manifested, in response to a differentiation stimulus, rhythmic motor reactions in the form of raising and letting down of one of the anterior paws. In some experiments, in response to a differentiation stimulus, circular circus movements were observed in the dogs. The circus movements were of various intensity; they were often accompanied by running, at a gallop, at a fast trot, or at a gentle trot. Upon impairment of differentiation inhibition (following repeated irradiation of the dogs), one observed also intersignal runs to the tables – phenomena not observed in these animals following their initial irradiation. However, all these disturbances related only to changes of the process of inner inhibition, whereas the positive conditioned reflex activity, in analogy with the results of the first irradiation in small doses remained intact. The conditioned reflex activity in all dogs following the second irradiation usually became restored to normal levels within 2-4 months.

For a more precise solution of the problem concerning the

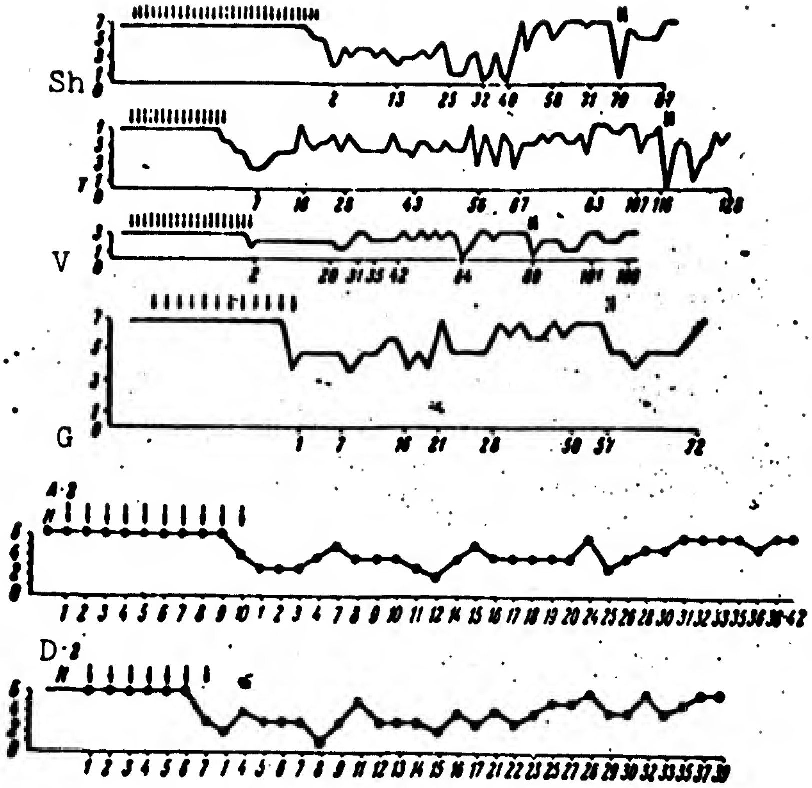


Fig. 26. Impairment of differentiations in the dogs Sharik (Sh), Tolstyak (T), Pal'ma (V), Soltan (G), Akkord (A-2) and Dzhoy (D-2) subjected to repeated irradiation with a dose of 28, 15, 19, 12, 10 *r* (at 1 *r* daily). On abscissa axis – days, during (a series of arrows) and after irradiation (marked with numbers); on the ordinate axis – the number of differentiation stimuli employed in the experiment. Two arrows on the right – administration of aminazine in a dose of 1 mg/kg.

summation of the harmful effect of small doses of ionizing radiation, or adaptation to the X-ray effect on the dogs Akkord and Dzhoy, experiments were conducted with repeated irradiation in small doses. These dogs were repeatedly irradiated after the conditioned reflex activity following previous irradiation has been restored and held (at its normal level) for 10 days.

It was found, following repeated irradiations of Akkord and Dzhoy (1 *r* daily) that a change in conditioned situation reflexes sets in at lower total doses (7-10 *r*, instead of 12-15 *r* of the first irradiation). Following repeated irradiation even with a smaller dose, a more lasting disturbance of the process of inner inhibition was observed (Cf. Fig. 26). For instance, in Akkord and Dzhoy, the disturbance of differentiation inhibition lasted 36 days. During the period of disturbance of the process of inner inhibition, an extension was observed of the latent period of the motor conditioned reflex (up to 1.5 seconds) to a signal employed following disturbed differentiation.

In a number of experiments, the turning on of the differentiation stimulus induced in the dogs rhythmic motor reactions, expressed in raising and lowering one of the paws, or turning the head in the directions of the positive and inhibition stimuli. Also, intersignal reactions were noted. During the period of impairment of differentiations an increased thirst was observed in the dogs. However, none of the dogs refused to perform after repeated irradiations with small doses. Besides, neither after the first, nor after the second irradiation with small doses, was there a reduction of the number of leucocytes in the peripheral blood.

Based on the above data, one may conclude that, following repeated irradiations with small doses (at a single irradiation with 1 r), all dogs manifested a more considerable and lasting disturbance of the process of inner inhibition of the cerebral cortex than after the first irradiation. These data have been confirmed by the observations of clinicians, indicating that in individuals subjected to the effect of small doses of ionizing radiation, the first to be disturbed is the inhibition process in the cerebral cortex (V.N. Zvorykin, 1961 et al.). The early disturbances of the process of differentiation inhibition, observed in our experiments on dogs, may take place on account of the fact that there has been developed in the animals, prior to irradiation, a complex conditioned reflex activity to the rhythmic systems of alternating positive and negative conditioned stimuli. This type of activity, elaborated under conditions of a soundproof camera represents a difficult task for the nervous system of dogs, as has been demonstrated by the investigations of P.S. Kupalov (1929, 1933), V.V. Siryatskiy (1926), M.K. Petrova (1945) and N.P. Murav'yeva (1958).

On the basis of experimental data obtained on 14 dogs, we may conclude that, upon an initial as well as repeated irradiation with total doses of 300, 100, 70, 40, 30, 28, 19, 15, 12, 10, 8 and 7 r, a rise in general excitability takes place on the first day, and after 1-5 days there is a decrease of the general motor activity of the animals.

In our experiments with the use of the method of conditioned situation reflexes, it was clearly demonstrated that, as early as within 20-30 minutes following irradiation, there takes place first of all an impairment of the course of the spatial conditioned reflex – the animal's orientation in the experimental chamber (the dog does not step on the rug, or it jumps on another table on which the animal has never received any food reinforcement), and only later a disturbance sets in of the delayed reflex and of the differentiation inhibition. As a result of the impairment of the process of inner inhibition, one observes in all investigated dogs a consecutive inhibition, as well as the appearance of intersignal reactions. With the weakening of the process of inner inhibition in the cerebral cortex there appear phasic states (paradoxical and ultraparadoxical phases). In addition, the animals manifest a number of motor reactions, not present prior to irradiation: circus movements, rhythmic raising and lowering of one of the extremities, shaking the head in the direction of the conditioned stimuli, an intensified orientation reaction to conditioned stimuli, etc.

