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RM-4870-ARPA
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PULSE TRAINS IN LATERAL GENICULATE AND RETINAL GANGLION NERVE CELLS

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PREPARED FOR:
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The RAND Corporation
SANTA MONICA • CALIFORNIA

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PREFACE

This study is a component part of an investigation conducted for the Advanced Research Projects Agency of the possible utility of a man in a missile-discrimination system. The several component studies involved various aspects of the mechanics of the human visual system, the desirable characteristics of false-color composite display systems, and the application of such systems to the ABM discrimination problem. This is one of three studies which address the neural processes of the human color-vision mechanism. One of these studies has been published in RM-4877-ARPA, A Digital-Computer Model of Spike Elicitation by Postsynaptic Potentials in Single Nerve Cells; the other, a summary of the work conducted on a model of information processing at the retinal level, is still in progress.

The primary concern of the present study is primate vision. However, due to a lack of recorded data in this area, vision in the cat is considered because the data obtained may provide information that is applicable to primate vision. On the other hand, data concerning vision in the rabbit are included to illustrate the marked differences among various species and the potential dangers of extrapolating information among such species.

The publications reviewed describe original experimental work and appeared no later than July 1966. An attempt was made to cover the significant aspects of the subject matter, but the review is by no means exhaustive.

A summary relating this study and the several other component efforts to the ABM discrimination problem is planned for future publication.

SUMMARY

There are three main classes of measurements of the events involved in visual perception and discrimination: (1) properties of the physical stimulus, (2) subjective reports or behavioral data, and (3) neuroelectric events. The study of the relationship between properties of the physical stimulus and subjective reports or behavioral data has given rise to an extensive literature on psychophysics. This Memorandum deals with data relevant to the relationship between properties of the physical stimulus and neuroelectric events. It is hoped that when the results of studying the relationship between properties of the physical stimulus and neuroelectric events are compared with the findings of psychophysics, it may be possible to establish correlations between subjective reports or behavioral data and neuroelectric events and thus bring the subject of visual discrimination into the realm of neurophysiology.

Although perception depends upon processing which occurs at the level of the cortex, there is a substantial amount of integration occurring at the lower levels which has far-reaching implications for perception. The neuroelectric events considered are those in the ganglion cells of the retina and in lateral geniculate cells. These have been chosen primarily because reasonably complete investigations of single cells are available only at these levels. Time series of impulses (spike trains) recorded from ganglion and lateral geniculate cells are reviewed in order that the correlations between features of these spike trains and characteristics of the visual stimulus may be examined. Spectral composition, intensity, spatial extent, and retinal location are taken as pertinent characteristics of the visual stimulus. As most investigations have not been concerned with details of temporal patterning or statistical analyses of the pulse series, descriptions of electrical activity are restricted for the most part to such measures as average frequency, the interval between stimulation and the "first" spike, or merely a qualitative statement of the response type.

The visual cells of cats have been investigated much more thoroughly than those of primates. Data concerning the vision of cats are in many

respects comparable to those obtained for primates and contain detailed information pertinent to several areas where primate data are less complete or nonexistent. Data concerning the vision of rabbits are also included to indicate the extent of differences between species.

CONTENTS

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I. INTRODUCTION

AN APPROACH TO UNDERSTANDING PERCEPTION

Figure 1 illustrates a concept of behavior. The school of

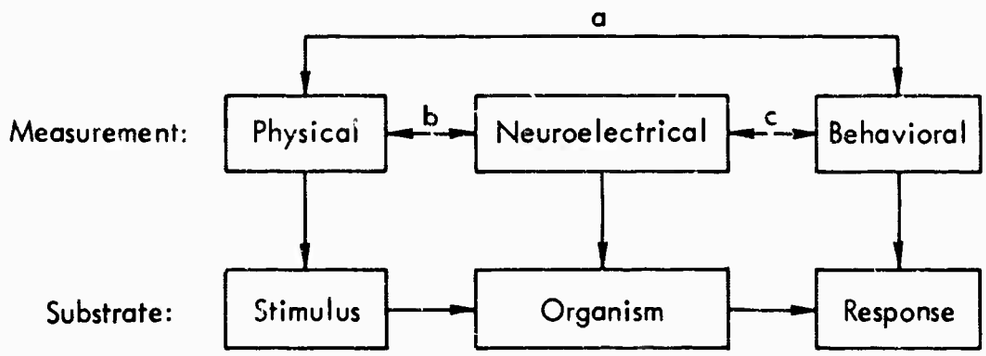

Fig. 1 — Orientation schematic

Behaviorism has maintained that the purpose of psychologists is to delineate relationships of type "a." Indeed, a considerable amount of data pertinent to these relationships has been obtained, including a relatively large amount of information in the realm of psychophysics. The program of psychophysics was to obtain quantitative relations between specific, elemental components of stimuli and those of subjective response. Psychophysicists maintained that perception could then be understood by superimposing the elemental components according to these relations.

Contemporary psychology has for the most part rejected the positions of both the behaviorists and the psychophysicists because their approaches have not adequately allowed for the active and nonlinear processes which occur within the organism. Theoretical psychology today is largely concerned with schemata intended to represent these

internal processes. The assumption is that these events are controlled by physiological structures and that the primary mediator is the nervous system.

An approach which complements this orientation consists of attempts to understand the behavior of underlying neural networks and the relation of their electrical activity to subjective sensations. In a sense, such an approach is an attempt to understand the authenticity and limitations of the psychologist's schemata and the properties of the constituent elements.

In recent years, a sizable volume of data pertinent to relations of type "b" has been obtained. Some data pertinent to relations of type "c" have been obtained directly, but usually these relations are inferred by comparing relations "a" and "b." The mere establishment of the relations "b" and "c" represents a major step forward, but consonant with the contemporary orientation is the realization that such establishment, per se, is not sufficient; little predictive power ensues.

To achieve satisfactory understanding, the behavior of the neural networks which mediate events within the organism must first be understood. Four classes of data are involved: behavioral, neuroelectrical, neuroanatomical, and neurophysiological. Each contains implications different from those of the other classes. Thus, to ignore any of these categories diminishes the level of potential understanding.

The data discussed in the following sections were reviewed as preliminary steps in a program with this orientation. The data concern those neuroelectric events in visual nerve cells which appear to reflect basic properties of the underlying networks and/or pertain to relations of type "b."

Perception is an active process which is influenced markedly by the organism's attentive state, momentary motivational distribution, metabolism, past learning, and set. It is highly nonlinear and depends upon gestalt organization of the stimulus field and may involve more than one sense modality. Furthermore, understanding of the process may require that it be viewed as the first stage in a generalized schema also involving stages of classification, assessment, and preparation to act.

Neural systems are sufficiently complex in both anatomy and physiology to be compatible with the psychological requirements. In the mammalian visual system, for example, interconnection patterns among the lateral geniculate nucleus (LGN) of the thalamus, brain-stem reticular formation (BSRF), visual cortex, and cerebral association areas, and those within each of these structures, are sufficiently complex to allow for literally infinite interaction possibilities. It is by no means clear how the neural networks effect the psychological processes, but Ref. 1 attempts to show how this might be done. Reference 2 contains an attempt to understand some of the subtle gradations which characterize neural behavior.

Although the perceptual process as a whole is complex, active, and plastic, it exhibits certain lawful characteristics. For example, the visual psychophysical relations involved in intensity encoding, spatial and temporal contrast effects, flicker fusion, and subjective-color phenomena are specific, quantitative, and repeatable. One suspects that these reflect basic behavioral properties of the underlying neural networks.

It is reasonable to hope that concepts of neural integrative mechanisms along with neuroanatomical data and the data reviewed here may provide for some understanding of these lawful characteristics of perceptual behavior.

THE BASIC NEURAL NETWORKS OF VISION

The fundamental neural pathway involved in vision[3,4] is shown in Fig. 2. The basic structures are the retinal network, the cells of the LGN, and the visual areas in the occipital lobe of the cerebral cortex.

The retinal network is characterized by cross-connection at every level, as is illustrated in Fig. 3. Each receptor makes connections with several bipolar cells, most of which are connected to some half-dozen other receptors as well. The same type of cross-connection occurs at the bipolar-ganglion junctions. Also, there are two classes of cells, amacrines and horizontals, which make transverse connections within the

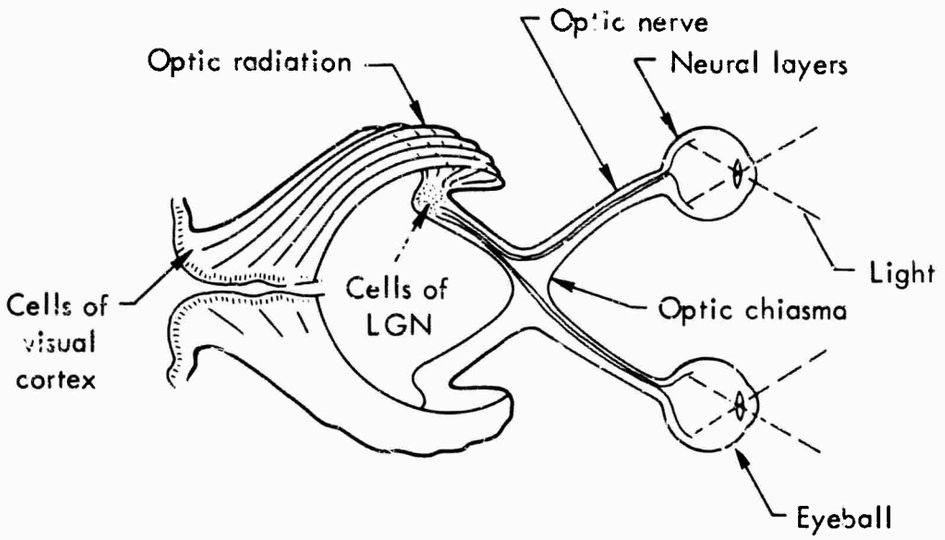

Fig. 2 — Fundamental visual pathway

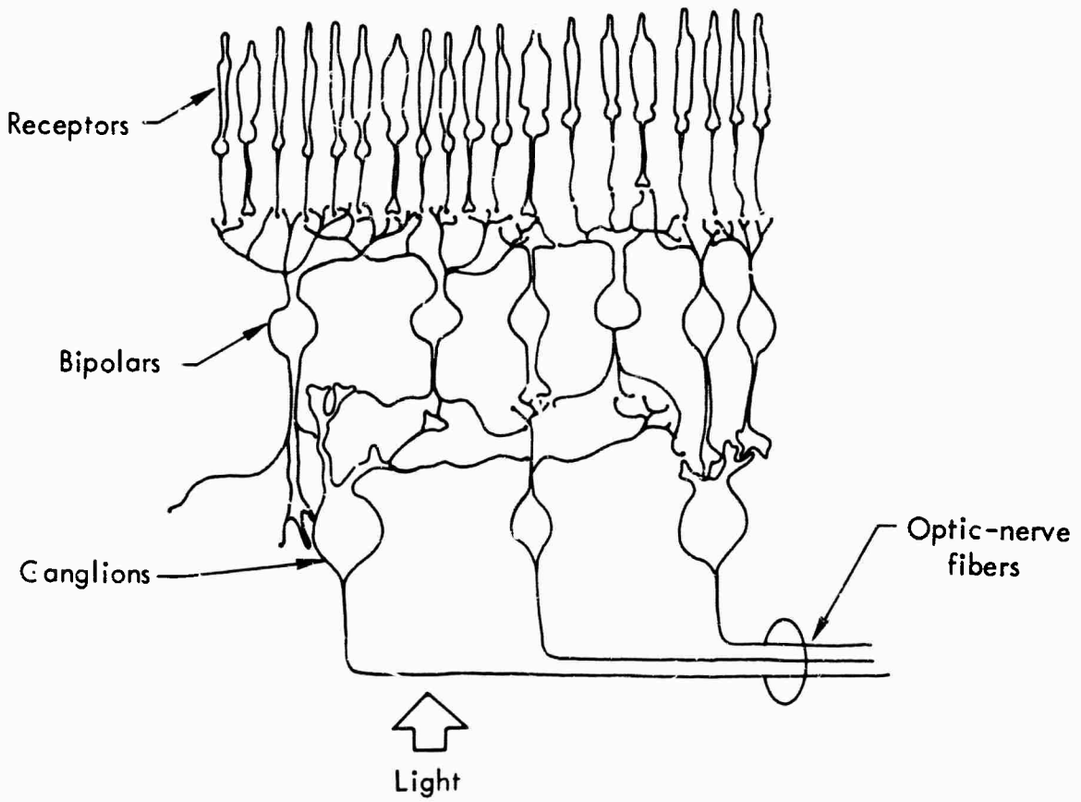

Fig. 3 — Retinal cross-connection

retina. The cells of the LGN incorporate cross-connection with the optic-fiber terminations and, in turn, cross-connect with the cells of the visual cortex.

