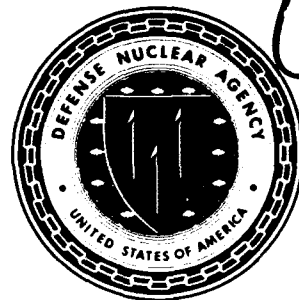


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DNA-TR-91-111

Animal Models of Ionizing Radiation Damage

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January 1992

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Technical Report

CONTRACT No. DNA 001-88-C-0120

92-01968



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Public reporting burden for this collection of information is estimated to average 1 hour per response including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503				
1. AGENCY USE ONLY (Leave blank)	2. REPORT DATE 920101	3. REPORT TYPE AND DATES COVERED Technical 880518 - 910518		
4. TITLE AND SUBTITLE Animal Models of Ionizing Radiation Damage		5. FUNDING NUMBERS C - DNA 001-88-C-0120 PE - 62715H PR - R99QAXE TA - B WU - DH009150		
6. AUTHOR(S) Lynda L. Pippin, DVM				
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Pathology Associates, Inc. 15 Worman's Mill Court Frederick, MD 21701		8. PERFORMING ORGANIZATION REPORT NUMBER		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) Defense Nuclear Agency 6801 Telegraph Road Alexandria, VA 22310-3398 MRCO/Collins		10. SPONSORING/MONITORING AGENCY REPORT NUMBER DNA-TR-91-111		
11. SUPPLEMENTARY NOTES This work was sponsored by the Defense Nuclear Agency under RDT&E RMSS Code B323075464 R99QAXEB06954 H2590D.				
12a. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution is unlimited.			12b. DISTRIBUTION CODE	
13. ABSTRACT (Maximum 200 words) This report is a survey of the English language literature of radiation biology between 1947 and 1987, for the purpose of compiling a literature base on the effects of radiation on animals, which have yielded results that can expand our knowledge about similar radiation effects on human beings. Articles were sought that reported exposure of adult mammals to external sources of ionizing radiation, having endpoints that included effects on the brain, the spinal cord, and behavior (Section 1 of the survey); the gastrointestinal, endocrine, and cardiovascular systems (Section 2); and the hematopoietic and immune systems (Section 3). Effects of interest were those that occurred within the first 12 months after exposure. The survey does not include articles reporting chronic or long-term delayed effects of radiation unless they provided insight into mechanisms of morphological and/or functional derangement. Information presented in the report is divided into subtopics (i.e., Brain—Morphological Changes). The brief introduction to each subtopic is followed by a condensed description of representative reports and a short summary of conclusions based on those reports. The articles reviewed are appended as a Bibliography, arranged alphabetically within subtopics. Articles discussed in the text are cited and assembled alphabetically as a "cited reference list"				
14. SUBJECT TERMS Radiation Immune System Cardiovascular System Behavior Brain GI System Endocrine System Ionizing Animal Spinal Cord Hematopoietic System				15. NUMBER OF PAGES 316
				16. PRICE CODE
17. SECURITY CLASSIFICATION OF REPORT UNCLASSIFIED	18. SECURITY CLASSIFICATION OF THIS PAGE UNCLASSIFIED	19. SECURITY CLASSIFICATION OF ABSTRACT UNCLASSIFIED	20. LIMITATION OF ABSTRACT SAR	

UNCLASSIFIED

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13. ABSTRACT (Continued)

in Section 4. Reviewed articles are also catalogued into tabular format, allowing the reader to easily identify articles that pertain to a specific topic, species, dose level, and type of radiation.

SUMMARY

This report, prepared by Pathology Associates Inc., Frederick, Maryland, under Defense Nuclear Agency (DNA) Contract DNA001-88-C-0120, is a survey of the English language literature of radiation biology between 1947 and 1987. Articles were sought that reported exposure of adult mammals to external sources of ionizing radiation, having endpoints that included effects on the brain, the spinal cord, and behavior (Part I of the survey); the gastrointestinal, endocrine, and cardiovascular systems (Part II); and the hematopoietic and immune systems (Part III). Effects of interest were those that occurred within the first 12 months after exposure.

The objective of the survey was to collate the literature about animals which yielded results that contribute to the basis of our knowledge about possible radiation effects on human beings. Emphasis was on usefulness to extrapolate effects on military personnel, with special interest on medical and tactical considerations. For these reasons, the survey does not include articles reporting chronic or long-term delayed effects of radiation unless they provide insight into mechanisms of morphological and/or functional derangement.

We have attempted to be as thorough as possible in the literature reviews, but do not claim that the survey is absolutely comprehensive. We believe it is solidly representative of the relevant literature and that the conclusions represent the conclusions of the scientific community. We apologize in advance to any authors whose work we may have overlooked or omitted.