Repeated irradiations of dogs in doses of 100-10-1 r, conducted at various periods following initial irradiations, but after a complete restoration of conditioned situation reflexes to normal levels, result in a more lasting and more pronounced disturbance of higher nervous activity of animals, than after the initial irradiations. The above cited data permit the conclusion that the damaging effect of each successive irradiation, even in small doses, might be combined with the previous effect and induce a greater impairment of the conditioned situation reflexes. Such a conclusion can be also based on the fact that, under the effect of pharmacological and physiological experiments conducted against the background of normal conditioned reflex activity (restored after the irradiations), certain disturbances could be elicited of the course of conditioned situation reflexes (even after 1-5 years following irradiation), analogous to those which had taken place directly following irradiation of the dogs (O.N. Voyevodina, 1956, 1960, 1961, 1962; P.S. Kupalov, 1959).

Chapter 6

CERTAIN PROBLEMS CONCERNING THE STRUCTURAL ORGANIZATION OF CONDITIONED SITUATION REFLEXES

Facts presented in previous chapters convincingly attest to the complex functional organization of conditioned situation reflexes. As pointed out, even in the case of elaboration of a conditioned reflex, for example, to an "elementary" sound stimulus, there is created in the higher parts of the brain a complex system of temporary associations, which unifies the work not only of the sound and motor but also the visual, cutaneous and other analyzers, i.e., a functional structure is formed with very complex neural processes extended in time and interrelated, which integrate the performance of various analyzers.

It is naturally of great interest to investigate the problem of the structural organization of neural processes which determine the complex reflex activity, in other words – the problem concerning the role of various analyzers in the diverse cerebral structures during the course of conditioned situation reflexes.

The normal course of conditioned situation reflexes is determined to a considerable extent by the correct spatial orientation of the animals. In the physiological department im. I.P. Pavlov (Institute of Experimental Medicine), as in the laboratories headed by I.S. Beritov (1959, 1961), E.Sh. Ayrapet'yants (1960), a number of investigations has been conducted of the neural mechanisms of the spatial orientation of animals.

According to the studies of M.M. Khananashvili, a precise spatial orientation of dogs is realized, in the first place, by the visual analyzer. When a conditioned motor reflex activity is elaborated in dogs and the visual function is temporarily excluded, the dog's behavior in the experimental chamber becomes substantially disturbed – even in cases where the conditioned stimuli have been previously employed for an extended period of time. We cite below the records of experiments on the dog Rik, prior to the exclusion of its visual function (report of 9/XI 1955), and following exclusion of vision (record of 11/XI 1955).

The cited tests indicated that, following the exclusion of the visual analyzer, the dog retains a general, rough spatial orientation. For instance, the animal starts running to the food receptacle, but is unable to localize it accurately, despite the fact that it has eaten previously at this trough hundreds of times. Following exclusion of the visual function, the orientation in the experimental chamber is realized by means of other analyzers –

Record of an Experiment of 9/XI 1955 on the Dog Rik

Интервал между раздр. (мин) [1]	Число применений условного раздражителя [2]	[3] Условный раздражитель	Время изолир. действия условного раздражителя (сек) [4]	Время запазд. условного раздражителя (сек) [5]	[6] Характер реакции на условный раздражитель и поведение в интервалах
2	61	[7] Свет—55 вт	5	1	[11] Бежит к кормушке
2	100	[8] Крест (дифф.)	20	—	[12] Стоит на коврике
	235	[9] Круг	5	1	Бежит к кормушке
1,5	9	Свет—150 вт	5	1	[11] » » »
1,5	62	Свет—55 вт	5	1	» » »
1	47	Метроном [10]	5	1	То же [13]

1) Interval between stimuli (in minutes); 2) the number of applications of the conditioned stimulus; 3) conditioned stimulus; 4) duration of the isolated action of the conditioned stimulus (in seconds); 5) duration of retardation of the conditioned stimulus (in seconds); 6) character of reaction to the conditioned stimulus, and animal's behavior during the intervals; 7) light – 55 w; 8) cross (differentiation); 9) circle; 10) metronome; 11) the dog runs to the food receptacle; 12) the dog stands on the rug; 13) the same reaction.

labyrinthine, cutaneous, sound, and olfactory analyzers. One can see from a cited record of the experiment (11/XI 1955) that the dog went from the table 1 directly to the rug, where it made a 90-degree turn and approached the steps leading to table 2. Here, the dog lifted its front paw, performed a few movements in the air until it touched the steps. After that, carefully feeling each step, the dog ascended to the table and immediately turned left to the food bowl. One can clearly see in the described motor activity of the animals the participation of the labyrinthine and cutaneous analyzers.

An analogous behavior of the dogs was observed by A.T. Selivanova in her experiments with a temporary disturbance of vision induced by the dilatation of the pupils with atropine-like substances (atropine, lachesine). It is a known fact that the administration of these preparations cause in dogs a dilatation of the pupil lasting from 4 to 24 hours.

Our investigations demonstrated that the use of sound conditioned stimuli, following exclusion of the visual function, contributes to a correct orientation in space, although at the start these stimuli do not ensure a precise orientation of the animals (Cf. record of the experiment of 11/XI 1955).

Record of the Experiment of 11/XI 1955 on the Dog Rik.

Within an hour prior to the start of the experiment, both eyes of the dog were covered with specially adjusted metal plates. When the dog was let in into the experimental room, it immediately approached table No. 1; carefully stretching one or the other forepaw, it touched the table prop and slowly reached the top of the table, turned right and came near the feeding trough where it made sniffing movements in search for the open bowl; after looking for the bowl for a period of one minute and not finding it, the dog descended to the floor, again carefully stretching one paw or the other and touching the table prop. It then went to the rug, stepped on it, remained there for 5 seconds only, went to table No. 2, carefully ascended it, approached the feeding trough, found the open bowl within 30 seconds and ate the pieces of meat in the bowl. It got down to the floor and went to the rug; it remained standing on the rug until it heard the sound of feed-trough No. 1; went to table No. 1, got up on the table, but could not for a long period of time find the open meat bowl. Only in response to the repeated sound did the dog find it and obtained its food reinforcement. After eating, the dog went back to the rug.

These experiments are in accord with the investigations of I.S. Beritov (1953, 1955, 1959); his data led him to the conclusion that the spatial orientation of the animals, following exclusion of the visual function, is effected mainly by the vestibular analyzer.

For instance, if the animal is placed with its eyes covered in a cage and transfer the cage to another corner, at a few meters' distance, feed the dog, and then carry the cage back to its original place, the dog would be able within a few minutes to repeat this route not only with open eyes but also when a protective cover is placed on the eyes.

According to I.S. Beritov, simultaneous exclusion of visual and vestibular reception produces a considerable disturbance of the spatial orientation of the animals.

The investigations of A.S. Batuyev (1959, 1960) also point to the important role of the visual analyzer in the spatial analysis in higher mammals. The author established the fact that, following bilateral exclusion of the peripheral visual analyzer (by means of enucleation) in cats, the animals cease to perform the sighting jump, and that this function of the analyzer is not fully restored by the other analyzer. On the other hand, a bilateral exclusion of the vestibular analyzer leads only to a transitory disturbance of this function. These results were obtained by A.S. Batuyev with the aid of the motor alimentary method of conditioned reflexes.