It is possible that centrifugal fibers synapse with retinal cells. Fibers from the BSRF synapse with cells of both the LGN and the visual cortex, and the LGN also receives input from the visual cortex. The cells of the visual cortex exhibit complex interconnection patterns and receive input from cerebral "association" areas.

The incidence of light upon the retinal receptors sets off a chain of electrical activity throughout the visual pathway. This activity has been extensively recorded under a variety of conditions with both microelectrodes and macroelectrodes. The former are used to record the behavior of single cells, and the latter are used to record the "average" behavior of a large number of cells. The relatively large body of data showing the responses of groups of visual cells is not reviewed here.*

In recent years a good deal has been learned about the electrical activity of single nerve cells. The picture that emerges is essentially the following:[2,5-7] The soma (or cell body) of a nerve cell is the site of low-magnitude (5 to 10 mv), graded, electrical activity which reflects an integration or synthesis of potentials transmitted to the cell by other neurons. The graded activity at the soma sometimes results in a relatively large (~ 70 mv), distinct potential change (impulse, spike, or pulse) which has a characteristic form and time course independent of the details of the preceding graded activity. It is a time series of such identical pulses which is transmitted by the cell to its synapses with succeeding nerve cells or effectors. Recordings of such outgoing spike trains taken from single retinal ganglion and lateral geniculate cells are reviewed here, and Refs. 8 through 21 provide a reasonably complete list of publications describing behavior of

*Access to this literature may be obtained, for example, through almost any issue of the journal Electro-Encephalography and Clinical Neurophysiology.

single cells of the visual cortex. Unit recordings from other cell types in the fundamental visual pathway are not available.

The first systematic investigation of the behavior of single visual cells was carried out in the 1930's by Hartline.[22] He used a macroelectrode but dissected optic fibers until only one fiber remained active. Since the advent of the microelectrode some years later, a very large volume of electrical data has been obtained from single visual cells in many species. This review is concerned with the single visual cells in primates, cats, and rabbits. References 23 and 24 contain relatively comprehensive examinations of the frog and the bush baby, respectively.

Section II discusses characteristics of the neural substrate against which responses to stimulation should be considered. Light and dark adaption, spontaneous activity, interaction among the LGN, BSRF, and the cortex, and posttetanic potentiation are reviewed.

Section III discusses receptive-field organization, and Sections IV and V contain descriptions of the effects of stimulus intensity and wavelength on response measures.

Section VI considers temporal characteristics of responses and the effects of stimulus temporal pattern.

Section VII contains the concluding remarks and a table summarizing salient aspects of the data.

II. SOME CHARACTERISTICS OF THE NEURAL SUBSTRATE

When the eye has been subjected to either complete darkness or a steady, low-intensity background light long enough for the electrical activity of an associated cell to reach a steady state, the cell is called dark-adapted or light-adapted, accordingly. Dark- and light-adapted states are distinguished by threshold levels and responses to monochromatic stimuli. Ganglion cell thresholds are considerably lower in the dark-adapted state.[25-28] In an investigation of the transition from light to dark adaption in cat ganglion cells, Barlow, Fitzhugh, and Kuffler[26] found that the change in threshold takes from 3 min to about 2 hr, depending on the intensity and duration of the light-adapting illumination. (They indicate that this process is approximately four times faster in humans.) Threshold curves to blue and red stimuli exhibit different time courses. The blue curve exhibits two distinct phases, the earlier phase being higher than in the red curve and the later phase being lower, while the red curve is essentially smooth. (The red curve and both phases of the blue curve resemble decaying exponentials.) These findings have been corroborated by Hughes and Maffei who observed[27,28] that the cat ganglion cells during dark adaption exhibited thresholds which in all cases decreased monotonically and attained the steady-state value in about 30 min. The differential responses in these two adaptive states to monochromatic stimuli are discussed in Section V.

SPONTANEOUS ACTIVITY

It is universally reported that the majority of ganglion and lateral geniculate cells exhibit pulse trains in either the dark- or light-adapted state in the absence of any stimulation aside from background illumination. These pulse trains are referred to as "spontaneous" activity.

Hughes and Maffei[27,28] report that cat ganglion cells exhibit systematic changes in spontaneous firing level during the course of dark adaption. When a diffuse light which has been on for several

minutes is turned off, the firing frequencies of about half the cells drop to zero and then increase exponentially with a time constant of about 30 sec to a maintained level about 50 percent below the original. The frequencies of the remaining cells exhibit a brief increase, a trough at about 35 sec, a second smaller and broader peak at about 55 sec, and a decline to a maintained level higher than the original in about 1 or 2 min. The dark-adapted steady levels of the latter cells tend to be higher than those of the former.

Kuffler, Fitzhugh, and Barlow[29] observed continuous, irregular, spontaneous activity in both light- and dark-adapted cat ganglion cells at the rate of about 20 to 30 spikes/sec (sps) in all cells at all levels of illumination. No systematic relationship was found between spontaneous firing frequency and intensity of background illumination. Some cells exhibited increases in firing frequency, some showed decreases, and others showed no change in frequency level as illumination was increased. In most cells, a 5- to 15-min transient "overshoot" in frequency followed a change in intensity. A histogram of first-order interspike intervals could be fitted quite well by a gamma distribution. The first serial coefficient differed significantly from zero, while the second and third did not. This indicates that the probability of firing at any given time depended only on the times at which the two immediately preceding spikes occurred.

Interspike-interval histograms of spontaneous activity in cat ganglion cells comparable to those described above have been obtained by Fuster et al.[30] They report that a change in illumination level produces a transient response and a change in steady-state frequency level but no change in the mode of a given cell. The mean mode of their data was 9.1 ms.

Spontaneous activity is reported in almost all of the publications on cat ganglion cells listed in the References of this Memorandum, and all findings appear to be consistent with the preceding analyses. Specifically, no tendency of spikes "clustering" into groups has been reported at this level.[31]

Hubel[31] reports spontaneous activity in the lateral geniculate cells of an awake or sleeping cat at 10 to 20 sps. In the awake cat,

the activity in the lateral geniculate cell appears to be random in the same manner as in the ganglion cell. In the sleeping cat, however, the spikes tend to group into clusters of 2 to 8 spikes, and in each burst the frequency is close to 500 sps. (This clustering is obliterated by a response to a specific light stimulus.)

Many other workers have also reported this tendency to cluster in the lateral geniculate cells of the cat.[32-41] Levick[36] and Bishop[35] have examined the spontaneous discharge of the dark-adapted lateral geniculate cells in some detail. Levick reports that many units exhibit mean discharge rates that are relatively stable for periods of 5 to 10 min but that it is uncommon for this stability to last longer than 30 min. He classifies the firing patterns into three groups: (1) the stable group, where the mean rate for two-thirds of the firing patterns is less than 10 sps, the most common range being 4 to 6 sps, (2) the irregularly unstable group, and (3) the regularly unstable group. Many of the firing patterns having a regularly unstable rate showed mean rates of discharge varying in a cyclic manner. The most common periods in these cycles were 0.3 to 0.5 sec and 1 to 20 min. Spontaneous activity was obliterated or severely depressed in 61 percent of the cells, following blockage of retinal discharge by increasing intraocular pressure. The remaining 39 percent exhibited either a brief transient and return to normal or no response at all to this blockage.

Bishop[35] examined interspike-interval histograms from the stable mean-rate data based on two levels of coarseness (100-ms and 8-ms "bins"). He found that 76 of 112 samples exhibited the burst activity and that the more coarse histograms appeared to resemble an exponential distribution, except for a depression (of varying depth) around the 8- to 16-ms bin.

Fuster[30] reports bursts of 3 to 5 spikes in the cat LGN at frequencies of about 500 sps occurring at intervals of 80 to 200 ms. About half the units investigated showed preponderant interspike intervals, in the ranges 2 to 3.5 ms and 6 to 10 ms.

Negishi et al.[41] report that bursts in the cat LGN have a mean of 4 spikes/burst, a mean duration of 20 ms, and a mean intraburst frequency of 274 sps and occur at a mean rate of 5.3 bursts/sec.

No detailed analyses of spontaneous activity in primate ganglion or lateral geniculate cells are available, but reports of Hubel and Wiesel[42] and the deValois group[43-50] establish that it does exist. In the lateral geniculate cells spontaneous activity occurs at the rate of 10 to 20 sps in the light-adapted state and is essentially unrelated to the level of background illumination, although a transient follows a change in level.[46]

Jacobs[51] reports that the cells of the monkey LGN (see Section V) show one of two changes in firing rate to a given shift in stimulus luminance: The frequencies of the excitatory cells increase with increasing brightness, and the frequencies of the inhibitory cells decrease with increasing brightness.

In both the ganglion and lateral geniculate cells of the rabbit,[52,53] spontaneous activity is characterized by a clustering of 2 to 3 spikes at frequencies of about 300 sps. The overall rate is about 20 to 40 sps in ganglion cells and about 10 to 20 sps in the LGN.

INTERACTION AMONG CENTERS

The firing patterns of ganglion and lateral geniculate cells are influenced not only by activity in the retinal receptors, but also by activity in the BSRF, as are most sensory channels.[54] Ogden and Brown[55] obtained evidence of an efferent influence on primate ganglion cells. Extracellular recordings at the level of ganglion dendrites revealed potentials whose properties are consistent with their hypothesis that small efferent fibers in the optic nerve excite the amacrine cells which in turn inhibit the ganglion cells.

It is reported that similar potentials could not be found in the cat retina. Ogawa reports that "direct recording from single optic tract axons [in the cat] has failed to reveal any evidence that they are activated by stimulation of the midbrain reticular formation..." Maffei and Rizzolatti[56] found no difference between the responses of cat ganglion cells to flashes of light in sleeping and waking states. However, two workers report that stimulation of the BSRF in the cat potentiates activity in some ganglion cells and inhibits it in others in both spontaneous firing[57] and light-induced discharge.[57,58]

In dark-adapted lateral geniculate cells of the cat, spontaneous activity is markedly affected by BSRF stimulation, the modification being characterized by a rise in frequency which exhibits a peak about 135 ms after stimulation and levels off at a rate substantially higher than the normal rate.[39] Injection of sodium pentobarbital, which depresses activity in the BSRF, obliterates this effect. Furthermore, in the presence of a flashing light stimulus, BSRF stimulation improves temporal resolution. The maximum frequency of a flickering light to which this type of cell responds is increased, and the firing is restricted to a particular phase of the cycle. When these cells are light-adapted, the effect on spontaneous activity is still present, but there is no discernible improvement in temporal resolution. When the brainstem connection to the nucleus is destroyed, the percentage of dark-adapted lateral geniculate cells which cease firing after retinal blockage increases from 61 to 85.[36]

Hernández-Peón[58,59] reports that BSRF stimulation reduces the population response of the cat LGN to a visual stimulus and that comparable depression is found when the cat is attentive to acoustic or olfactory stimulation. Suzuki and Taira,[60] however, report that the effect of BSRF stimulation on the response of single cells in the cat LGN to optic-tract stimulation differs markedly among cells and usually exhibits a time course involving both facilitory and inhibitory phases. Considering responses of all the cells, they report that more time was involved in facilitory than in inhibitory phases. Furthermore, population responses for this case showed marked facilitation to this stimulation.