In this effort, we encountered many articles, particularly in the older literature, that were incompletely reported. Important data that were omitted for some reports included number of animals per treatment or total number of animals; untreated control animals; age or strain of animals; one or more parameters of radiation exposure (total dose, dose rate, radiation type or energy, beam filtration, distance, etc.); time interval between exposure and observation; and other experimental factors. Only in recent years do the majority of the reports include data on husbandry conditions and diet composition, but there is still no uniformity in description of experimental parameters. Reviewers are thus obliged to accept the reported results at face value or to "discount" them to a degree proportional to the completeness of the description of the experimental conditions. Our practice was to apply an informal analysis to experiments that lacked complete description, seeking whatever "central tendency" might emerge for comparison to similar experiments. This approach permitted tentative overall conclusions to be reached, although judgments about specific details in particular experiments remained tentative. In many instances, we found a small number of well-executed studies that confirmed the conclusions suggested by earlier, less complete work.



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The format for this report includes a brief introduction to each subtopic, intended to provide a concise statement of the current understanding of that subtopic. This is followed by a condensed description of representative reports concerning the subtopic, more or less in historical sequence, a short commentary indicating our impressions of the strengths or weaknesses of the available data, and a short summary of our conclusions.

Appended are reading lists of the articles reviewed, arranged alphabetically within subtopic. The reading lists follow the same subtopic outline as the text. Articles discussed are cited in the text and are assembled alphabetically as a "cited reference list" after the respective subtopic. The articles are also catalogued into tabular format, allowing the reader to easily identify articles that pertain to a specific topic, species, dose level, and type of radiation.

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SECTION 1

RADIATION EFFECTS ON BRAIN, SPINAL CORD, AND BEHAVIOR

1.1 INTRODUCTION.

Historically, investigators have associated neural function with integrity of neurons. A review of the neural effects of ionizing radiation in animals forced the reviewer to abandon that simplistic approach. The "sensitive volume" to receive radiant energy includes both neurons and non-neuronal tissue, whether or not the nervous system per se is in the target field. Non-neuronal tissue volume is the greater of the two, even within the nervous system, where it is composed chiefly of glia and vasculature. Normal neural function requires normal function of the supporting glia and vasculature, so neural malfunction can result directly from neuronal damage, indirectly through damage to supporting structures, or by both routes. Moreover, the vital integrative role of the central nervous system (CNS) depends upon balanced levels of excitation and inhibition, generated through stimuli from all possible somatic and sensory sources. Even when the CNS is not in the radiation field, it will be the recipient of aberrant input from other irradiated sites (e.g., the abdomen) and thus will experience perturbation in its balanced function.

Interpretation of behavioral changes after irradiation, without regard to structural change, is similarly complex. Behavior formerly motivated by food reward may be confounded by anorexia following intestinal exposure. Performance on highly conditioned discrimination tasks may improve temporarily after heavy irradiation, presumably because radiation-induced malaise reduces curiosity and distractibility.

There are qualitative and quantitative differences in response among the various animal species, but no central unifying dogma to explain the seemingly random variations. Until more is known about comparative neurophysiology, reviewers must be content to simply catalog the differences. Although extrapolation to humans of those effects described in animals is beyond the scope of this report, a number of the articles reviewed did make comparisons with human data. Those data are relatively sparse, however, and are derived from nuclear industrial accidents, from Japanese survivors of the atom bomb detonations, from radiation therapy patients, and from volunteers. In virtually all instances, the number of comparable subjects is small, and the subjects are heterogeneous in most demographic characteristics. Rarely have exposure factors been known with confidence, except in radiation therapy patients. In these cases, large variations exist in pretreatment morbidity and in the exposures employed. Despite these problems, the "central tendency" in histologic changes, electrophysiologic observations, and behavior patterns reported for humans exposed to ionizing radiation is consistent in its broad aspects with that observed in more detail in animals. We are convinced that data available to date from well-controlled animal experiments provide a valid basis from which to extrapolate judiciously and to rationally predict radiation effects in humans.

1.2 BRAIN.

1.2.1 Morphologic Changes.

Studies by light microscopy consistently show relatively few structural changes in neural tissue at early times (days to weeks) following neural exposure to

radiation. When changes are detected, they first tend to affect preferentially neural supporting tissues rather than neurons. These observations and the lethality pattern resulting from exposure to increasing doses of radiation ("CNS death" requiring the greatest dose) led early to the dogma that neurons were relatively radioresistant.