As shown by the investigations of E.Sh. Ayrapet'yants, A.S. Batuyev, V.A. Kislyakov and K. Lebentrau (1960), the spatial orientations, following exclusion of vision in cats and monkeys, are restored to a considerable extent by the compensatory mechanisms of vestibular as well as proprioceptive analyzers.

Experiments with the exclusion of the peripheral part of the analyzer convincingly attest to the fact that, although in dogs and cats the precise spatial orientation takes place mainly via the visual analyzer, the entire complex reflex activity is the result of a coordinated performance of various analyzers. But the question still remains, as to what is the structural, spatial organization of the neural processes in the central nervous system during the realization of conditioned situation reflexes, in other words – what is the role of various projection and association fields of the large hemispheres, and what is the role of other parts of the brain in this complex reflex activity?

For an answer to this question, we performed a number of surgical interventions on the cerebral cortex, as well as the cerebellum.

Long time ago a hypothesis has been advanced in physiology concerning the special role of the so-called associative fields of the cerebral cortex in the most complex unifying neural activity (Luciani, 1886; Flechsing, P., 1894; Demoor, I., 1899, et al.). This point of view was frequently subjected to experimental verification, and in a number of investigations – to sharp criticism (L.A. Orbeli, 1908; L.G. Voronin, 1948); however, it is still actively supported by a number of physiologists, psychologists and clinicians (Pribram, Penfield). In order to study the role of the so-called associative field of the cerebral cortex in the elaboration and course of conditioned situation reflexes, we removed in dogs the frontal lobes (investigations of V.I. Syrenskiy), as well as the parietal lobes and secondary optic fields (investigations of M.M. Khananashvili). The surgical removal of the frontal area field was performed on both hemispheres; as a result of such an operation, also fields No. 6 and 4 suffered partial damage (the cytoarchitectonic designations of the fields of the large hemispheres of the dogs are given according to the chart of M.M. Gurevich and G.Kh. Bykhovskaya (1933).

It was found that following this operation there is observed a number of substantial changes in the previously elaborated complex reflex activity. During the first few days after the operation, the animals are in an inhibited state, but toward the 7th day a restoration of conditioned reflex activity takes place. On the 7th day the dogs react correctly to the signal stimuli; just as before the operation, the dogs remain on the rug during the intervals between the conditioned stimuli. However, on the 12th-14th day after the operation, marked behavioral changes were observed in these animals: their motor activity increased, the dogs were constantly running about the experimental room, without scarcely stopping at their usual place; without any visible cause, they jumped on the table and ran to the feeding trough, and then would run along the walls of the room. During the following days, the jumps on the table with the food container, unconnected with the signals, became more frequent, and the motor activity continued to increase. The increased motor activity was observed also outside the experimental room – in the cage and in the street.

Within about a month after the operation, these disturbances began to disappear gradually, and within 2-3 months after the operation the conditioned reflex activity in the process of the experiment, as well as the dog's behavior outside the experimental room started to revert to norm, i.e., to the preoperation level.

Hence, according to the data of V.I. Syrenskiy, the behavior of experimental dogs, following removal of the frontal area, undergoes a number of changes which proceed in the following order:

first period (3-5 days) – general inhibition state;
second period (4th to 10th day) – temporary restoration of conditioned reflex activity; this period, taking into account subsequent changes, can be regarded as the latent period;
third period – maximal motor disturbances (11th to 30th day);
fourth period – gradual attenuation of these disturbances (30th to 60th day);
fifth day – period of complete restoration of the function.

These data lead us to the conclusion that removal of the frontal lobes alters the normal course of the motor function of the animals.

Investigations carried out during the last decade in a number of laboratories point to the important role of frontal areas in the normal course of neural processes, not only within the motor analyzer but also other analyzers. According to the works of N.A. Shustin (1959), carried out with the aid of motor-alimentary and secretory-alimentary methods of conditioned reflexes, the processes of inhibition and excitation in the higher parts of the brain come weaker after the enucleation of frontal lobes; the excitation process is characterized in this case by a rapid exhaustion; the basic properties of neural processes – strength, equilibrium and mobility – show deterioration. These disturbances last many months.

Furthermore, as per the data of N.A. Shustin, the enucleation of frontal lobes leads to the disturbance of trace reflexes which had been elaborated to visual and sound stimuli. This observation is in accord with the investigations of Konorski (Cf. also: Konorski a. Lawicka, 1959), who demonstrated the role of frontal lobes in the normal process of retarded reactions in dogs. As is known, Pribram (1955) and Mishkin (1957) in their studies of monkeys, also point to the role of frontal lobes in the normal process of retarded reactions.

It is of interest to point out that I.S. Beritov (1961), in his analysis of the experiments of Y. Konorski, as well as of A.N. Bregadze and other authors, arrives at the conclusion that the prefrontal zone, possibly together with the premotor zone, represents the associative field, in which the labyrinthine and aural sensations become integrated into a complete spatial perception, or a complete image.

As mentioned above, the investigations of V.I. Syrenskiy pointed to increased motor activity following removal of frontal lobes in dogs. Similar changes in motor activity, following enucleation of frontal lobes, were observed also by other authors (N.I. Afana'yev, 1913; Kennard, 1941; N.A. Shustin, 1959, and other authors). Afanas'yev as well as Anokhin (1949) attributes these hyperkineses to the elimination of the function of frontal lobes, whereas Turner (1954), Ward (1948), Y. Kornoski (1956) et al., are of the opinion that these changes are caused by the damage to the adjoining cerebral formations.

Hence, the obtained facts are given a contradictory interpretation, possibly due to the fact that in the above stated works the investigations were carried out on various animal species, with the use of different surgical procedures; however, according to V.I. Syrenskiy, the decisive cause of observed disturbances is due to the irritation of cerebral tissue. This conclusion is arrived at on the basis of the following facts:

1) the increased motor activity does not originate immediately following the operation, but after a certain period of time. Were the elimination of the function of frontal lobes the dominant factor responsible for these changes, the disturbances would have been manifested immediately after the operation, but under no conditions after a period of normal activity;

2) the observed periods of change coincide, as to time, with the dynamics of degeneration of the neural tissue. It is known from literature data that the degenerative process begins during the very first days after a cerebral trauma, but its clear manifestation is observed only toward the 8th-15th day (Kh.A. Khodos, 1948).

As mentioned above, the period of the start of the greatest manifestation of motor disturbances, following extirpation of frontal lobes, coincides precisely with the 8th-15th day.

Hence, the degenerative process during the period of its greatest development and its accompanying inflammatory and regenerative phenomena may represent the factors which irritate the cerebral structures associated with motor activity. In this connection, the question arises, as to which excitation of the neural structures leads to the development of hyperactivity, observed after the removal of frontal lobes. This is a difficult question, since the frontal lobes are connected via well developed pathways with various cerebral structures – with the adjoining cortical areas and with various subcortical structures. A number of facts obtained by V.I. Syrenskiy permit the assumption that subcortical formations play an important role in the increased motor activity, observed following removal of frontal lobes.