A state of waking defined by electroencephalographic recording can be reproduced by stimulation of the BSRF. Maffei and Rizzolatti[56] confirm that the bursts of spontaneous activity in single cells in the cat LGN are absent in the waking state and report that responses of these cells to flashes of light are markedly higher in the waking state, whether that state is attained naturally or by stimulation of the BSRF. Furthermore, no response to light was altered by BSRF stimulation in the awake cat.

However, another source[61] reports that the potentials which accompany deep sleep facilitate a population response in the cat LGN to optic-tract stimulation. Possible resolution of this point is offered by Dagnino et al.[62] who report that population responses in the cat LGN to optic-tract stimulation are larger during the waking state than during light sleep, but larger yet in deep sleep.

It is reported[63-65] that the responses of cells in the cat LGN to optic-tract stimulation are influenced also by stimulation of the visual cortex. The effect is inhibitory, has a latency of about 10 ms, is maximally effective in 60 to 100 ms, and lasts from 400 to 700 ms.

Dodt[66] has reported activity in rabbit ganglion cells as a result of stimulating the contralateral optic tract. The responses are quite distinct from typical antidromic responses, which were not attained with any visual stimulus tested. From this he inferred the existence of a centrifugal influence in this species. The impulses obtained often occurred repetitively at frequencies of 400 to 600 cps. Increasing light adaption lengthened the latencies of the responses and in some cases obliterated them.

In dark-adapted lateral geniculate cells of the rabbit, spontaneous activity is virtually unaffected by retinal blockage.[53] However, if the brain-stem connections are severed, many units cease their activity, and those that remain active are silenced by retinal blockage. There is a general correlation of activity in these cells to the activity of the EEG.

Fuster and Doctor[67] report that BSRF stimulation does not affect the lateral geniculate response to light flashes but that injection of sodium pentobarbitol results in depression of that response.

PLASTIC BEHAVIOR

In addition to the temporal characteristics of responses (see Section VI), some relatively long-lasting variations have been observed which appear to reflect a plasticity of the underlying neural structures. Such effects have been investigated thoroughly in the cat LGN.

Hernández-Peón et al.[68] report that the population responses in the LGN of most cats to a series of 1-ms flashes presented at a frequency

of 125 to 200 cps exhibited marked habituation. The diminution of response size always followed a waxing and waning course and involved from several hundred to several thousand flashes. In cases where habituation required relatively few flashes, reinitiation of the flashing stimulus after only a few minutes of suspension produced responses to the first flashes which were as large as the original responses. However, in cases where habituation was established with many thousands of flashes, responses to a reinitiated flashing stimulus remained diminished for up to 24 hr. Extraneous stimulation of acoustic or visual modalities brought about an immediate recovery of the diminished potentials. These responses were not merely transient responses to the extraneous stimulus but persisted after its cessation.

The administration of an anesthetic dose of Nembutal enhanced the potentials which were diminished by habituation. Furthermore, habituation could not be reestablished in an anesthetized animal.

These authors report that the optic-tract response remained unmodified while the LGN habituation was observed.

A series of investigations* have shown that the responses in the cat LGN to stimulation of optic-tract fibers are influenced by conditioning shocks applied to those fibers prior to stimulation. Such responses in an awake, unanesthetized cat following conditioning with a single shock are inhibited for up to 2 sec, the inhibition being a maximum of 60 percent at about 40 to 80 ms. In anesthetized cats, single-shock conditioning is followed by a facilitory period reaching a maximum of about 113 percent at about 5 ms, an inhibitory phase reaching a maximum of about 60 percent at about 20 to 40 ms, a relatively rapid rise for about 150 ms, and a much slower rise to the control level which may take up to 2 sec.

Conditioning of the optic tract with repetitive shocks applied at a frequency of 400 cps for 20 ms in an awake, unanesthetized cat results in LGN responses to test shocks which are greatly depressed immediately after conditioning, and responses attain control level only if obtained some 15 to 50 sec after conditioning. Morlock and Marshall[70] report

*See Refs. 37, 38, and 69 through 74.

that responses to test shocks applied after this period have the same amplitude as control responses, but Bishop[37] suggests that a prolonged depressive period may exist in this case.

The responses of the anesthetized cat under the same conditions show an initial (and immediate) depressed period, a rise to a peak at about 40 ms, and a subsequent, second subnormal period which may last from 5 min to several hours, depending on the intensity and duration of conditioning. Evarts and Hughes[71] have shown that the 40-ms peak in the above case corresponds to responses greater than the control responses (and thereby constitutes posttetanic potentiation) only if the conditioning tetanus is applied while the LGN is in a depressed period. Otherwise, the peak corresponds to responses about equal in magnitude to the control responses.[70]

Morlock et al.,[69] recording subthreshold activity in this situation (anesthetized cat, tetanic conditioning), have found that the amplitudes of excitatory postsynaptic potentials (EPSPs) are modified in precise accordance with the postconditioning time course given above. About 90 percent of the EPSPs observed showed this change, while the remainder showed no change.

BASIC RESPONSE TYPES

Against this background of spontaneous activity and interconnection, cells respond in one of two ways to a light stimulus. First, the firing frequency may increase during light stimulation, reaching a maximum (usually of the order of 50 to 100 sps with typical intensities) in about 100 ms and then declining to a still-elevated steady-state value in about 300 or 400 ms. The second type of response is characterized by a decrease in firing frequency during the presentation of the stimulus and a response very similar to that described above, but in this case the response occurs when the stimulation is stopped. These response types are known as the "on" and "off" responses, respectively.*

*These definitions are not intended to describe the diversity and variability of temporal patterns associated with different types of stimuli.

(As indicated, the "off" response is associated with firing reduction during presentation of the stimulus in almost all cases, and this condition is to be assumed for all "off" responses described in this Memorandum unless the contrary is explicitly stated.)

Figure 4, taken from recordings of the deValois group,[75] shows "on" and "off" responses in two lateral geniculate cells of the macaque monkey. The top line on each of the four records is the signal marker with upward deflection indicating that the light is on, and the duration of the flash is 500 ms. The top two records show "on" responses, and the bottom two records show "off" responses. Note the spontaneous activity exhibited by these cells and its inhibition prior to the "off" responses.

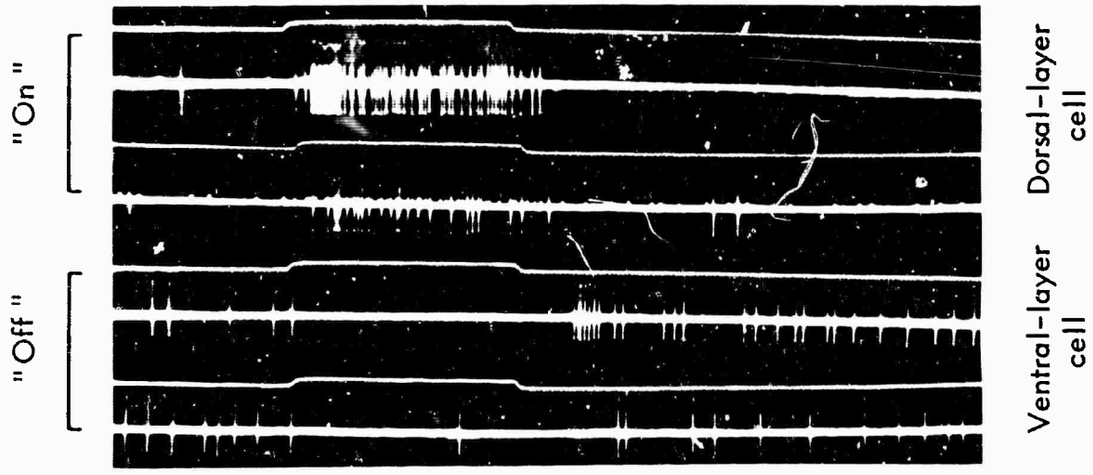

Fig.4—Single-cell records from a dorsal-layer cell and a ventral-layer cell of the lateral geniculate nucleus

Some cells exhibit a combination of both types of response to certain types of light stimulation, and these responses are called "on-off" responses. Although the relative strengths of the response types in these cells may be altered by changes in light intensity, it is generally true that the type of response characteristic of a given cell does not

change with light intensity. Changes in stimulus location or wavelength, however, may alter the response type. These cases are discussed in Sections III and V.

III. RECEPTIVE-FIELD ORGANIZATION

RECEPTIVE FIELDS

The concept of a receptive field is to be considered a property of a given cell. It may be defined as that retinal area populated by the set of receptors which when stimulated by light cause a marked change in electrical activity of the cell.* The size of a cell's receptive field is influenced by stimulus intensity, spectral composition, size, and state of adaption. However, an apparently basic feature of receptive-field organization has been revealed by small (dia ≈ 0.1 mm), circular, white stimuli of moderate intensities. The following discussion relates to this type of stimulation.

Hubel and Wiesel[42] have examined receptive-field organization in 112 light-adapted, primate ganglion cells. They found that all cells were one of two types: those whose receptive fields contained a roughly circular "core" region which gave exclusively "on" responses and an annular region surrounding this core which gave exclusively "off" responses; or, conversely, those whose receptive fields contained a core region giving "off" responses and a peripheral region giving "on" responses. Responses containing both "on" and "off" components could be obtained only when portions of both regions of the field were stimulated simultaneously. A salient feature of the results is the antagonistic nature of the two receptive-field regions: Stimulation of the periphery tends to inhibit the response of the core as well as elicit the opposite response type, and vice versa.

Hubel and Wiesel also noted two interesting aspects of field geometry revealed by plotting receptive-field diameters against the distance from the fovea, as shown in Fig. 5, where 1 deg is approximately equal to a linear dimension of 360, 250, and 100 μ on the retina of the primate, cat, and rabbit, respectively. First, core diameters tend to

*It is likely that there are receptors within the field thus defined which do not influence the cell, but on a coarse scale the receptors which do influence the cell are in general contiguous. Such fine-grain heterogeneity as may exist is not relevant to results obtained with the stimulus sizes dealt with here.

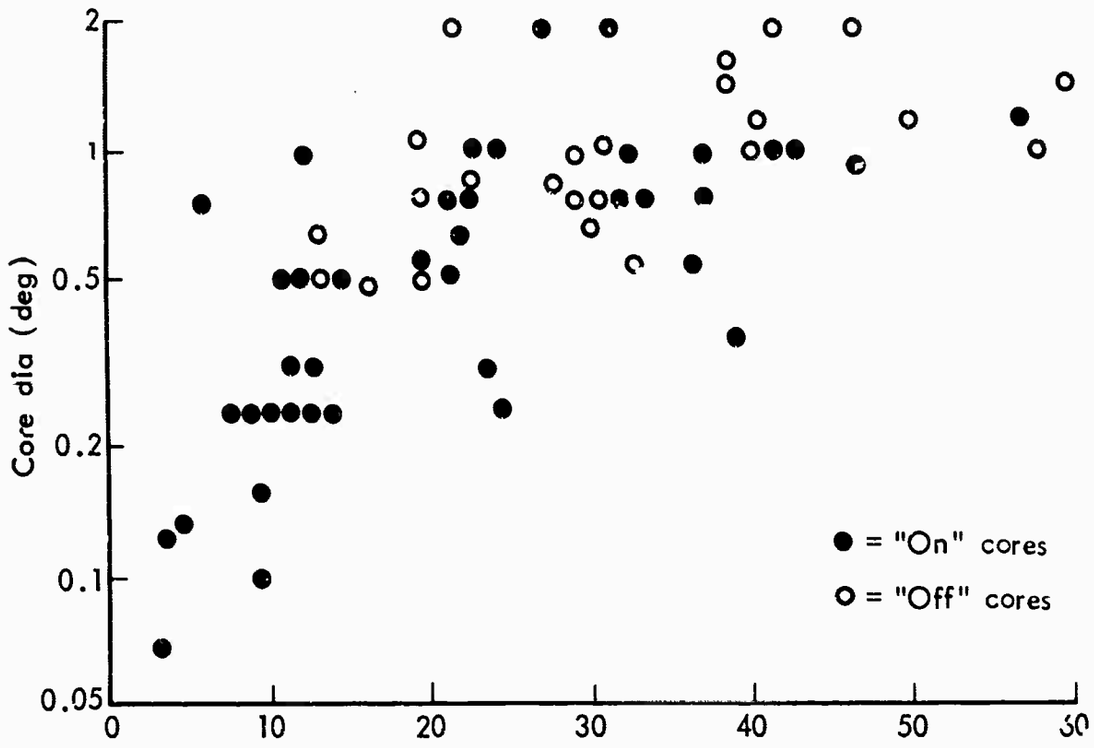

Fig.5—Spatial distribution of the receptive-field diameters

become significantly smaller as the fovea is approached. Second, there is an apparent preponderance of "on" cores near the fovea. The validity of the last statement is questionable because of the relatively small size of the sample. Periphery diameters were not measured explicitly, although the comment is made that "for most fields the total diameter was many times that of the centre." In many cases it was necessary to use spot and background intensities about 2 log units higher than normally used in cat cells in order to obtain a response from the annular periphery. Gouras[25] observed that the effect of the annular periphery disappeared at low stimulus intensities.