The structural resistance of neural tissue, which requires kilorad for disruption detectable in a few days by light microscopy, is now seen as paradoxical since electrophysiologic decrements are present promptly after absorption of a few rad, and behavior is altered promptly by millirad. Although electron microscopic examination of neurons reveals ultrastructural changes at earlier times and lower doses than does light microscopy, neurons are synthesizing DNA during only a small fraction of their lifetime and they indeed are relatively resistant to morphologic alteration from direct effects of radiation. In contrast, their normal function requires closely regulated ion fluxes and membrane polarity and depends on innumerable chemical, electrical, and physical interaction with cells of diverse types. Direct damage to those cells, e.g., supporting glia or endothelium, or to effectors in the autonomic nervous system, becomes the limiting factor in integrated neural function. Functional deficits occur at radiation doses that are orders of magnitude below those required to cause direct physical disruption of neurons.

The dominant pattern of histopathologic change in the CNS is one of vascular damage with edema and hemorrhage, followed by glial loss and proliferation. As neuronal change occurs (led by pyknosis, reduction of dendritic arborization, loss of synaptic integrity, and demyelization), it is complicated by associated sclerosis, neovascularization, and infiltration by immune competent cells. The latter may contribute to loss of additional neurons.

The time course for these events is measured in weeks and months, long after acute chemical signs have resolved, and the changes most often are accompanied by cognitive and motor performance deficits. At lower doses, the early post-exposure period may have been free of signs referable to neural dysfunction. Survivors recovering from doses that did produce early functional change may relapse with a more permanent debility. The following section documents changes noted in selected representative studies. Early reviews include those by Haymaker (26) and Van Cleave (53).

1.2.1.1 Electromagnetic Radiation. The earliest systematic study of radiation change in the brain appears to be that of Lyman, et al. (33) and Scholz, et al. (49), reported in units of 4-20 human erythema doses of x-rays (approximately 100-500 rad) applied to the heads of dogs. Meningitis and perivascular edema were present at 5-6 weeks post-exposure without neuronal injury. After 5-6 months there were degenerative changes in blood vessels and correlated areas of necrosis, predominantly of white matter. Observations such as these have been repeated in the decades since that time. In rabbits given 200 kvp x-rays through a 3x4 cm field on one side of the head, Russell, et al. (47) reported neurological signs after 3-4 months following 2.85 krad exposures, and after 8 months in animals given 2.44 krad. Animals examined before signs appeared had multifocal necrosis of capillary walls and of adjacent brain tissue (probably glia). There were also small hemorrhages in the exposed half of the brain, mainly in hippocampus, mid brain and basal ganglia. They described little or no gliosis or nerve cell damage. After neuronal signs appeared, lesions were more extensive, involving even the opposite side of the brain. Necrosis was more prominent and was associated with thrombi, vessel wall necrosis, and gliosis.

High doses of radiation are associated with acute changes, predominantly inflammatory in nature. Rabbits given 4.2-9 krad to the head (260 kvp x-ray) had meningitis within 2 hours, and those receiving 9 krad also has vasculitis by 6 hours (19). After 2.5-30 krad of whole-body exposure to Ba¹⁴⁰-La¹⁴⁰ gamma rays, macaque monkeys had inflammatory changes in brain vessels and meninges as early as 2 hours after the highest doses, while damage to glia and neurons was negligible. Damage was greater in grey matter than in white (25). Comparable results were reported in other macaques exposed to 10 krad Co⁶⁰ gamma rays, head-only or whole-body. Transient vasculitis and meningitis were maximal at 8-24 hours and then subsided. There was pyknosis of cerebellar granule cells as well. Davidoff and co-workers (14) reported prominent damage to neurons in macaque rhesus monkeys in which exposed brain was irradiated with 1-5 krad of 200 kvp x-rays. In 4-8 months the brains had patch demyelination and damage to cerebral and cerebellar ganglion cells. Later "cavitation" of white matter was accompanied by gliosis. Occasional thickening and hyalinization of vessels was considered not significant, although by 8 months, the "end stage" nature of the lesion could have obscured any earlier role played by damaged vasculature.

In a similar study in Syrian hamsters, Scholz, et al. (50) gave 40 krad of high intensity x-rays through a 1.0 cm diameter port to the closed surface of the head at 2.14 krad/sec. Tissue "sponginess" and slight damage to cellular elements were detected at 7 hours after 20 krad or more, although no increase in vascular permeability to trypan blue was evident at that time. Later, small hemorrhages and tissue staining with trypan blue occurred and preceded development of necrosis. Fully developed necrosis, including neurons, glia and vessels, was described after only 3 days following 45 krad, 6 days after 10 krad and 8 days after 5 krad. The authors concluded that all cells were affected simultaneously. Hager (23) examined some of the same brains with the electron microscope and reported abundant exudative lesions at earlier times, suggesting that vascular damage preceded changes in glia and neurons.