As is known, there is a definite group of pharmacological substances which, according to a number of investigations, acts mainly on the cerebral cortex. One of them, in particular, is chloral hydrate. On the other hand, substances such as nembutal and aminazine affects mainly the subcortical structures. Taking into account the pharmacological data, we investigated the effect of chloral hydrate, nembutal and aminazine on the motor activity originating after the removal of frontal lobes. It was demonstrated that nembutal and aminazine, in contrast to chloral hydrate, check the excessive motor activity in dogs with extirpated frontal lobes. Thus, it can be assumed that subcortical formations participate in the genesis of motor disturbances which are observed following the removal of frontal lobes.

A number of researchers include also the parietal zone in the associative parts of the cerebral cortex. An opinion was expressed long ago that this zone functions as the highest associative center (Demoor, 1899). However, subsequent experiments have not confirmed this point of view (L.A. Orbeli, 1908). At present, there is no basis whatsoever to ascribe to this zone the highest integrative function. As the same time, certain facts make it possible to state that the parietal zone plays a definitive role in the interaction mechanisms of various cortical analyzers (L.G. Voronin, 1948; B.F. Sergeyev, 1958; M.M. Khananashvili, 1962).

This interpretation of the parietal zone corresponds to its anatomohistological structure. As is known, this zone borders on the cortical parts of the cutaneous-motor, aural and optic analyzers, and its anterior part approaches in its structure to the structure of the cutaneous analyzer of the cerebral cortex.

All this renders still particularly interesting the problem of the role of the parietal zone in the course of the conditioned situation reflexes, i.e., the type of reflexes which, as stated above, are realized with the participation of various analyzers.

The effect of the removal of the parietal part of the brain on the conditioned situation reflexes has been investigated by M1M. Khananashvili (1961, 1962). His investigations showed that, as a result of the removal of the parietal part of the brain, a number of changes of the function of the optic analyzer take place, accompanied by an impairment of the fine differentiation of the form of objects, of the retardation of the conditioned reflex, and of the interaction of the optic and cutaneous analyzers. At the same time, no disturbance is observed in the operated animals of their positive conditioned reflexes; the correct spatial orientation within the experimental room remains unaltered, and there is only a transitory (for 10 days) impairment of the differentiation stimuli, characterized by the difference in their spatial arrangement.

These disturbances of conditioned reflex activity are more strongly expressed if, in addition to the field 7 of the parietal zone, one removes also the so-called associative optic fields of the cerebral cortex – the fields 18 and 19. But also in this case, the animals retain all conditioned reflexes which were formed prior to the operation.

Hence, the results of exclusion of the frontal and parietal associative zones of the large hemispheres indicate the definitive role of these areas in the realization of conditioned situation reflexes.

We regard the changes taking place after the removal of the parietal and frontal zones, as resulting from the disturbance of the normal course of neural proce‿es in various cortical analyzers. The obtained results also attest to the fact that the associative areas of the cerebral hemispheres should not be regarded as special and sole parts of the brain which accomplish the complex synthesis of the work of various analyzers. This function, as pointed out also by investigations cited below, requires a coordinated performance of various parts of the cerebral hemispheres.

We investigated also the effect of removal of the cortical nucleus of the motor analyzer on the conditioned situation reflexes (M.M. Khananashvili, 1962). These investigations showed that a bilateral removal of the sigmoid gyrus considerably impairs the complex conditioned reflex activity of the animals. Following an operation, there is a protracted worsening of the analysis of optic and sound stimuli, a disturbance of differentiation stimuli which are reinforced on various tables, as well as an impairment of the spatial conditioned reflex of the location of the dog during the intervals between the conditioned stimuli.

The effect of the removal of the sigmoid gyrus on the optic function has been described in detail in our reports in the publications of M.M. Khananashvili (1959 and 1962); here, we consider it essential to dwell on the disturbances observed in regard to the spatial orientation of the experimental animals.

It can be seen in the reports of the experiments on 13/I and 19/I 1959 that, prior to the operation of removal of the motor zone of the cerebral cortex in the dog Nayda, two visual conditioned object stimuli were reinforced in different parts of the room — on various tables. They were stable conditioned reflexes, and the dog clearly differentiated the spatial localizations. After the operation the dog ceased to differentiate the optic stimuli in regard to the localization of their reinforcement, and in every case it ran to table 1. Restoration of the spatial differentiation of stimuli was noted only toward the end of the second month after the operation.

Prior to the operation, during the intervals between stimuli, the dog remained standing on square No. 26 of the floor of the experimental room. This conditioned reflex to localization was also of a stable nature. After the operation, the dog would stop at other squares also, i.e., there was a clearly manifested disturbance of this reflex.

Investigations of A.S. Batuyev (1960) showed that removal of the cortical end of the motor analyzer disturbs the precise evaluation of spatial relations also in cats. A.S. Batuyev interprets these results as the sequel of elimination of the proprioceptive control of motor reactions.

Apparently this mechanism plays an important part also in the disturbances of spatial conditioned reflexes which we observed after removal of the sigmoid gyrus. However, it is our opinion that removal of the cortical end of the motor analyzer leads to the elimination of one of the principle sources of the afferent impulsation which enters the cerebral cortex, namely — the proprioceptive impulsation. This leads inevitably to the reduction of the cortical tonus, and it is manifested, as pointed out above, to a marked weakening of the analyzer function of other projection zones of the cortex (for instance, the optic and aural zones).

This change of the function of cortical analyzers may represent the leading factor in the disturbance of the precise spatial

Record of the Experiment on 13/I 1959. Dog Nayda.

1 Интервал между раздр. (мин)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Время запаздывания условного рефлекса (сек)	6 Характер реакции на условный раздражитель и поведение в интервалах
1	86	[7] Свет—55 вт	5	1	[11] Бежит на стол 1
1	65	[8] Круг	5	1	[12] То же
1	40	[9] Крест	20	—	Стоит на месте [13]
1	66	Круг	5	1	[11] Бежит на стол 1
1	17	Свет—200 вт	5	1	» » » 2
1	51	[10] Звонок	5	1	» » » 1

1) Interval between the stimuli (in minutes); 2) the number of applications of the conditioned stimulus; 3) conditioned stimulus; 4) duration of action of the conditioned stimulus (in seconds); 5) duration of retardation of the conditioned reflex (in seconds); 6) character of the reaction to the conditioned stimulus, and the behavior during the intervals; 7) light – 55 w; 8) circle; 9) cross; 10) bell; 11) the dog runs to table 1; 12) the same; 13) the dog remains in situ.

Record of the Experiment on 19/I 1959, on the 4th Day After the Operation. Dog Nayda.