No description of receptive-field organization in primate lateral geniculate cells has been found.

Kuffler[76] had previously described the same sort of receptive-field organization in cat ganglion cells, and his description has been corroborated many times.* He reported that although it was necessary

*See Refs. 29, 31, and 77 through 84.

in some cases to change the adaptive state, stimulus intensity, area, or location, it was possible to obtain either the "on" or "off" circular core and opposing annular periphery in all units. The antagonism of the two regions was emphasized.

Information concerning the size and retinal distribution of receptive fields of cat ganglion cells has since been obtained. Core diameters tend to be smaller (~ 0.25 mm or less) in the centralis than in the periphery (~ 0.5 to 1 mm), while periphery diameters are about 1 to 3 mm throughout the retina.* Core thresholds are about the same throughout the retina. However, Wiesel reports that thresholds for diffuse stimuli are higher in the centralis than in the periphery, and this is probably due to the higher ratio of the periphery diameter to the core diameter in the centralis.(78) Also, he reports that the number of "on" cells is approximately equal to the number of "off" cells in both the centralis and the periphery.

In dark-adapted cat ganglion cells it has been found that the effects of the opposing periphery are absent.(77,83) The length of time necessary for the periphery effect to disappear is about 50 percent longer than the time for the threshold transition under the same conditions. Furthermore, the effects of the opposing periphery are diminished when background illumination is increased.(76,79)

McIlwain(80) has recently shown that a cat ganglion or lateral geniculate cell may be influenced by the motion of a black disc some 10 mm from the receptive-field center. Such stimulation facilitated the response to a spot light on the core and, in a few cases, elicited a direct response. The frequency and amplitude of the motion seemed to be critical, and a stationary disc had no effect. This phenomenon has been corroborated by Levick et al.(85)

Rodieck and Stone(83) were unable to find any cat ganglion cells responding preferentially to specific directions of stimulus motion.

As might be expected, the receptive-field organization of lateral geniculate cells of the cat is very similar to that of the species'

*See Refs. 76, 78, 79, 81, and 83.

ganglion neurons.* The one significant difference appears to be that the degree of suppression of the core by the periphery is much higher in lateral geniculate cells.[32,80,87] In fact, many lateral geniculate cells in the cat do not respond to diffuse light.[33,86] (Figure 6 on p. 23 illustrates this point.) Bishop and his colleagues[86,87] report that some lateral geniculate cells of the cat respond only to specific features of a visual stimulus (e.g., preferential sensitivity to a stationary black spot, large or small stimuli, rapid oscillatory movements, or specific direction of motion). Hubel,[31] however, explicitly reports that he found no preferential sensitivity to motion within the receptive field.

Recent work has shown that receptive-field organizations in rabbit ganglion[52,88-90] and lateral geniculate cells[91,92] are more diverse. Barlow, Hill, and Levick[88-90] report that about half of the rabbit ganglion cells are of the core and opposing annulus variety (25 percent "on" core and 23 percent "off" core) and that the remainder are preferentially sensitive to motion. Forty percent of the cells exhibit a maximum response to motion in a particular direction, a null response to motion in the opposite direction, and graded levels of response to motion in intermediate directions. These cells are distinguishable from the classical variety in several respects: (1) The preferential response to motion has not been explained by a simple temporal property of the classic field; (2) the same direction preference is shown for spots that are lighter or darker than the background illumination; (3) the discharge is very insensitive to light intensity; and (4) the receptive fields are homogeneous with respect to response type (most give "on" and "off" responses at all points, though some give only "on" responses at all points). The direction-sensitive mechanism appears to be associated with "subunits," which extend about 0.25 deg and of which there are about a dozen in a given receptive field. The direction sensitivity is thus distributed over the field and is not associated with one given boundary. There is an optimum velocity for this effect, the

*See Refs. 31, 33, 79, 80, 82, 86, and 87.

most common magnitude being about 5 deg/sec. The remaining 12 percent of the cells are also preferentially sensitive to motion, but the salient stimulus feature in these cells is speed rather than direction: Some cells with large receptive fields respond only to rapid motions, and some with small fields respond only to slow motions.

Receptive-field organization is similarly diverse among light-adapted lateral geniculate cells of the rabbit.[91,92] Arden[91] reports that the classical core and opposing periphery arrangement is seldom found in these cells. Of 129 cells studied, he found 47 cells which exhibited receptive fields homogeneous with respect to response type. These fields were commonly oval in shape, a typical dimension being 6 deg. The majority of the remaining cells[92] had irregularly shaped receptive fields of great variety, the one common factor being that most boundaries (between adjacent regions and external limits) extended along tangential or radial lines in a polar-coordinate system centered on the optic axis. Many of these receptive fields were quite large; others were relatively small and exhibited "tails" on an otherwise circular field. Areas and organizational patterns changed markedly with stimulus intensity.

Furthermore, the response character of the rabbit cells differs from that reported in other species. "Off" responses are essentially uncorrelated with inhibition during stimulus presentation.[52,91] Responses are brief, and in many cells ascertainment of a response is possible only through synchronization of pulses to a flickering stimulus.[53,91]

Over the years many investigators have obtained responses in ganglion cells of various vertebrates with diffuse light stimulation. These responses contain varying amounts of both "on" and "off" response types.* They most probably represent the confluence of two opposing types of influence[95] and reflect the two antagonistic receptive-field regions described by Kuffler. In cats the combined response is more commonly obtained from the "off"-core cells,[78] but it is also obtained from some "on"-core cells.[76,78,79]

*See Refs. 22, 93, and 94.

DISTRIBUTION OF SENSITIVITY

Figure 6 shows the effect of the size of illuminated retinal area on response thresholds in cat ganglion and lateral geniculate cells.* The core diameter of this unit is about 1 deg. The threshold decreases as the number of active core receptors is increased. However, as the opposing periphery is invaded, the threshold rises.

Wiesel[78] reports that similar results are obtained by using constant-intensity stimuli of increasing area and by measuring latency or average frequency.

Figure 7 shows the firing frequency of a response in a ganglion cell in the cat as a function of the position of a spot stimulus (3-min dia) within the receptive field. The upper curve represents the average firing rate during an 88-ms period just after the light was turned on, and the lower curve represents the average firing rate during the last 400-ms of the "on" period. Corroborating information is given in Refs. 33, 76, 77, and 84.

Rodieck and Stone[83] report responses to combinations of spot stimuli in ganglion cells of the cat are approximately equal to the sum of the individual responses.

Hubel and Wiesel[42] report comparable area effects in a primate ganglion cell, and as indicated earlier, no studies of primate lateral geniculate cells utilizing small-diameter stimuli have been found.

In rabbit ganglion cells of the direction-sensitive variety, threshold intensity is proportional to the reciprocal of the area illuminated within 20 min of arc of the field center and approximately proportional to the square root of that quantity (Piper's law) from 20 min of arc to 3 deg.[89,90]** Thomson[52] reports that response frequency exhibits a Gaussian-like dependence on distance from the field center and that latencies are smallest at the center. However, Barlow and Levick report that latencies are not systematically related to position in the receptive field.[90]

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*See Ref. 78 for more quantitative data relative to this effect in cat ganglion cells.

**It is tempting to associate the demarcation line of these regions with the motion-sensitive "subunit" size, as is pointed out in Ref. 90.

It has been reported that the logarithm of threshold intensity in lateral geniculate cells of the rabbit (averaged for three similar cells with homogeneous fields) bears a positive linear relationship to the logarithm of the area stimulated.[91] Also, the response frequency increases as the stimulus is moved closer to the field center.

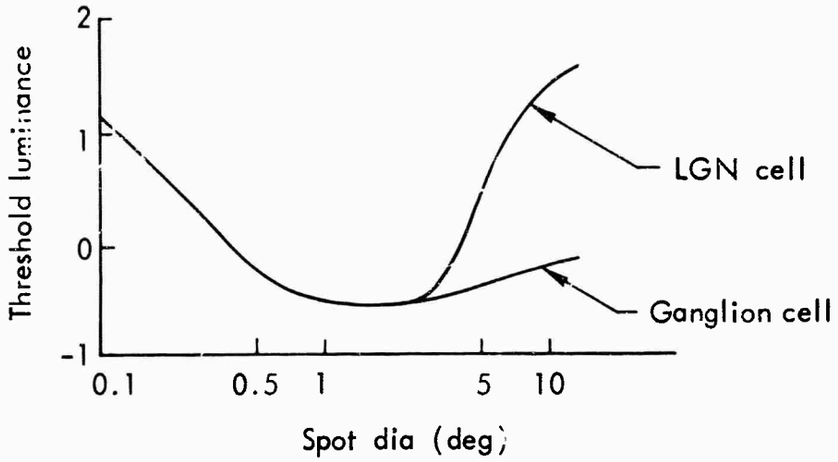

Fig.6 — Effects of diffuse light on response thresholds in associated ganglion and lateral geniculate cells of the cat[33]

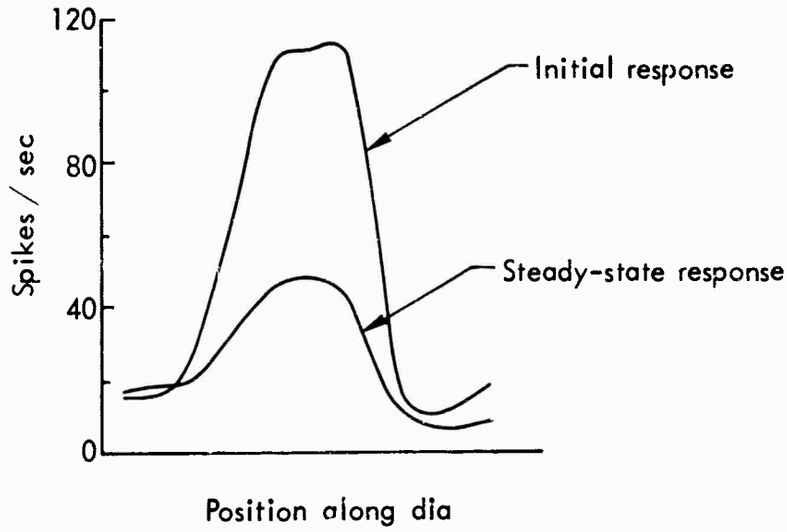

Fig.7 — Effects of spot light on firing frequency in a cat ganglion cell[83]

IV. THE INFLUENCE OF STIMULUS INTENSITY

The most readily obtained and often used measures of "strength" of a spike-train response to a given stimulus are the time interval between the stimulus onset and the first spike and a characteristic frequency of the train (usually an average over the first 100 to 500 ms following light onset or cessation in visual cells). The effect of stimulus intensity on these measures is considered in this section.

Diffuse stimuli have been used in most investigations of intensity effects. This situation, as pointed out in Section III, results in the confluence of two opposing factors in most ganglion and lateral geniculate cells. As a consequence, there is a relatively high degree of diversity in the results. However, the relations of stimulus intensity to response strength may be classified into six groups, as illustrated in Fig. 8.