1.2.1.2 Particulate Radiations. Beams of particulate radiation have special value in the study of radiation effects on the CNS because they deposit the majority of their energy in a very localized volume of tissue, at the end of their tracks. In some experiments, these beams in high doses have produced direct damage to neurons. Zeman and co-workers (57) exposed mice to microbeams of 22 Mev deuterons. With a 0.025 mm beam, nerve cell destruction was produced with 400 krad and more without concomitant light microscopic damage to blood vessels. Beams of 0.25 and 1.0 mm produced generalized necrosis with prominent vessel damage, by contrast. In other work (39, 40), the same group produced nerve cell pyknosis in the cerebral cortex and cerebellum 8 days after an 8 krad dose, and pyknosis of cerebellar granule cells and glia in 2 days with 72 krad. Granule cells were more sensitive than Purkinje cells. Vessel damage again was present with the 1 mm beam but not with a slit microbeam.

Rats exposed to 10, 20, 30, or 40 krad via a 3 mm beam of 185 Mev protons showed vascular changes after 14, 6, 3, and 1 days, respectively (31). These were evidenced by increased trypan blue permeability before nerve cell damage was manifest. No changes except impaired capillary circulation were found at the 10 krad dose. Anderson, et al. (1) summarized this early high-energy proton work.

Vogel, et al. (55) exposed monkeys to 850 rad of 14 Mev neutrons. After 14-22 months, there was fragmentation of myeloma sheaths and decreased numbers of oligodendroglia. The cerebral cortex was atrophic, but blood vessels appeared unchanged as did residual neurons. Further demyelination, astrogliosis, and microgliosis was seen later. The authors believed that myelin was particularly susceptible and that myelin damage was independent of oligodendroglial damage.

The brain stem and hypothalamus were consistent in their increased sensitivity to vascular lesions (25). In 21 macaque mulatta monkeys exposed to various doses of x-rays (e.g., 1.5-6.0 krad) penetration of trypan blue was more marked in hypothalamus and medulla (11) than in other parts of the brain. Within 2 weeks of exposure, edema, astrocytic degeneration, swollen oligodendroglia, and vasculitis were observed in the dyed areas. The astrocytic damage occurred at 3.0 krad and above, and was especially interesting since there may be a 1:1 relationship between astrocyte integrity and normal blood-brain barrier impermeability. Astrocytic glia have foot processes closely applied to capillary walls where the barrier is present, but in those brain regions lacking the barrier (choroid plexus, area postrema, neurohypophysis, pineal body), no glia are present about the vessels. Hence disruption of the vessel-glial unit may be more important to barrier function than is endothelial damage alone, and the sensitivity of the barrier may reside in astrocytes rather than, or in addition to, endothelium. In another study (3), beams of 23 Mev x-rays were directed laterally through the temporal lobes of monkeys and caused perivascular necrosis in the hypothalamic, supraoptic, and paraventricular muscle and the brain stem white matter, while the temporal lobes and basal ganglia had minimal damage.

1.2.2 Effects on Blood-Brain Barrier.

Trypan blue, after intravenous injection, can be found in all tissues of the body except the CNS. Clemente and Holst (11) first demonstrated trypan blue permeability in brain vasculature in irradiated monkeys. Griffin (22) studied mice cranially irradiated with 0.5, 1.0, 1.5, or 2.0 krad of 250 kvp x-rays administered at 200 rad/min. Methotrexate, to which the blood-brain barrier is normally impermeable, was given intraperitoneally to groups of 5 BALB/C mice simultaneously with irradiation or 1, 2, 3, or 6 days later. The animals were killed and their brains homogenized and examined 24 hours after administration of the chemical. Detectable levels were found only in brains of mice irradiated with 2.0 krad, including those administered the methotrexate 6 days after radiation exposure. Regrettably, the homogenization precludes detection of differential regional permeability of the barrier. The topic has practical significance, however, since exposures in the 2 krad range may be achieved during radiation therapy in humans and subsequent administration of pharmacologic agents could prove toxic as a result of altered barrier permeability.

Remler and Marcussen (41) reported a careful study of three cats in which they monitored the permeability produced by 6 krad of proton irradiation to 0.25 cm³ of the left cerebral cortex. Anesthetized cats served as their own control, first establishing an electroencephalogram (EEG) after penicillin was given intravenously. Penicillin leaking from a cerebral vessel causes epileptic spikes on the EEG. Two-minute EEG tracings were made at intervals up to 80 days after irradiation. Each cat had a unique response, although all showed significant blood-brain barrier leakage. One had an 8-fold increase in spike count by day 14, then gradually returned to normal by day 45. Another had a 9-fold increase by day 14, which

increased to 12-fold by day 21 before returning to normal by day 80. In the third animal, the spike increases began later, at 21 days, reached a 40-fold increase by day 35, and did not begin to subside until day 62. The authors stated all returned to normal by day 80. The important contribution of this study is the demonstration of the individual variations in onset, extent, and duration of the penicillin leaks, variations that would be obscured by destructive techniques which permit only one observation per subject and require that the data be pooled. Demonstration of this individual variability explains the various outcomes reported by other investigators who did not use non-invasive techniques. Indeed an equally important observation was ignored by the authors, who revealed that two cats were eliminated from the study because their pre-evaluation EEG examination revealed "significant epileptic spike activity." If two of six cats were "positive" before irradiation, the sensitivity of all blood-brain barrier tests must be suspect. The authors did not describe the results in three of the six cats irradiated.