1	1	[1] Звонок [2]	5	1,5	[5] Идет к кормушке 1
1,5	1	Свет—55 вт	5	2	[6] То же
1	1	[3] Круг	5	2	» »
1	1	[4] Крест	20	2	» »
1	2	[3] Круг	5	3	» »
1	1	Свет—200 вт [2]	5	2	» »

Annotation: In view of the motor disturbances, the dog does not jump on tables, and the food bowls are placed on the floor.

1) Bell; 2) light – 55 w; 3) circle; 4) cross; 5) the dog walks to the food container; 6) the same.

orientation of animals.

It is of interest to note that, according to the investigations of I.S. Beritov, the temporal zone plays an important part in the spatial orientation of animals. I.S. Beritov arrives at this conclusion on the basis of his experiments with the removal in dogs of the temporal zone of the cerebral cortex. The author demonstrated that a dog with damaged temporal lobes, is able with the aid of vision to clearly differentiate the location of food reinforcement, but with its eyes closed the dog cannot find the food reinforcement locus based on labyrinthine stimuli.

The obtained facts lead I.S. Beritov to the conclusion that the temporal zone plays an important role in the mechanism of animals' orientation based on labyrinthine stimuli. In his subsequent investigations I.S. Beritov established that this function is mainly connected with the anterior parts of the temporal zone – the anterior parts of Sylvian sulci.

Hence, our observations on animals with extirpated parts of the cerebral cortex, as well as the studies of other authors, indicate a complex structural organization of conditioned situation reflexes, and determine the importance of various zones of the large hemispheres in regard to the complex reflex activity.

At the present time, thanks mainly to the studies of the associates of L.A. Orbeli, it has been generally accepted that the cerebellum exerts a definitive effect on the normal course of conditioned reflex activity (N.N. Livshits, 1947; A.I. Karamyan, 1949; V.K. Krasusskiy, 1950; A.I. Aleksanyan, 1953, et al.).

Analogous data have been lately obtained also in other physiological laboratories (R.S. Miukhina, 1952; I.S. Beritov, 1960; L.S. Gambaryan, 1959, 1960; V.V. Fanardzhyan, 1960, et al.).

The results of these investigations are well known, and we shall not dwell on them in detail; we shall only point out that in the majority of cases the above-mentioned studies were concerned with the effect of the removal of the cerebellum on the conditioned reflex activity, elaborated by means of secretory or motor-defensive methods. It is therefore natural that the question arose on the role of the cerebellum, and first of all the new cerebellum, in the complex reflex activity, elaborated according to the method of conditioned situation reflexes. The investigations of I.V. Malyukova dealt with this problem.

Prior to an operation, the conditioned reflexes were elaborated in the dogs with reinforcement on two tables. In the intervals between conditioned stimuli, the animal was placed on a certain square. We cite the experimental record of 15/IV 1959 on the dog Dzhek, prior to the operation.

Following elaboration in the dogs of stable conditioned reflexes, the new cerebellum was removed.

As a result of the operation, one observed in the dogs well-known cerebellar disturbances – ataxia, atonia and rigidity of the muscles. These disturbances became gradually less pronounced during the 3-6 weeks following the operation, and after this period they became negligible.

The operation induced a number of serious disturbances in the conditioned reflex activity. In dogs one observed an impairment of differentiation of conditioned stimuli, as related to food reinforcements placed in various locations: the movement (motor reaction) originating in response to the action of the conditioned stimulus was often directed not to the food bowl, where the dog was supposed to feed in response to a given stimulus, but to another bowl. These faulty reactions were at first of constant nature and resembled obsessive reactions. We shall cite an example. The dog Dzhek, when the tone of 600 cps was switched on (usually

Record of the Experiment of 15/IV 1959. Dog Dzhek (Prior to the Operation).

1 Интервал между действием условных раздражителей (сек)	2 Число применений условного раздражителя	3 Условный раздражитель	4 Время действия условного раздражителя (сек)	5 Латентный период условного рефлекса (сек)	6 Поведение собаки при действии условного раздражителя
50	200	7 Свет	5	0,6	12 Подбегает к столу 1, прыгает на него
45	106	8 Метроном (левый)	5	0,8	12 Подбегает к столу 2, прыгает на него
50	94	9 Тон	5	0,6	12 Подбегает к столу 1 и прыгает на него
60	100	10 Метроном (правый)	10	—	13 Стоит на коврике
70	96	11 Звонок	5	0,6	12 Подбегает к столу 2 и прыгает на него
90	95	9 Тон	5	0,8	12 Подбегает к столу 1, прыгает на него
70	101	10 Метроном (правый)	10	—	13 Стоит на коврике
60	201	7 Свет	5	0,6	12 Подбегает к столу 1, прыгает на него
55	107	8 Метроном (левый)	5	0,6	12 Подбегает к столу 2, прыгает на него
50	101	10 Метроном (правый)	10	—	13 Стоит на коврике
45	97	11 Звонок	5	0,6	12 Подбегает к столу 2, прыгает на него

1) Interval between the action of conditioned stimuli (in seconds); 2) the number of applications of the conditioned stimulus; 3) conditioned stimulus; 4) duration of action of the conditioned stimulus (in seconds); 5) latent period of the conditionex reflex (in seconds); 6) behavior of the dog under the effect of the conditioned stimulus; 7) light; 8) metronome (le t); 9) tone; 10) metronome (right); 11) bell; 12) the dog runs to table ... and jumps on it; 13) dog stands on the rug.

reinforced from the feeding trough No. 1), went to trough No. 2. If at this time the food was set at trough 1 (a knock), the dog would turn the head to trough 1, would stop at times, but ran nevertheless to table 2, lowered its snout into the empty bowl, remained standing for a few seconds, and would only then walk to table 1. In some tests this reaction would remain for 5-8 sound signals, despite its constant reinforcement from trough No. 1 (record of the experiment on 20/VII 1959. The dog Dzhek).

As a result of the operation, one further observed a considerable increase of the latent period of conditioned reflexes

Record of the Experiment on 20/VII 1959. Dog Dzhek (Within 6 Weeks After the Operation)

1 Интервал между действием условных раздражителей (сек)	2 Число применений условного раздражителя	3 Условный раздражитель	5 Время действия условного раздражителя (сек)	6 Латентный период условного рефлекса (сек)	4 Поведение собаки при действии условного раздражителя
120	202	7 Свет	20	—	10 Стоит на коврике, смотрит на лампу
100	96	8 Тон	30	25	11 Идет к кормушке 2 (вместо 1), смотрит в нее, потом идет к кормушке 1
120	97	»	50	15	12 Идет к кормушке 2 (вместо 1), поворачивается на стук кормушки 1, стоит 5 сек, после чего продолжает двигаться ко 2-й, смотрит 10 сек в пустую кормушку, потом идет к 1-й и получает подкормку
100	98	»	45	20	13 Такая же ошибочная двигательная реакция, подкрепление в кормушке 1
110	99	»	50	15	14 То же самое
120		Метроном 9	50	10	15 Неправильно идет к кормушке 1 (вместо 2)

1) Interval between the action of conditioned stimuli (in seconds); 2) number of applications of the conditioned stimulus; 3) conditioned stimulus; 4) behavior of the dog under the effect of the conditioned stimulus; 5) duration of action of the conditioned stimulus (in seconds); 6) latent period of the conditioned stimulus (in seconds); 7) light; 8) tone; 9) metronome; 10) the dog stands on the rug, looks at the lamp; 11) dog goes to table 2 (instead of 1), looks into the bowl, then goes to table 1; 12) dog goes to table 2 (instead of 1), turns to the sound of the feeding trough 1, stands still for 5 seconds, continues moving in the direction of bowl 2, looks for 10 seconds into the empty bowl, walks to bowl 1 and receives the food reinforcement; 13) the same erroneous motor reaction, then reinforcement at bowl 1; 14) the same response; 15) incorrect move in the direction of bowl 1 (instead of 2).

to visual as well as sound stimuli (approximately 10-12-fold as compared with the preoperation value), also an impairment of the spatial conditioned reflex in regard to the location of the dog (on a definite square) during the intervals between conditioned stimuli. All above-enumerated disturbances improved slowly and were observed for a period of 5-9 months after the operation.