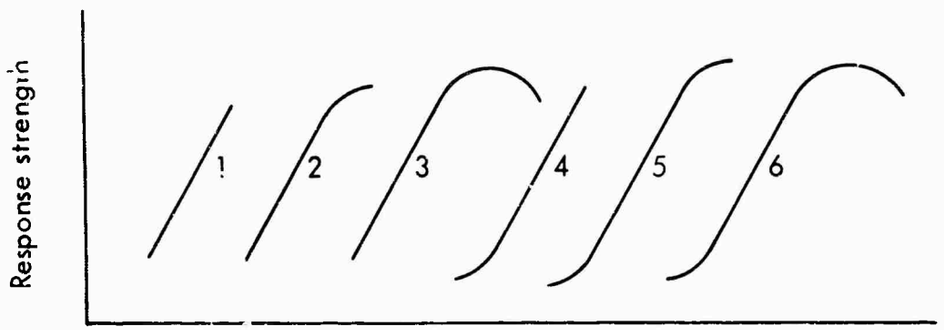

Fig. 8 — Relation of response strength to stimulus intensity

There are few data relative to intensity influence on responses in primate ganglion cells. Hubel and Wiesel[42] found that in an "off" cell "a decrease in intensity of the [spot] white light produced even weaker 'off' responses."

Firing frequency in lateral geniculate cells of the primate is systematically related to the intensity of a diffuse stimulus.* Increasing the light intensity increases the rate of firing in a cell that has been excited by this stimulus and decreases the rate of firing in a cell that has been inhibited. The difference between the frequency associated with the stimulus and the spontaneous frequency is usually related to the logarithm of stimulus intensity as in form 5 of Fig. 8. However, the slopes vary widely among cells, and in some cells responses are irregularly related to light intensity.

The results of two investigations[79,96] of the dependence of the response in cat ganglion cells on diffuse light intensity are consistent, although the scatter in parameter values is large. "Off" responses in both "off" cells and "on-off" cells exhibit a dependency of form 3. Both investigators report curves of type 2 or 3 for the "on" response in "on" cells. The "on" response in "on-off" cells, however, seems to be anomalous. Suzuki et al.[79] report frequency dependencies which are essentially flat over relatively wide intensity ranges and which consistently exhibit single depressions, often at the intensity level associated with the peak of the "off" response from the same cell.**

Fitzhugh,[98] averaging frequencies based on 10-ms "bins" over many cat ganglion cells, found a relation between the logarithm of frequency increase above spontaneous level and the logarithm of diffuse light intensity which was linear over a wide range and leveled off at high intensities.

Brown and Wiesel[99] report a ganglion cell of the "off" variety which exhibits increasing latency in the "off" response to increasing light intensity.

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*See Refs. 45, 46, 50, and 51.

**The "on" response in "on-off" cells differs further from other types of response in showing shorter latencies,[97] decaying faster,[79] and exhibiting spectral responses distinguishable from those of the other types (see Section V). Hartline[22] found that in the frog the only response measure linearly related to the logarithm of stimulus intensity was the reciprocal of latency in this response type.

Suzuki et al.[79] report response dependencies on diffuse light intensity in lateral geniculate cells of the cat to be of the same form as their counterparts in cat ganglion cells (form 3 in "off" and in "on" responses, and the relatively flat, anomalous behavior in the "on" response of "on-off" cells). Erulkar and Fillenz,[34] however, investigating the same situation, report that an increase in intensity was followed by an increase in response duration and in total number of spikes in some cells, and by a decrease in these two measures in others. (It should be noted that these statements do not necessarily imply a decrease of some average frequency based on a fixed time period in either case.) With increasing intensity, some cells exhibited an increase in first-spike latency and others exhibited a decrease. Neither of these behavior patterns was associated exclusively with either "on" or "off" responses. In "on-off" cells the latency dependencies for the two responses were of opposite types (one increasing, the other decreasing). It is reported that these inverse latency curves are of form 2, but the data show large scatter at high intensities, and the curves exhibited appear to be consistent with a linear relationship throughout the intensity range. There is great variability among the slopes of these curves, ranging from a 10- to 300-ms latency change in a 10^4 intensity increase.

Suzuki and Kato[65] report a relation of type 5 between the magnitude of a response in the cat LGN and the intensity of a shock delivered to the optic tract. When the response was conditioned by stimulation of the visual cortex (see Section II), the response was diminished, but the form of the relation remained unchanged.

As indicated earlier, those rabbit ganglion cells which are preferentially sensitive to motion are very insensitive to light intensity.[88,89] Thomson, however, reports more conventional cells in the rabbit retina which respond to increased intensity with an increase in frequency and a decrease in latency.[52]

In the lateral geniculate cells of the rabbit, it is reported that an increase in diffuse light intensity does not seem to be correlated with frequency per se but that it does result in improved synchronization of the spikes to the flashes of a flickering light.[53]

V. THE INFLUENCE OF STIMULUS WAVELENGTH

The effects of stimulus wavelength are usually displayed as curves in a plane: The abscissa is the stimulus wavelength, the ordinate is response measure, and a parameter sometimes represents the stimulus intensity. In some cases, response measures (inverse first-spike latency or "average" frequency) are plotted directly. In other cases, the reciprocal of the energy necessary to achieve either (1) an arbitrary level of either response characteristic or (2) threshold is used as a measure of "sensitivity." Response measures that are plotted directly are referred to as spectral response curves, and the others are referred to as sensitivity curves.

Consider first the responses of primate ganglion cells. Gouras[25] has shown that there exists a critical level of light intensity below which spectral response curves, based on latency or number of spikes, exhibit a broad peak at about 510 mμ. Above 510 mμ this peak shifts. Below the critical level, monochromatic lights whose intensities are balanced for scotopic vision produce identical effects in a given ganglion cell, while above this level, a sensitivity curve resembles the spectral sensitivity of peripheral-cone vision.

In a preliminary investigation using monochromatic light, Hubel and Wiesel[42] found three types of primate ganglion cells: (1) cells giving "on" responses to all wavelengths, (2) cells giving "off" responses to all wavelengths, and (3) cells in which a change in wavelength caused a change in the type of response. There were "indications of some variability in the spectral sensitivity peaks" of cells in groups (1) and (2). Only 3 cells out of 100 were of group (3), and these cells gave "off" responses to long wavelengths (> 500 mμ). Furthermore, cells of groups (1) and (2) responded "briskly" to white light, while those of group (3) were relatively insensitive to it.

DeValois and his colleagues* have probed the electrical activity of single lateral geniculate cells in monkeys in relation to diffuse, monochromatic light stimulation. Three classes of cells have been

*See Refs. 43 through 51, 100, and 101.

found, and each class is relegated exclusively to two adjacent lateral geniculate laminations.[43-45,50]

Cells in the two dorsal layers give "on" responses to all stimulation regardless of wavelength,[43-45] and some cells are characterized by a relatively low level of spontaneous activity. Spectral response curves, based on firing frequency, are of two types: those with narrow single peaks and those with double peaks. Cells with receptive fields in the fovea are virtually all of the narrow, single-peak variety and do not exhibit peak shifts with varying levels of background illumination. Single peaks appear at 510, 550, 590, or 620 mμ. A commonly occurring type of cell exhibits a narrow peak at 440 mμ and a lesser peak at 510 mμ, all cells with a peak at 440 mμ having another at 510 mμ. Furthermore, many cells exhibit a peak at 510 mμ and a lesser one at 440 mμ, although some show only single peaks at 510 mμ. Cells with receptive fields in the retinal periphery are more likely to display multiple peaks and do exhibit peak shifting with a change in background illumination. Another commonly occurring type of cell shows double peaks in the red and green regions.

Another class of cells consists of those in the two ventral layers which give "off" responses to all wavelengths.[43-45,50] Most of these cells exhibit spectral response curves with broad single peaks around 510 or 550 mμ, although a few curves do have narrow peaks. Thresholds, measured by decreased firing frequency during light stimulation, are 2 to 3 log units lower in these cells than in the "on" cells. Also, a higher level of spontaneous activity is encountered here.

The cells of both of the above classes are quite sensitive to light intensity,* showing the same type of logarithmic dependence that they show to white light (see Section III). They are reported to be quite insensitive to shifts in wavelength when the standard and test wavelengths are balanced for equal photopic brightness.

The third class of cells consists of those of the intermediate layers whose response type changes with a change in the wavelength of the stimulus.** Figure 9 shows the forms of spectral response curves

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*See Refs. 46, 48, 50, and 51.

**See Refs. 44, 45, 47, and 50.

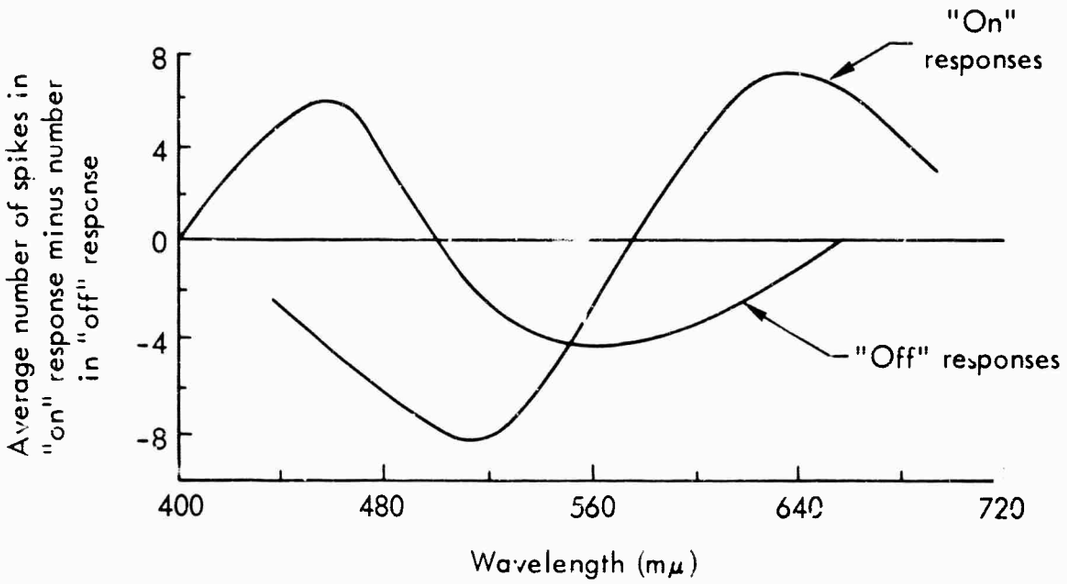

Fig.9 — Spectral response curves for several dark-adapted cells[45]

for several dark-adapted cells. These curves are based on the average firing frequency in an "on" or "off" response to constant-energy stimulation.

The cell at the lower end of the spectrum (green or blue) may give either an "on" or an "off" response, but the response at the other end of the spectrum (red or yellow) is always of the opposite type. The "on" and "off" regions are separated by a range of about 20 mμ, through which the cell elicits essentially no response. The cells are characterized by an almost complete absence of response to white light, even of very high intensities. Although these curves show "considerable variation both in terms of the sensitivity peaks and the relative balance between the two opponent processes,"[47] they fall into one of two classes: opposing response peaks of red and green and opposing response peaks of blue and yellow.