These same authors (42) used 6 krad proton irradiation at 900 rad/min to open the blood-brain barrier in the left cerebral cortex of 50 rats. Thirty unirradiated animals served as controls. The radiation exposure did not affect the normal EEG. Kainic acid given subcutaneously at 0.5 mg/kg does not cross the blood-brain barrier in normal rats, but it does at 1 mg/kg, at which time it causes transient (10 min) scattered sharp waves on the EEG. When irradiated animals were challenged with 0.5 mg/kg, intense, highly localized (to the irradiated area) epileptiform bursts resulted; these lasted 1-10 seconds and recurred for about 90 minutes. The result was repeatable for about one week after radiation, presumably the duration that the blood-brain barrier was "open." This dose of radiation increased the permeability of the blood-brain barrier in the same manner (as demonstrated with similar convulsants) as does trauma, cold, heat, electric current, and osmotic shock, according to the authors. They were concerned primarily with radiation plus kainic acid as a technique for studying focal epilepsy. Kainic acid is a potent agonist of glutamate and a strong epileptogen. Given the predilection of rabbits to experience spontaneous epileptiform seizures shortly after heavy head irradiation, possibly they should be investigated for the activity of endogenous glutamate agonists that cross their blood-brain barrier after irradiation.

In a carefully documented study in 160 Sprague Dawley rats, Rene, et al. (43) demonstrated that fluid transudation across the blood-brain barrier in irradiated animals occurs via increased transendothelial transport in pinocytotic vesicles. The 80 irradiated rats were exposed to a whole-body pulse of 15 krad of mixed gamma-neutron radiation from a TRIGA reactor. Eighty rats served as unirradiated controls. Half of each were injected with horseradish peroxidase (HRP) 5-30 minutes before sacrifice, and all were killed 2 hours after irradiation. The brains were fixed either by immersion (to demonstrate HRP in vessel lumens) or perfusion. Electron microscopically, the irradiated medullas examined had increases in the number of HRP-containing micropinocytotic vesicles in endothelial cytoplasm, in capillary basement membrane, and beyond the membrane. No increase in tracer was seen in junctional channels between endothelial cells. The endothelial tight junction is usually considered the major barrier to protein loss from brain capillaries (8), but was apparently not altered by 15 krad in this experiment. Molecules smaller than the 40kd HRP tracer, that contribute to edema formation, may use the tight junctions or diffuse directly through the endothelial cells. Nerve and glial cells had "little observable differences" when compared to unirradiated animals.

Lundqvist and co-workers (32) used ^{99}Tc uptake to monitor vessel permeability in Sprague Dawley and Wistar rats exposed to 50, 70, 100, or 150 Gy of 200 Mev protons, via a beam of either 5 or 7 mm diameter. Uptake increased to a maximum 20-30 days after irradiation, with relatively little difference among the irradiated groups. Histopathologic examination of 2-3 animals per time point revealed vascular lesions, hemorrhage, and local gliosis in the irradiated region (visual cortex) at 27 days, together with cytolysis of neurons. At 57 days, there were marked necrotic areas with disintegrated blood vessels and glial scavenger cells. The changes were similar for 100 and 150 Gy, 5 mm, and 7 mm beam diameters. Minor hemorrhages and focal glial scavenger cells were seen on days 26, 39, and 58 after 70 Gy via the 7 mm beam, and small foci of necrosis were present on the latter two days. The vascular injury is consistent with that described by other workers and is corroborated by the small histopathologic samplings, thus establishing another non-invasive method for use in studying this phenomenon.

1.2.3 Electrophysiology.

The literature on electrical activity of nerve tissue after irradiation is difficult to summarize because of the many differences in experimental design, measurement techniques, and potential for misinterpretation. These are superimposed upon the complexity of the radiobiology literature generally, namely the variety of animal subjects, types of radiation, temporal factors, and completeness of reporting.

Generally there is evidence that at lower doses and earlier times, irradiation increases the overall state of CNS excitability. Thresholds for evoking arousal, recruiting, and certain reflexes appear lowered. Radiation stimuli below 1 rad have shown to affect arousal responses. The mechanism is uncertain, but could be direct interaction with neurons or receptors.