These experiments clearly attest to the importance of the neocerebellum in the course of neural processes which control the higher neural activity of animals.

Recently, thanks to the wide use of the stereotaxic method in investigations of the function of subcortical structures, numerous and substantial facts have been obtained which indicate the important role of a whole series of subcortical formations in conditioned reflex activity. Our task does not include a detailed review of these works, especially since we did it in a special publication (P.S. Kupalov and M.M. Khananashvili, 1963); here, we shall only touch upon one problem which is widely discussed now in physiological literature. We speak of the role which is played by the reticular formation of the brain in conditioned reflex activity.

As is known, according to the ideas of a number of researchers (Gastaut, 1958; Hernandez-Peon and associates, 1961 et al.), the reticular formation of the mesencephalon represents the substance where the closing of temporary associations is taking place. This formation, in the opinion of the authors, plays an important and ever leading role in the integrative activity of the brain. This concept of the role of the diffuse activating system of the mesencephalon was experimentally checked in the investigations of A. Kreindler, J. Ungher and D. Volanskiy (1959); using the method of situation reflexes, as well as the method of electrocutaneous protective conditioned reflexes, these authors inflicted in the dogs a damage to the reticular formation of the mesencephalon.

The activity of experimental animals, upon elaboration of the conditioned situation reflexes with the P.S. Kupalov method, was as follows. In a large experimental room, in response to certain stimuli, the dog would run to a feeding trough where it received its food reinforcement. In the intervals between stimulations, the dog remained at a strictly defined spot. It was found that, upon destruction of certain areas of the reticular formation, of a diameter of 4 mm, bilaterally, one observed motor disturbances – pareses – and, following their disappearance, within 3-4 weeks a complete restoration of conditioned situation reflexes would take place. Toward the end of this period, the preoperation EEG picture was also restored.

These investigations attest to the fact that the closing of temporary connections during the formation of conditioned situation reflexes cannot be attributed to the function of the reticular formation of the mesencephalon.

Numerous investigations of Soviet physiologists (P.K. Anokhin, O.S. Adrianov et al.) indicate that this closing does not take place during the formation of other, even less complex, conditioned reflexes.

The facts described in this chapter indicate a complex structural organization of the conditioned situation reflexes. Various cerebral structures take part in the formation of such reflexes, and the most complex analysis of external stimuli under these conditions is realized by the large cerebral hemispheres.

CONCLUSION

The strictly objective study of the performance of the brain, begun by I.P. Pavlov, has led to the discovery of entirely new rules of its activity and has determined the only correct, materialistic approach to the investigation of this highest form of organized matter, and to the creation of a new science of the performance of the brain – the physiology of higher nervous activity.

As is known, at the basis of ideas and generalizations of I.P. Pavlov in regard to the function of the higher centers of the brain and, in the first place, the cerebral hemispheres, were his studies carried out basically on the salivary gland, which was used as a peripheral organ, which reflected in its activity the neural processes taking place in the brain. In this connection, among the scientists who have a negative attitude to the materialistic teaching of I.P. Pavlov, there is a widespread opinion that the facts established in the Pavlovian laboratory characterize neural processes which determine the elementary cerebral activity, whereas the complex motor activity of animals and man and their behavior are not subordinated to the rules established by I.P. Pavlov, and they follow their own, special laws of cerebral activity, or are a product of supermaterial force – the soul.

It should be admitted that the absence during a long period of time of systematic investigations of complex forms of behavior of animals by the method of conditioned reflexes and the insufficiently complete analysis of the natural motor activity of animals from the point of view of the basic rules of higher nervous activity, contributed to the viability of this concept.

At the present time we already possess a number of studies devoted to the analysis of complex forms of animal behavior from the point of view of the general rules of higher nervous activity. These studies conducted in various physiological laboratories convincingly attest to the fact that Pavlovian method of conditioned reflexes makes it possible to investigate also neural processes which control the natural motor activity of animals. However, we still do not have a systematic description of the rules governing the formation and course of such activity in a dog, i.e., in an animal on which the rules governing the cerebral performance by the method of secretory conditioned reflexes have been investigated.

The present monograph represents a systematic study of the behavior of dogs under conditions of their natural motor activity with the use of the method of conditioned situation reflexes. This method, developed by P.S. Kupalov in 1942, enables us to investigate in detail the rules governing the formation and course of complex forms of the behavior of animals, to analyze this behavior and, thus, to study the neural mechanisms which control this behavior.

Experimental data cited in the monograph show that, under free mobility in the experimental room, the animals easily and rapidly form conditioned associations with the definite localization of the food and with the entire experimental set-up as a whole. The rate of formation of the first conditioned motor reflex to the usual conditioned stimuli differs in various animals, depending on the functional state of the cerebral cortex, physical intensity of the employed conditioned stimuli, the number and quality of unconditioned stimuli, individual peculiarities of the nervous system of the dogs, and a number of other causes.

The motor conditioned reflexes, elaborated according to the method of conditioned situation reflexes, are stable and durable. From the moment of formation of the first conditioned motor reflexes the animal's behavior during the experiment is determined by the conditioned stimuli. In the intervals between the action of conditioned stimuli, the location of the animal in a definite part of the room and its posture also become positive conditioned agents, and the animal actively and voluntarily goes to this spot, assumes a definite posture and remains on this spot until the next positive conditioned stimulus is turned on.

With the formation of the second, third and subsequent conditioned motor reflexes, i.e., in the course of training, the conditioned reflexes develop more rapidly.

The "law of force" established in the laboratory of I.P. Pavlov, according to the classical salivary method, is clearly manifested also during investigation of the natural motor activity of the animals. Under these conditions, the dependence is elicited of the manifestation of this law on the functional state of the cerebral cortex which, in its turn, depends in our experiments on the alimentary excitability of the animals. For instance, a reduction of alimentary excitability contributes to the elicitation of the "law of force," while a rise of excitability masks this law. Extraneous stimuli, as factors of external inhibition, inhibit the response motor reaction to a weaker conditioned stimulus more easily, than in the case of a stronger conditioned stimulus. With the progress of training, the manifestation of the "law of force" may level off and disappear. The "law of force" is more clearly manifested in cases of complicated motor activity.