Spectral curves have been obtained from the red-green cells by monochromatic light adaptation.[47]* Adaptation to a wavelength corresponding to one of the spectral peaks of a cell results in complete elimination of the type of response associated with that peak, the

*No information pertaining to this aspect of behavior in blue-yellow cells has been found.

opposite response type now occurring at all wavelengths. The wavelength of the optimum response is some 30 mμ closer to the spectrum center than in the dark-adapted case. The curves obtained in this manner show very little variation from cell to cell, as seen in Fig. 10.[47]

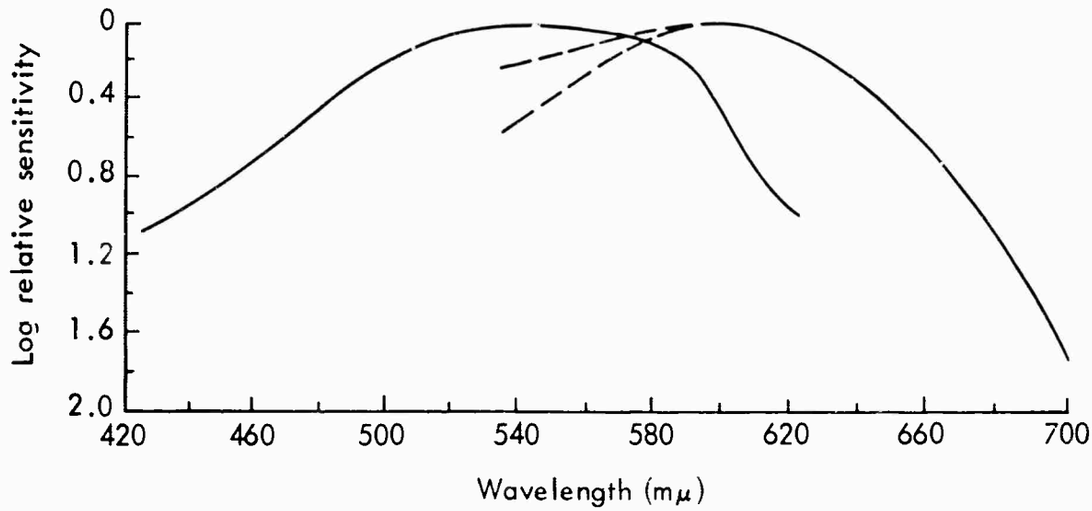

Fig. 10 — Spectral curves in red-green cells adapted to monochromatic light[47]

All the above observations relating to these "on-off" cells of the intermediate layers are based on constant-energy stimulation.* When adapted to monochromatic light, the sensitivity of these cells to changes in wavelength has been investigated on the basis of constant-luminosity stimuli.[48] Both the red-green and blue-yellow cells have been found to be quite sensitive to wavelength changes throughout the spectrum. This is particularly true of the red-green type in the region of 560 to 610 mμ and of the blue yellow type in the regions of 470 to 500 mμ and 550 to 600 mμ. These cells in general are very insensitive to intensity changes compared to the other two classes of

*The two single-peak spectral response curves of light-adapted red-green cells, based on stimuli balanced for photopic illumination, dictate a curve of $\Delta\lambda$ versus λ which matches psychophysical-hue discrimination data.[47]

cells; however, they do show some intensity sensitivity, and this is inversely related to the wavelength sensitivity.

In an examination of the LGN of the squirrel monkey,* Jacobs[49,100] attempted to correlate the increase or decrease in frequency during light stimulation to the intensity and wavelengths of monchromatic stimuli. He found that the cells fall into one of three groups: those giving "on" responses to all wavelengths, those giving "off" responses to all wavelengths, and those whose response type changes with wavelength. The spectral curves of all cells of the first two groups exhibit broad spectral peaks between 530 and 590 mμ. There is a good deal of variability in the data, and secondary peaks and depressions are often observed. The response frequencies, averaged over (1) several excitatory cells and (2) several inhibitory cells as functions of wavelength and intensity, exhibit roughly linear relations to the logarithm of intensity. A spectral sensitivity curve, based on the intensity necessary to obtain a given frequency, matches the photopic luminosity function. Similarly, responses averaged over four additional cells giving "off" responses only can be made to approximate the scotopic luminosity curve.

Jones[101] reports that cells of the LGN of the owl monkey respond to diffuse monochromatic stimulation with either increases or decreases in firing rate. No cell was found which changed its response type with a change in wavelength. Spectral sensitivity plots of 143 cells reflected 3 classes of cells with peak sensitivities at about 500, 530, and 560 mμ.

Granit[93,102,103] reports sensitivity curves taken from dark-adapted cat ganglion cells which approximate both the rhodopsin absorption spectrum and the human scotopic sensitivity curve (exhibiting broad peaks at about 500 mμ). Furthermore, in the light-adapted cells studied, about 36 percent showed sensitivity curves approximating the human photopic curve (exhibiting broad peaks at about 560 mμ).[93,104]

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*This species is deficient in retinal cones, exhibits an essentially unlaminated lateral geniculate body, and has a severe discrimination loss at the red end of the spectrum.

Suzuki[79] reports "off" responses, "on" responses, and "off" components of "on-off" responses in light-adapted ganglion cells of the cat which exhibit sensitivity curves with broad peaks at about 500 mμ, the "on" response in "on-off" cells being anomalous. Also, at low intensities spectral response curves in all response types show a broad peak at about 500 mμ, and at higher intensities the peaks are one of two types: either a broader peak at 500 mμ or a flat plateau over the entire spectrum except for the red end, where there is a precipitous drop. Donner[96] describes a light-adapted cell whose spectral response curves show the latter type of intensity dependence. In general, he reports "on" responses exhibiting spectral response curves of the broad 500 mμ-peak variety and more irregular "off" curves exhibiting various shapes and multiple peaks.

Neither sensitivity nor spectral response curves having narrow peaks have been discovered in cat ganglion cells. Granit, however, has obtained such narrow-peaked sensitivity curves indirectly by subtracting curves obtained in different adaptational states.[105] (See Ref. 106 for a review of Granit's attempt to find these "modulators" by indirect methods.)

Lennox[97] reports that cat ganglion cells giving strong responses to red stimulation are correlated with fast-conducting optic fibers and that those giving strong responses to blue stimulation are correlated with slow-conducting optic fibers. Cohn's report[32] is consistent with this in that responses to blue light occur in the lateral geniculate body about 5 ms later than responses to yellow or white light.

Suzuki[79] reports sensitivity curves obtained from light-adapted lateral geniculate cells in the cat which are similar to those found in ganglion cells. The spectral response curves of these cells, however, were more complicated. At low intensities the curves exhibited the common broad peak at 500 mμ, but as the intensity was increased this peak disappeared and two maxima (420 through 480 mμ and 520 through 600 mμ) appeared. This behavior was reported for all response types.

Cohn[32] failed to find any modification of pulse pattern in the LGN of the cat in correlation to the differing wavelengths of light with which he stimulated the retina.

Hill and Marg[107] report that rabbit ganglion cells exhibit spectral response curves with peaks at one of two wavelengths: 500 or 460 mμ. It is probable that the peak at 500 mμ is associated with rabbit rhodopsin and that the peak at 460 mμ is associated with the rabbit cone pigment.

It has been reported[108] that sensitivity curves (of both varieties) based on rabbit ERG, i.e., potentials representing a large number of retinal cells, are the same in both the light- and dark-adapted states and approximate closely the rhodopsin absorption curve.

Evidence of an absence of clear-cut wavelength effects in the lateral geniculate cells of the rabbit has been reported:[109] Eighty-nine of 106 sensitivity curves from 51 cells were put into 7 groups according to the location of spectral peaks (435, 445, 460, 505, 515, 580, and 635 mμ); in 2 groups (445 and 505 mμ) the responses were inhibitory, and the other responses were excitatory.

VI. TEMPORAL FEATURES

RESPONSES TO SUSTAINED STIMULI

No systematic investigation of the time course of responses to sustained stimuli in single, primate ganglion cells has been found. Figure 11 shows examples of four such responses based on spike trains recorded from an "on"-core unit and an "off"-core unit by Hubel and Wiesel.[42] The frequency values are based on the numbers of spikes in successive 100-ms intervals. The responses obtained by stimulating the core of the receptive field exhibit firing frequencies whose steady values during stimulation differ from the spontaneous rates. The one response which corresponds to stimulation of only the periphery, on the other hand, shows a steady level during stimulation which is the same as the spontaneous level. The latencies of the core responses are about 50 ms, while the latency corresponding to only periphery stimulation is about 90 ms. The responses of both cells reach a peak in about 100 to 200 ms; the responses of both cells to core stimulation and of the "off" cell to peripheral stimulation indicate a depression occurring about 700 ms after onset or cessation (as the case may be) of stimulation.

Any inferences based upon details of these curves must be highly tentative because there is a degree of variability among responses, and characteristics of these four examples may not be representative.

Donner[96,110] reports that "on" and "off" responses to diffuse light stimulation in cat ganglion cells show time courses which rise in about 100 ms to a plateau which is maintained for another 100 ms and then decline to a steady level in about 300 to 500 ms. There is a systematic relationship between the rise time of the response and the wavelength of the stimulus; that is, wavelengths of 460, 520, and 600 mμ correspond to rise times of 300, 220, and 150 ms, respectively. In general, the rise time decreases with increasing stimulus intensity.

Ogawa et al.[111] report poststimulus histograms taken from responses to diffuse light stimulation in dark-adapted ganglion cells of the cat which show the form exhibited in Fig. 12. As these curves

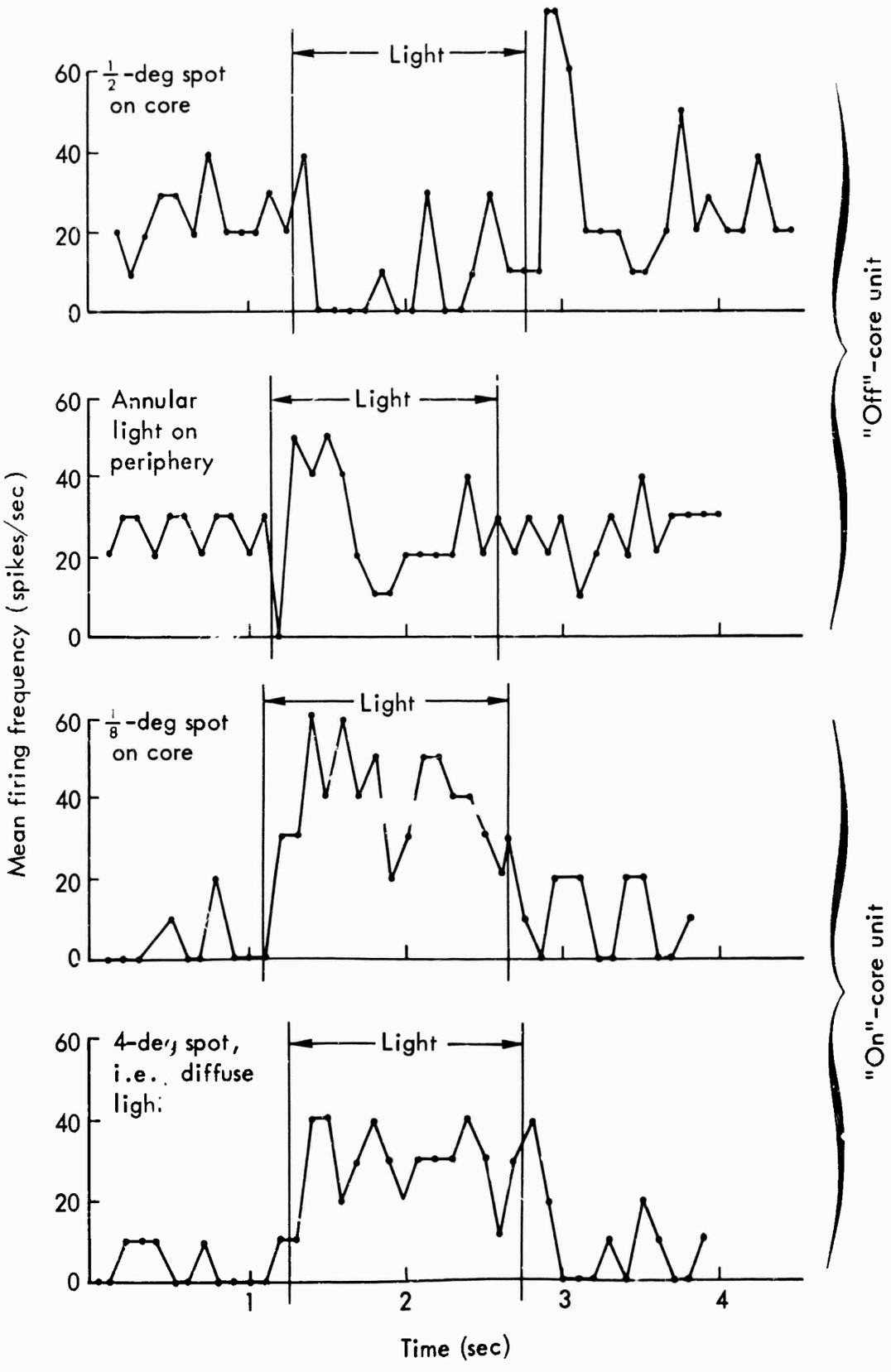

Fig.11— Time course of responses in primate ganglion cells based on the number of spikes in 100-ms intervals