In large doses, radiation depresses the CNS and certain specific reflexes. The physical and chemical correlates are not understood. Effectors may include a combination of derangements of conductivity and excitability of the neuron, of synaptic transmission, of the neurosecretory process, and of the integrity of the supporting tissue. These possibilities ignore further functional considerations, of altered stimuli arriving at the unexposed CNS from irradiated non-neural systems (e.g., abdomen) or of the effects of high levels of motivation or conditioning.

The above introduction to the topic of electrophysiology indicated the difficulty in summarizing radiation effects; that difficulty certainly applies specifically to EEG responses. As with other measures of CNS electrical activity, the EEG appears to reflect increased excitability at doses of radiation even below 100 rad. Depression, as reflected in the EEG, occurs at doses between 2 and 10 krad and is reversible at the lower range but persistent until death at the upper range.

1.2.3.1 Electroencephalographic Responses. After observations that irradiation would arouse rats from sleep, EEGs on sleeping rats were recorded during radiation exposures (18). (EEGs are described as "desynchronized," "activated," or showing "arousal"; all mean conversion from high-voltage, low-frequency patterns to low-voltage, high-frequency patterns.) Hunt and Kimeldorf (28) established that behavioral arousal in sleeping or inactive rats could be elicited by a 1-sec exposure of head or body to 1 rad/sec of 250 kvp x-rays. Head exposure was more effective than body alone, but whole-body exposure was more effective than either.

Cooper and Kimeldorf (13) designed a study to identify the afferent pathway for the EEG change. They recorded EEGs from rats with transected spinal cords exposed to whole-body, body-only, or head-only x-ray, 250 kvp at 0.5, 1.0, or 1.5 rad/sec. An activation pattern was observed under all conditions except that in which body-only exposures were monitored in rats with transected spinal cords. They concluded that the intact spinal cord was necessary; agents transmitted via the circulatory system could be ruled out, as could impulses via the intact vagal nerves. This does not preclude high doses of radiation from transmitting signals by these routes, however.

Olfactory structures of the head are sensitive inducers of EEG activation. Activation was not seen with head irradiation by 35 kv x-ray (HVL 0.076 mm Al) at 2.0 rad/sec (12) in intact rats, but could be elicited with 1 rad/sec of 100 kvp x-ray (HVL 0.075 mm Al). Latency times to EEG response were on the order of 0.5 to 1.5 seconds. Surgical or chemical ablation of the olfactory bulb markedly reduced the EEG activation induced by radiation exposure (27). The authors concluded that skin receptors were unlikely to contribute as radiation sensors. Clearly, rats can detect very small doses of ionizing radiation.

At higher doses, cats given 400 rad whole-body x-rays (250 kvp) at 35 rad/min underwent EEG desynchronization immediately after exposure. The changes persisted for several hours and were associated with restless behavior. The changes in EEG and behavior were not produced by 400 rad to head alone or body alone. Both changes were also present but barely detectable after 200 rad (17, 24).

Bailey, et al. (4) inserted Tantalum¹⁸² wires unilaterally into the parieto-occipital region of 12 monkeys. EEG tracings recorded after 500 rad were desynchronized and slower on the irradiated side and faster on the opposite side. Changes were maximal after 6-8 weeks, followed by reversion to normal by 3 months. Slow waves and decreased voltage reappeared on the irradiated side and by 2 years, two of the animals showed epileptic spike patterns and fast activity. The EEG pattern was more indicative of general cerebral damage than of a focal lesion.

In the same dose range, the earliest definitive study was provided by Eldred and Trowbridge (15), who reported few definitive changes in the EEG of monkeys exposed to 400-800 rad of whole-body x-rays.

Brooks (9) used whole-body exposures in monkeys and found transient depression in frequency and voltage after 1 krad. Up to 2.5 krad, the EEG returned to normal in 5-10 minutes; after 5 krad, the recovery was transient. Monkeys exposed unilaterally (one cerebral hemisphere) to 3.5 krad x-rays showed marginal EEG changes after 6 weeks, definitive ones at 8 weeks (29).

Burros given head exposures to 200, 400, and 600 rad Co⁶⁰ gamma rays showed no EEG changes up to 7 days after 200 rad, but 400 and 600 rad produced diffuse high-voltage slow waves within 48 hours (38).