Our investigations showed that formation of conditioned situation reflexes, their extinction, the development of differentiations and conditioned inhibition, reorganization of reflexes, etc., are subordinated to the same laws which had been previously established in the laboratory of I.P. Pavlov with the aid of the classic salivation method.

During the study of differentiation of conditioned stimuli in various experimental variants, it was established that the course of this process depends to a considerable extent on the spatial factor.

A special approach was used in the study of rules governing the differentiation of positive stimuli, reinforced from various food receptacles located in various parts of the experimental room. This method proved to be suitable for further investigation of the role of the spatial factor in the differentiation of stimuli and in the general behavior of animals.

In the study of the problem of spatial differentiation of sound stimuli situated in various parts of the room, our attention was attracted to the fact that serious disturbances of higher nervous activity can be induced by gradually reducing the distance between the locations of the sources of differentiated stimuli. Apparently, this method is suitable for inducing experimental neuroses under conditions of the natural activity of animals.

Our investigation, as well as those of V.V. Yakovleva and other authors, made it possible to establish the definite conditioned reflex significance of various parts of the experimental room. It was elicited, for instance, that the part of the room in which the animal stands during the turning on, for example, of positive conditioned sound stimuli, acquires the property of a positive conditioned agent, whereas the part of the room in which the animal finds itself during the action of inhibition stimuli acquires the property of a negative conditioned agent. Thus, various spatial segments become conditioned stimuli which differ as to their meaning, and these stimulating agents, together with other conditioned and unconditioned stimuli control the complex motor activity of the animals. It was also found that the differentiation of various spatial segments proceeds according to the same general rules of higher neural activity which have been established in the laboratory of I.P. Pavlov with the method of secretory conditioned reflexes.

The conditioned reflex which controls the constant position of the animals during the intervals between the action of conditioned stimuli requires special attention. It represents one of the first conditioned reflexes elaborated in the animals in our experiments and is also the initial link, which precedes the reaction taking place in response to the turning on of each distant stimulation; as such, this reflex turns out to be particularly susceptible to various functional or surgical disturbances of the cerebral hemispheres.

The importance of the spatial factor as a stimulus, which determines to a considerable degree the animal's behavior under normal conditions, is indicated also by the experiments in which one shifted the position of the sources of sound and visual conditioned stimuli, as well as the rug on which the animal stayed in the intervals between the action of conditioned stimuli, also the shifting of the source of the unconditioned stimulus (food receptacle) from one spatial segment to another. It has been established in these investigations that the above-mentioned changes in the experimental set-up affect the normal course of previously elaborated conditioned reflex activity, and in a number of cases seriously impair it. It turned out that the extent of the disturbance of higher nervous activity depends on the extent of the change of location of the sources of conditioned and unconditioned stimuli, as well as on the stability of formed conditioned reflexes, their complexity, and the individual peculiarities of the nervous system of the experimental animals. Disturbances of higher nervous activity were more pronounced when the conditioned stimuli were shifted to a greater distance from their previous location, and are less marked when the distance is small. It was further elicited that disturbances of higher nervous activity, which result from the shifting of conditioned and unconditioned stimuli, are more pronounced when the conditioned reflex activity is not stably formed, as well as in cases where a complex conditioned reflex activity was elaborated in the animals. Our obtained data also indicate that disturbances of higher nervous activity, following the shifting of stimuli, are most easily induced in animals with a deliberately weakened nervous system and in animals with a normally weak type of nervous system.

All above-stated attests to the high sensitivity of the nervous system to changes in the spatial arrangements of the circumjacent stimuli.

In our investigation of the behavior of animals in an environment resembling the natural one, we often observed various forms of manifestation of voluntary and involuntary reactions. A satisfactory solution of this problem is possible only on the basis of a materialistic world outlook. Idealism, based on the fantastic concept of supernatural forces, proved to be inadequate not only for the correct understanding of the physiological essence of the voluntary and involuntary but even to make some approach to their scientific analysis. The idealists, as is known, separate artificially the voluntary from the involuntary, and regard the voluntary as a product of the activity of the supernatural source – the soul. They connect voluntary activity with the antiscientific concepts of free will. Most prominent physiologists-materialists have taken a determined stand against such interpretation of the voluntary principle. E.M. Sechenov, in his time, criticized the idealistic concept of free will; he stated that voluntary movements in humans emerge in the process of their development and represent reactions developed under the influence of environmental conditions.

In acknowledging the voluntary principle, materialism does not separate it or tear it away from the involuntary one; it considers that both are determined by the internal and external environmental medium of the organism. Our investigations cited in this monograph attest to the correctness of this concept.

Involuntary reactions, as is known, are characterized by the fact that they are regularly induced by definite stimulations. For instance, the shaking-off reaction appears in response to stimulation of the fur and skin, the sneezing reaction – to the stimulation of nasal mucosa, etc. However, as shown by the investigations of V.K. Fedorov and L.S. Gorshkova (V.K. Fedorov, 1955), R. Floru (1952) and V.V. Yakovleva (1952), the above-mentioned involuntary reactions can be changed to voluntary ones. It suffices to systematically reinforce with food occasional or deliberately induced shaking-off, sneezing, or other involuntary movements. After a few of these combinations, the animals begin to perform these reactions actively in a given experimental set up, without any special irritation of the skin, nasal mucosa, etc. The active reproduction of involuntary reactions by the animals is conditioned by the experimental set up and by the definite state of the animal.

Following reinforcement of their accidental movements with food, the dogs would start performing them also actively and regularly. This was demonstrated on the examples of the animals approaching the rug and standing on it, licking the electric lamp, pressing a rubber bulb with the paw and striking the loud speaker with the paw.

Combinations of the neutral stimulus with various motor acts would lead to the elaboration of a corresponding conditioned motor reflex. A comparison of data obtained during the elaboration of an active reproduction by the dogs of motor acts, on the one hand, and formation of classic conditioned reflexes to a definite external stimulus, on the other, showed that the differences between a voluntary and conditioned reflex reproduction of an unconditioned reflex are relative, although there is much in common between them - first of all, the fact that temporary associations lie at the base of both processes.

The relative nature of the difference between these two reactions is attested also by the fact that an involuntary reaction can be changed into a voluntary one, and a voluntary reaction may acquire the character of an involuntary one. This fact again corroborates the correctness of Pavlov's idea when he stated that there is only a relative difference between voluntary and involuntary reactions.

As our investigations have demonstrated, most complex motor acts are formed on the basis of involuntary as well as on previously elaborated voluntary reactions. The process of their formation is realized in accordance with the mechanism of formation of temporary associations of various complexity. This convinces us once again that it is possible to investigate even the most complex behavior pattern of animals by the method of conditioned reflexes.

In order to elicit the neural mechanisms which control the complex motor activity of animals, we extensively employed various pharmacological substances. We proceeded on the assumption that the action of chemical substances, as stated by I.P. Pavlov, is contributing to a precise physiological analysis. With the aid of chemical agents it is possible to separate and isolate things which no instruments are able to separate. In our investigations we also posed and solved certain problems which are of special interest to pharmacology.