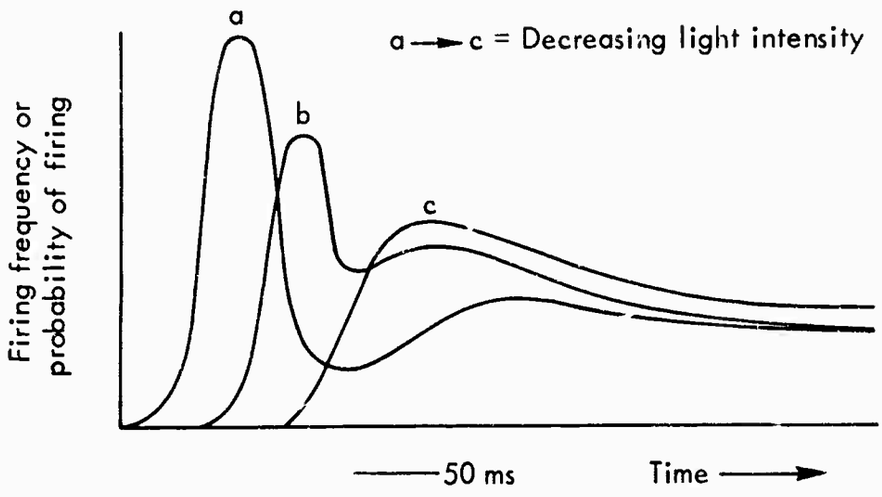

Fig. 12 — Time course of responses in cat ganglion cells[111]

are based upon the superposition of responses in the same cell to several repetitions of stimulation, the ordinate is to be interpreted as either firing frequency or probability of firing.

Although investigators have referred to "on" and to "off" responses to sustained stimulation in single, lateral geniculate cells in both primates and cats, no explicit discussion of their time courses has been found.

OSCILLATORY RESPONSES

Doty et al.[112,113] have reported that population recordings taken with macroelectrodes in the optic tracts of cats and monkeys exhibited oscillations in response to 10-μs flashes of light. The frequency of oscillation was between 50 and 160 cps and was "definitely not a function of intensity."[112] The "on" response in the monkey to a bright 10-μs flash showed a latency of about 10 ms, oscillated at a frequency of 150 to 160 cps, dropped abruptly in amplitude and frequency after a few cycles, and lasted for about 100 ms. The amplitude and regularity of the oscillations were augmented by repeated flashes at 0.3 cps. In the monkey, oscillations followed each flash at stimulus frequencies up to 20 flashes/sec. Removal of the forebrain

did not affect the behavior. As the flash duration increased beyond 50 ms, the amplitude of the oscillations declined; the oscillations were not obtained with flash durations longer than about 500 ms.

Similar oscillatory activity has been recorded in single, cat ganglion cells. Steinberg[114] reports that single ganglion cells in the cat responded to a single 10-μs flash with 3 to 6 bursts after a latency of about 16 ms and then were inhibited for 50 to 150 ms. The first burst was the longest and had the highest frequency, sometimes approaching 900 sps. He often found a secondary excitatory period, sometimes followed by another inhibitory period and a third excitatory period.

In response to rhythmic flashes regular grouping of the bursts was developed in every unit studied, including "on," "off," and "on-off" types.* The mean intergroup period was 10 ms (8 to 20 ms). The grouping evolved as follows: There was always an initial high-frequency burst (regardless of the adaptive state and number of previous flashes) and then an irregular series of spikes; in each subsequent response the spikes were progressively more grouped. The grouping was enhanced by adaption to a sustained light.

As discussed in Section II, Fuster et al.[30] reported that interspike-interval histograms taken from records of spontaneous activity in single, cat ganglion cells exhibited a mean mode of 9.1 ms. They reported also[30] that histograms taken from responses in the same cells, obtained with either steady or flickering stimuli, exhibited different shapes and different frequencies from the spontaneous case. Some of the flickering responses developed another mode corresponding to the frequency of stimulation, but the original mode remained prominent and unchanged in value.

Ogawa et al.[111] have also reported that single ganglion cells in the cat tend to fire in both the driven and spontaneous state at a preferred interval of about 20 ms.

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*The grouping of bursts under consideration here occurred between stimulus flashes which were presented at frequencies of 0.1 to 5 cps. Thus, the situation is somewhat different from that discussed on p. 38.

Negishi et al.[41] report that single cells in the LGN of the cat responded to a 10-μs flash with an increase in firing frequency to a value of 20 to 100 sps in 20 to 40 ms, a decrease to about 37 sps at 60 to 80 ms, and an oscillation in frequency which terminated at a value of about 30 sps in close to 500 ms.

They report that cells whose latencies in responses to single 10-μs flashes are between 20 and 60 ms and those whose latencies in such cases are greater than 60 ms exhibited responses whose latencies increased and decreased, respectively, with increasing stimulus frequency. The cells responded maximally to stimulus frequencies of 9 to 12 cps.

Fuster et al.[30] report that interspike-interval histograms based on recordings taken from responses to flashing light stimulation in single lateral geniculate cells in the cat are different from those based on spontaneous activity in the same cells (see Section II) only in that the incidence of small interval values is increased; no new peaks are observed, and the overall profile is maintained.

FLICKER FUSION

References 111 and 115 through 117 describe investigations of responses in cat ganglion cells to flickering stimuli in relation to the psychophysical relations of flicker fusion.[118] The responses were reported to exhibit a transient phase at the onset of stimulation which involved a more or less continuous outburst of spikes. The response evolved into a series of bursts which were produced on a one-to-one basis with the stimulus flashes after a period of about 1 sec for light- and dark-adapted cells with high stimulus intensities and about 1 min for dark-adapted cells with low or moderate stimulus intensities. As stimulus frequency was increased from 0.5 to 20 cps, the number of spikes in the individual bursts decreased. In this process the bursts appeared to be "cut off from behind forward."[111] At stimulus frequencies above 20 cps, spikes were usually produced on a one-to-one basis with the stimulus flashes. At higher frequencies the relation of the response to the stimulus became progressively less certain.

Poststimulus histograms were about the same for "on" and "off" cell types. In both types of cell the latencies of the excitatory and

inhibitory effects varied together, and the latency of inhibition was somewhat smaller than the latency of excitation; for example, 20 ms for inhibition as compared to 25 ms for excitation at one level of light intensity. The latencies did not appear to be correlated with flash frequency.

Dodt and Enroth[117] defined the fusion frequency by noting when the strict relationship between flash and discharge ceased. Ogawa et al.[111] defined it by noting when the firing pattern no longer permitted discrimination of a flickering light from a steady light. Both definitions result in relations between fusion frequency and stimulus intensity which match the psychophysical data. Figure 13 shows the results obtained by Ogawa et al.

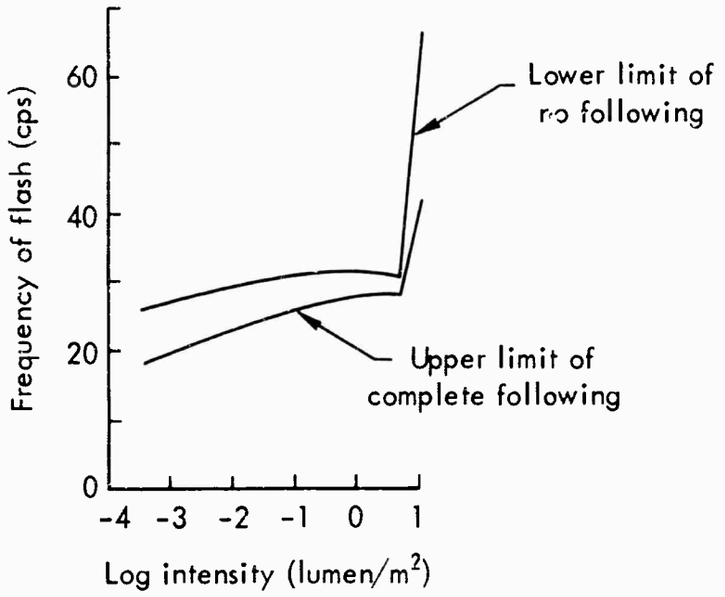


Fig. 13 — Relation of flicker-fusion frequency to flash intensity in an "on"-core unit of the cat[111]

Enroth[115,116] reports also that the average frequency in the last three bursts prior to fusion which had four or more spikes each was related linearly (slope about 0.25) to the fusion frequency. Enroth was recording from large ganglion cells of the cat's retinal periphery, and Ogawa et al. were recording from the smaller cells in the area centralis.

MISCELLANEOUS STIMULUS PATTERNS

Rodieck et al.[87,119] have recorded the responses to moving stimuli in single ganglion and lateral geniculate cells in the cat. Light-adapted ganglion cells[119] were classified into one of two groups on the basis of their responses to white and black pieces of cardboard moving at 10 deg/sec across their receptive fields. The defining response types are shown in Fig. 14. The type-1 response was obtained from "on" cells to white stimuli and from "off" cells to black stimuli; the obverse combinations gave the type-2 response.

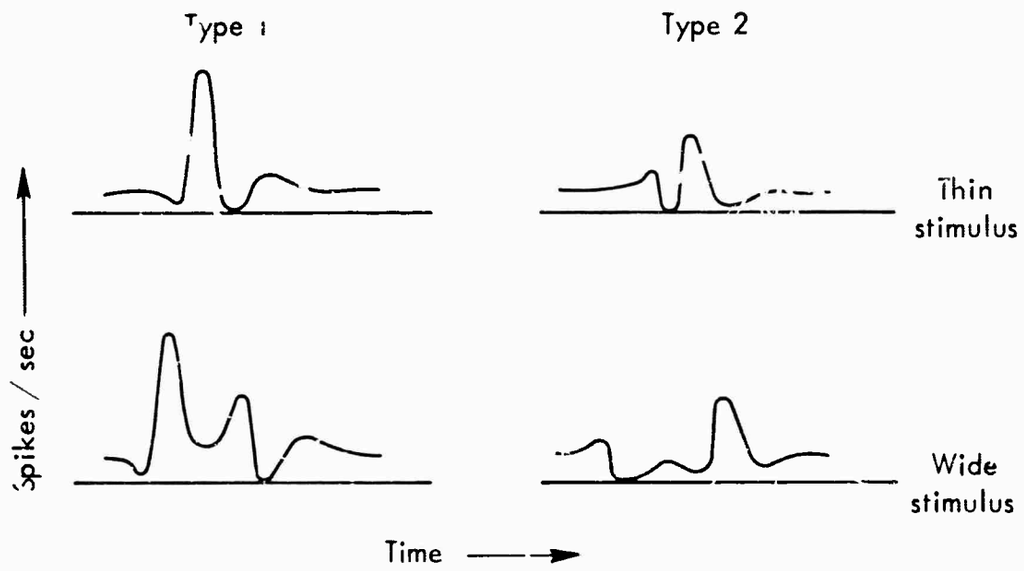


Fig. 14 — Responses in light-adapted cat ganglion cells to moving stimuli[119]

The response types were insensitive to the shape of the stimulus, but the relative proportion of the center response increased as the width of the stimulus was increased. The response curves became more symmetric as the speed of the stimulus was reduced, and no cells were found to respond preferentially to motion in a specific direction.

In light-adapted cells the response curves were of the same form at all levels of background intensity, but the amplitudes could be

reduced by about 30 percent by a hundredfold change in intensity. In the dark-adapted case the first suppression (left to right) shown in the curves of Fig. 14 was absent; there was a unimodal elevated phase, followed by a suppression which was much smaller than in the light-adapted cases.