In a careful, coordinated study of clinical, EEG, visual, and histopathologic responses of monkeys, Caveness, et al. (10) exposed 24, two-year old monkeys to 3.5 krad of x-rays, delivered at 350 rad/min from a 250 kvp machine. Exposure

was limited to the right visual cortical area of the occipital lobe and was said to be limited in depth to 1 cm. There was individual variation in EEG response, but between 18-22 weeks, high-amplitude slow waves appeared in an "appreciable number" of the animals, and in all but one that remained at 44 weeks (3-6 animals remained, pending serial sacrifice). There were non-specific changes, characteristic of general brain injury from many causes. Monkeys examined histologically at the time of appearance of these EEG changes had disruptions of cell and myelin architecture, vascular and glial reactions, and inflammation in the exposed site.

EEG effects were also documented in other species. Immediately after whole-body exposure of rats to 9 krad (98 rad/min), the EEG waves were slowed. This observation was associated with a small decrease in brain serotonin (52). Nair, et al. reported EEG depression almost to electrical "silence" after 10 krad (295 rad/min) exposure to rats. This response occurred immediately and lasted for about 48 hours post-irradiation (37). Guinea pigs showed a slowing of the EEG with abnormal spiking and increased amplitudes for 1-3 days after exposure to 2.0-6.0 krad (180 kv x-rays) (2). In rabbits following 500 rad whole-body x-irradiation, the EEG activity was severely depressed within 15-20 minutes post-irradiation (56). This depressed response continued for about 48 hours after exposure to whole-body or head-only radiation.

Other EEG evidence of radiation-induced neural alteration included the appearance of spontaneous spike discharges. Post-irradiation spiking was recorded from the hippocampus, nucleus ventralis anterior and centrum medianum of the thalamus, the brainstem reticular formation, and the posterior hypothalamus in cats (16, 24) and rabbits (5, 34, 35, 36). These responses occurred following 200 or 400 rad (250 kv) x-ray whole-body exposure in cats and 400, 600, or 900 rad gamma rays (Co^{60}) head-only exposure in rabbits.

Other studies have tried to isolate EEG responses to radiation exposure by focal irradiation of specific areas of the brain. Schoenbrun (48) reported changes in the hippocampal electrical activity of cats following focal irradiation of the hippocampus with x-rays. In rabbits with unilateral lesions of the mesencephalic reticular formation, slow high-voltage waves appeared in the EEG from the intact side only following exposure to 700 rad whole-body gamma rays (Co^{60}) (30). No EEG effects were seen in the lesioned side.

These studies indicated that doses of radiation produce some functional alterations in neural tissues and/or sense organs which can be observed through the EEG. It appeared that the hippocampus, hypothalamus, and midbrain are especially radiosensitive. However, the EEG changes seen could result from radiation-induced changes in other structures in the brain which merely manifest themselves through cortical structures.

1.2.3.2 Electroconvulsive Sensitivity. Radiation-induced alterations in seizure thresholds have been documented in dogs (17, 35), cats (53), monkeys (46), rabbits (2, 20, 21), guinea pigs (7), rats (51), and mice (6). Weak stimuli associated with normal handling procedures often produced convulsions in these animals. Rosenthal and Timiras (44, 45) concluded after studying electroconvulsive seizure thresholds in irradiated rats (500 rad of x-rays [250 kv]) that irradiation caused an increase in brain excitability manifested by the lower electroconvulsive seizure threshold. They also noted a shorter clonic phase of the seizure, which was attributed to a post-irradiation decrease in the brain's ability to sustain the increased

excitability state. Similar maximal electroshock convulsive pattern seizures were also seen in rats following low exposure levels. This decreased threshold was seen following doses as low as 15 rad (180 kv x-rays) and lasted 2-3 weeks.

1.2.4 Summary: Brain.

The morphologic changes in the brain include general similarities among the animal species, as well as specific differences. This is also true for alterations in the function of the blood-brain barrier. To separate primary from secondary effects, real inter-species differences from effects of study design, or effects on function without discernible structural change, has not been easy and the task is still incomplete.

Because the complete perceptive, integrative, and responsive functions of the nervous system must all be intact to assess the effect of, and relative sensitivity to, noxious agents including radiation, this research requires intact organisms. When the object of our search for knowledge is man, only the higher orders of mammals can appropriately model the human nervous system. The studies must be repetitive over time, different exposures and different brain regions and be evaluated for endpoints that measure both structure and function. Noninvasive or nondestructive biomarkers, specific as possible for structure or function of individual cell types, must be used in combination to elucidate these interactions. The resolution of markers must be improved if substantial progress is to be made in sorting out causes from effects.

For example, the use of horseradish peroxidase to delineate ultrastructural channels of transport for small protein molecules could be combined with different enzyme histochemical determinations specific for integrity of endothelial cells, for neurons and for astrocytic or oligodendrocytic glia, to probe differential susceptibility of these cells. Modern concepts of neurobiology embrace the interdependence of neuron function and integrity of the supporting tissues; the redundancy of function by various regions of the mammalian nervous system makes evaluation of isolated lesions, and repair, very uncertain. The reader soon develops the conviction that crude, simple tools are being used to probe a sensitive, highly complex system.