We used the following preparations: analgesic substances of the opium group: dicodide, thecodine, lidol, promedole, morphine; cholinolytic preparations: amizyl, amedine, apophene, diphacyl, lachesine, atropine, etc; adrenergic substances: adrenalin and sympatholytin; tranquilizer of the central nervous system - aminazine). They belong to various pharmacological groups, but all of them mainly affect the central nervous system.

The use of these preparations showed that, upon administration to animals of minimal doses from the group of cholinolytic preparations which, according to literature data, inhibit cortical activity, the following disturbances set-in in the course of conditioned situation reflexes:

a) the food-getting voluntary motor reactions are altered or disappear altogether;

b) the active inner inhibition weakens, the differentiation of conditioned sound or optic stimuli, identical in intensity but located in various places are disturbed, i.e., there is an impairment of differentiation in regard to the reinforcement locus, etc.;

c) one of the first trigger components of the complex motor reaction drops out (the dog does not occupy the initial location in the experimental room — it does not stand on the rug, or on a definite square);

d) there is an increase in the latent periods of conditioned reflexes, up to a complete disappearance of the response motor reaction to the action of the stimulus. One observes in the first place the disappearance of a motor reaction to the action of weak conditioned stimuli, or stimuli connected with the differentiated one ("associated pair");

e) at the height of intoxication, there originate as a rule phenomena of diffuse cortical inhibition, with phasic states (equalizing, paradoxical and ultraparadoxical phases).

All this leads to the assumption that the components of conditioned situation reflexes, which are disturbed under the effect of cholinolytic preparations, are particularly closely linked with the cortical activity and are of cortical origin.

It was further elicited, that preparations which, according to literature data, exert a predominantly inhibiting action on subcortical formations (of the group of analgesic, adrenergic and tranquilizing substances — aminazine, in particular), in minimally active doses do not alter the voluntary motor reactions, have no effect on the differentiation inhibition and do not impair the conditioned reflex structure, although the entire conditioned reflex activity proceeds at a lower functional level. Simultaneously with reduction of the cortical tonus, there is a clearly manifested disturbance of unconditioned reflex activity, the general motor activity, the shaking-off, alimentary, and other reflexes. With the increase of the amount of administered substances, disturbances emerge which are connected with the direct effect of the preparation on the cerebral cortex: the dogs do not manifest the previously elaborated voluntary motor reactions, often fail to stand on the rug, their differentiation inhibition is weakened, etc.

On the other hand, substances which inhibit the peripheral effector link of the conditioned reflex arch, i.e., exert a peripheral effect and do not penetrate the central nervous system through the hematoencephalic barrier, induce disturbances in the behavior of animals only when large doses are administered.

These investigations, with the use of pharmacological substances, as well as investigations which involved surgical interventions in the large cerebral hemispheres, revealed certain facts of the structural organization of conditioned situation reflexes.

For instance, experiments with the removal of various part of the cerebral cortex established the fact that the conditioned situation reflexes are realized as a result of the complex interaction of cortical analyzers, as well as of the interprojection parts of the cortex.

Our investigations revealed the special role of the nucleus of the motor analyzer of the cerebral cortex during the normal course of conditioned situation reflexes, in the analysis of spatial stimuli.

It was also ascertained that frontal lobes and the parietal zone of the large hemispheres, as well as the cerebellum, take part in the realization of conditioned situation reflexes; a surgical injury to these structures induces characteristic disturbances of the conditioned situation reflexes. For instance, whereas, according to previously published investigations of M.M. Khananashvili (1962) conducted by the method of conditioned situation reflexes, the extirpation of the parietal zone leads to impairment of the analysis of the most complex visual conditioned stimuli, while the removal of the frontal zone leads, in the first place, to the rise of the motor activity of animals, and following extirpation of the cerebellum a most clearly manifested disturbance of the spatial analysis of conditioned stimuli takes place.

Investigations with extirpation of various parts of the cerebral hemispheres and cerebellum showed that conditioned situation conditioned reflexes represent the function of the higher part of the brain and, first of all, of the cerebral cortex. This conclusion has been confirmed in experiments with the use of pharmacological substances. As mentioned above, most distinct disturbances of conditioned situation reflexes are observed under the effect of substances which affect mainly the cerebral cortex.

At the present time, an extensive use of atomic energy and isotopes is taking place in industry, agriculture and medicine; hence, an ever-increasing number of people are in contact with radiation energy. This renders of particular importance the thorough study of the effect of ionizing radiation on the living organism.

Taking account of this circumstance, we employed the method of conditioned situation reflexes in the investigation of the effect of ionizing radiation on the higher parts of the central nervous system.

The unique nature of investigations described in our monograph consists of the fact that the effect has been investigated of various X-ray doses on the most complex forms of the behavior of animals. The effect of single, as well as repeated, irradiations was investigated.

The obtained results indicate that, upon daily irradiation of animals with a 1 *r* dose, the symptoms of disturbance of higher nervous activity are manifested as early as following 8 irradiations, and these disturbances are maintained for a long period of time, even after further irradiation of the animals has been discontinued. It is interesting that, in the first place, there is a disturbance of the most complex conditioned reflex activity, including the activity which requires a precise analysis of spatial relations. These disturbances set in prior to changes in the blood picture, usually observed upon irradiation of animals. Thus, irradiation of animals with an X-ray dose of 1 *r* has a definite effect on the central nervous system.

Even more serious and lasting disturbances of higher neural activity were observed in animals following irradiation with doses of 10 *r*, and over. Also in this case the disturbances would first appear in the most complex nervous activity. The obtained results attest to the particular sensitivity of the higher parts of the animal's brain to ionizing radiation. These data can be utilized in medical practice for the early diagnosis of radiation sickness.

Hence, the formation and course of complex motor activity is determined by a number of factors – the functional level of the higher parts of the brain, the intensity of conditioned and unconditioned stimuli, their spatial arrangement, as well as the spatial arrangement of the animal in the experimental environment, etc. All this, together, comprises the situation which determines the conditioned reflex activity of animals. Combination of the concrete factors of this situation leads to a strictly determined regular course and an easily reproduced activity pattern, under given identical conditions. Precisely for this reason, our employed method of investigation of higher nervous activity, which takes into account the complex range of factors affecting the animal in the process of formation of its behavior pattern, has been named the method of conditioned situation reflexes. The use of this method widened our knowledge of the nervous processes which control the behavior of animals; further application of this method may lead to the elicitation of new, at present still obscure, rules which govern the work of the brain.

All above stated enables us to assert that with the aid of the method of conditioned reflexes it is possible to study objectively and analyze the most complex forms of animal behavior. We think it essential to underline that our obtained data speak convincingly in favor of the fact that the most complex forms of the behavior of animals proceed on the basis of general rules governing the higher nervous activity – rules, established by I.P. Pavlov and his pupils and followers by means of the method of conditioned secretory reflexes.

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