Responses of lateral geniculate cells to comparable stimuli were more difficult to interpret.[87] The classification and number of observed cells were as follows: "on," 42; "off," 48; "on-off", 4; binocular, 4; large-field, 13; direction-sensitive, 5; other, 14. Figure 15 is based on the discussion in Ref. 87 and is intended to represent the responses in the "on" and "off" cells.

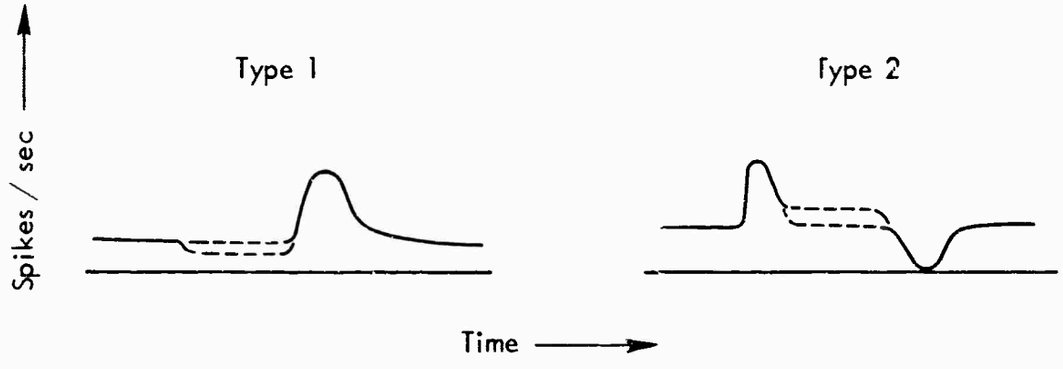


Fig. 15 — Responses of lateral geniculate cells in the cat to moving stimuli

The type-1 response was obtained from "on" cells with black stimuli and from "off" cells with white stimuli. The type-2 response was obtained with the obverse combinations. Response patterns in these cells were the same when the stimuli were moved across chords of the receptive field as when the stimuli were moved across a diameter and were the same in the light- and dark-adapted states.

Hughes and Maffei[120] report that spike frequencies, recorded in ganglion cells in the cat which are responding to diffuse light stimulation of sinusoidally varying intensity, are approximately sinusoidal except at high frequencies. They define parameters L_o, L, ω, R_o, R, and θ by the equations

$$\text{Stimulus intensity} = L_o + L \sin \omega t$$

$$\text{Response frequency} = R_o + R \sin (\omega t - \theta)$$

The following relations among these parameters are reported. The dependence of R_o on L_o was weak and exhibited an optimum in most cases. The parameter R_o was independent of ω below 5 or 10 cps, exhibited a peak at about 20 cps, and declined to the low-frequency value at about 50 cps. They state that R_o also depended on L, but this is not fully discussed.

For values of ω less than about 1 cps, R was proportional to L to the 0.75 power; for higher values of ω, R rose faster with L. The value of R was relatively independent of ω except for a range of ω between about 5 and 50 cps, where it exhibited a single sharp peak. The frequencies corresponding to the peaks were higher in "off" cells than in "on" cells.

For small values of ω, θ was about 315 deg for "on" cells and about 140 deg for "off" cells. At high frequencies both cell types exhibited linear relationships between θ and ω, and all appeared to approach lines with slopes of -65 ms.

Enroth-Cugell and Jones[121,122] found diverse responses in ganglion cells of the cat to diffuse stimuli which were increased exponentially, held constant, and decreased exponentially at various rates of rise. Most cells showed a transient increase in spike frequency during the increasing and decreasing phases. Usually the amplitude of the response increased monotonically with the rise rate, but some cells showed maximum responses with rise times in the range of 500 to 1500 ms. Some cells exhibited decreased frequencies during the latter half of the rise period, followed by an increase in frequency during the

constant period. In these cells inhibition in any phase of a response to an abrupt stimulus was much less pronounced than in most other cells.

There was much diversity and apparent irregularity among responses associated with the decreasing period. These responses were influenced in most cases by the stimulus rise time, decay time, and duration of the constant period. The responses of one cell, for example, changed from inhibitory to excitatory, as only the duration of the constant period was changed.

The responses of some cells changed with adaptive state, while those of others did not.

VII. CONCLUDING REMARKS

Salient features of the data reviewed in this Memorandum are summarized in Table 1. The following would be valuable additions to the existing data:

1. Single-cell data from ganglion cells of the primate fovea, including information about the time course of response to sustained, brief, and flickering lights; receptive-field organization; spectral sensitivity; dependence on stimulus intensity; and determination as to whether or not all foveal units are "on" types.
2. More detailed studies of ganglion cells in the periphery of the primate retina.
3. Data from lateral geniculate cells in the primate in relation to small-diameter stimuli, and in particular, information about receptive-field organization and temporal features of behavior.
4. Single-cell studies from bipolar cells in cats and primates.
5. A theory of the behavior of the underlying circuitry at any level in any species.

In Fig. 1 relations between neuroelectric activity and subjective responses are labeled type "c." Relations of this type are indicated with varying degrees of specificity by the data reviewed in the preceding sections. Neural substrates for each of flicker fusion, intensity encoding, spatial and temporal contrast, and wavelength encoding are indicated. Furthermore, the data of Donner[96,110] and the observed "oscillatory" activity suggest a possible basis for subjective-color phenomena.

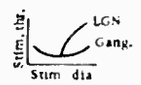
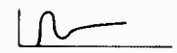
It should be clear that the data are sufficiently abundant to meet the requirements of the approach outlined in Section I, particularly with regard to the cat. A cogent theory of the behavior of the underlying structures in this species would be more valuable than additional data from ganglion or lateral geniculate cells.

Tentative, working hypotheses might be that the influences of attention and motivation are mediated primarily in the LGN and the cortex

Table 1

Table 1

SUMMARY OF SALIENT CHARACTERISTICS OF RETINAL GANGLION AND LATERAL GENICULATE SPIKE TRAINS

Cell Type	Spontaneous Activity	Receptive Field	Area of Stimulus	Intensity of Stimulus	Wavelength of Stimulus	Temporal Features
			Primate			
Ganglion	Resembles that in cat ganglion cells.	Small circular core regions giving "on" or "off" responses, and opposing annular periphery. Core dia are smaller towards the fovea. Perhaps "on" cores predominate near the fovea. Annular periphery absent in dark-adapted state.	No quantitative information.	No quantitative information.	There are 3 classes of cells: 1. "On" response - all λ 2. "Off" response - all λ 3. Response type changes with λ (~ 3% of total and relatively insensitive to white light).	Stimulus flashes < 50 ms in duration cause oscillations ~ 150 cps; enhanced by repetitive flashing.
Lateral geniculate	Rate = 10-20 cps. Unrelated to level of background illumination.	No information.	No information.	Discharge frequency essentially proportional to log intensity. There is much diversity in slopes among cells.	Same trichotomy as for primate ganglion cells. The "on" cells exhibit narrow spectral peaks, the "off" cells broad ones. "On-off" cells relatively insenaitive to white light.	No quantitative information
			Cat			
Ganglion	Rate = 20-30 cps. Interspike intervals exhibit gamma distribution and only the first serial coefficient is significantly different from zero.	Core and opposing periphery. Effects of annular periphery are not present in the dark-adapted state. Also, an influence reaching over 1 cm and selectively sensitive to motion.	Stimulus threshold vs stimulus dia:  Firing frequency exhibits dependence on stimulus dia consistent with this curve.	Discharge frequency essentially proportional to log intensity. There is much disparity in slopes among cells. "On" response in "on-off" cells is anomalous.	Spectral response curves in dark-adapted cells approximate rhodopsin absorption spectrum; ~ 35% of those in light-adapted cells approximate photopic vision spectrum. Other results nebulous.	Time course for response to sustained stimulus:  Short flashes cause oscillations ~ 100 cps, enhanced by light-adaptation or repetitive flashing. Cells tend to fire at preferred intervals of ~ 10-20 ms. Flicker fusion corresponds to psychophysical data. Latencies of inhibition smaller than those of excitation. Response to sinusoidal stimulation maximal at frequency ~ 5-50 cps; maxima at higher stimulus frequency in "off" cores than "on" cores.
Lateral geniculate	Rate = 10-20 cps. Interspike intervals exhibit Poisson distribution except for small values of interval. Pulses tend to cluster in the sleeping cat.	Same arrangement as in cat ganglion cells with stronger influence of annulus on core. Some cells not of core-annulus type have been reported.	Stimulus threshold vs stimulus dia shown above.	Same as in cat ganglion cells.	Essentially the same as in cat ganglion cells.	Response to flash lasts up to 500 ms. There are plastic effects lasting from ~ 2 sec to several min. Response to flashing stimulus maximal at stimulus frequency ~ 9-12 cps.
			Rabbit			
Ganglion	Rate = 20-30 cps. Tendency for pulses to occur in groups of 2 or 3.	Widely diverse arrangements and cells with preferential but brief responses to speed and direction of motion "Off" response not necessarily associated with inhibition of spontaneous activity.	Threshold is proportional to 1/A within 20' of field center and to $1/\sqrt{A}$ from 20' to 3 deg in cells with homogeneous fields.	Light intensity does not affect frequency magnitude but improves synchronization of pulses to light flashes.	Spectral response curves show peaks at either 500 or 460 mμ.	Not reviewed here.
Lateral geniculate	Rate = 10-20 cps. Tendency for pulses to cluster in groups of 2 to 8.	Essentially the same as in rabbit ganglion cells.	log threshold is proportional to log area illuminated.	Same as in rabbit ganglion cells.	Sensitivity curves based on latencies yield peaks at one of seven wavelengths.	Not reviewed here.

by the BSRF which, in turn, is responding to input from hypothalamic and cortical centers. The electrical behavior corresponding to the concept of set might also involve the brain reticular formation and/or cortical centers, while gestalt interpretation might be relegated to cortical centers.

The data indicate that the elemental relations of psychophysics reflect properties of retinal behavior. Indeed, electrical correlates of flicker fusion, intensity encoding, and spatial and temporal contrast are seen in the spike trains of ganglion cells. The data of deValois suggest that information about color vision may be further amplified in the LGN in primates.

These tentative suggestions might be useful guidelines in formulating investigations of specific underlying networks. In particular, the concept that the psychophysical relations are mediated primarily in the retina, along with the neuroelectrical and neuroanatomical indications that centrifugal control at this level is small, suggests that the retina would be a potentially fruitful point of focus for initial theoretical attempts.

It is necessary to be cognizant of possible differences between species. The electrical data reviewed here and anatomical data* suggest that the networks of the periphery of the primate retina are similar to those of the cat retina, but that the primate foveal networks are different and that the LGN of the cat is different from the primate LGN.

There are many electrical and anatomical[125-131] data taken from the cat retina but few behavioral data. On the other hand, there is a large amount of anatomical[3,131-140] and behavioral[118,141-143] data pertinent to the primate retina, but few direct electrical data.

A significant obstacle in the approach suggested here (one which applies in a general sense to the discussion of Section I) is the absence of a cogent and generalized theory of neural behavior. Ideas do exist, however,[2,144] and it is precisely this situation that makes the problems challenging and intriguing.

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*See Refs. 3 and 123 through 138.

From this point of view, it is suggested not only that more research in the networks of the retina is promising for a fundamental understanding of some elemental aspects of perception, but also that the cat retina in particular is a very propitious subject of study for solutions to basic questions of neural integration.

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10. ABSTRACT

An examination of the relationship between the physical stimulus and the neuroelectric events involved in visual perception and discrimination. The data indicate that certain elemental relations of psychophysics reflect properties of retinal behavior. Electrical correlates of flicker fusion, intensity encoding, and spatial and temporal contrast are seen in the spike trains of ganglion cells. The concept that some psychophysical relations are mediated primarily in the retina, along with the neuroelectrical and neuroanatomical indications that centrifugal control at this level is small, suggests that the retina would be a promising point of entry for understanding some of the neural mechanisms subserving vision.

11. KEY WORDS

Neurophysiology
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