It is impossible to conceive how we might have derived the yet-imperfect understanding we have of CNS injury and repair, or how we might continue to progress in that understanding, without the use of animal models.

There are static probes of structure, or in the case of enzyme histochemistry, of a single function. Before a quantum advance in our comprehension can occur, we will need a variety of sensitive monitors of dynamic electrophysiologic function. For example an organism may well compensate for a scarred, static lesion, a non-functional site, by providing the missing integrative function from another site. A more global evaluation of the animal would reveal the paradox of normal function despite a structural lesion. Today only sensitive electrophysiology could detect an appropriate elicited response to reveal the source of compensation. Ability to evaluate chemically the quantity and quality of specific neurotransmitters could provide comparable information from sites regulated neurohumorally.

1.3 SPINAL CORD.

1.3.1 Clinical Manifestation.

Fortunately, the difficulties encountered in describing brain-related clinical symptoms subsequent to radiation exposure are not such a problem in describing spinal cord-related clinical symptoms. Functional disturbances induced by localized x-irradiation of the spinal cord manifest themselves clinically as paralysis. Items such as whether or not paralysis occurs, time between exposure and clinical symptoms, and the length of time of paralysis, can be compared. Similar results are seen in the species studied.

Early studies by McLaurin, et al. (13) exposed the monkey spinal cord to x-rays. Paralysis occurred following 2 daily exposures of the monkey spinal cord to 5 krad of x-rays or one exposure of 7.5 krad. Later, Breit (4) showed that localized x-irradiation of the dog spinal cord produced paralysis after two daily doses at 500 rad/hr with a total dose of 2 krad.

In four, 1-yr-old male cats, a dose of 4.0 krad of x-rays to the thoraco-lumbar spinal cord produced paralysis at 3 months (2). Clinical signs in these cats began as a sudden weakness followed by over-retraction of the limb, rendering it unable to support the weight of the animal; but with time, some improvement was seen.

Studies involving the rabbit spinal cord have included exposure to x-rays and protons. X-irradiation of the upper thoracic spinal cord in rabbits with 3-11 krad at 250 rad/day resulted in paralysis of the hindlimbs at 4 to 33 weeks post-irradiation. Proton irradiation (185 Mev) of the thoracic spinal cord produced symptoms dependent on the width of the beam slit and the total dose. With a total dose of 20.0 krad given in a 1.5 mm wide beam, the rabbits showed symptoms including flaccid paralysis on day 9 in some animals to no paralysis in other animals (9). In contrast, a 10 mm wide beam with the same total dose resulted in partial paralysis after three to four days followed almost immediately by total paralysis. Paralysis was also brought about quickly by 40.0 krad given in a 1.5 mm wide beam, indicating a dose dependence.

In the rat, a single dose of 3.5 krad to the thoraco-lumbar region of the spinal cord produced paraplegia after 83-211 days. Development of the paralysis was gradual, beginning with weakness which progressed to muscle wasting and flaccid paralysis of the limbs in 2-3 days (3). Van der Kogel (19) produced similar results in rats irradiated in the cervical as well as in the thoraco-lumbar area. Other investigators have shown that the time between exposure and the appearance of paralysis is the same whether the dose is given as a single or fractionated exposure as long as the total dose is the same. For example, White and co-workers (21) reported a minimum latent period of 100-140 days at high doses (>2.0 krad) regardless of the exposure schedule. And as one would suspect, the mean latent period for the development of paralysis increases as the dose decreases. Masuda, et al. (12) showed that the minimum gamma ray dose causing paralysis in rats was almost the same whether 2 fractions were given at a 15-day or 1-day interval.

As described above, clinical manifestations of localized irradiation of the spinal cord are not immediate; the period of time between exposure and clinical symptoms increases as the total dose decreases. It is also apparent that some repair does occur in these tissues over a period of time since clinical symptoms do improve somewhat.

1.3.2 Electrophysiology and Spinal Reflexes.

In order to evaluate the immediate transient changes in the neurophysiology of the spinal cord after radiation exposure, one must look at electrophysiology and reflex activity. Unfortunately, studies of the electrical activity and reflexes of the spinal cord are complex by their very nature, so there are few results from which to draw conclusions. Generally, studies have shown that localized radiation exposure of the spinal cord may result in inhibition and/or excitation. Evidence has shown that as the dose increases, depression and complete loss of function usually follow an initial episode of excitation. For both electrophysiology and spinal reflex studies, the cat appears to be the species of choice.

1.3.2.1 Electrophysiology. Local x-irradiation of the spinal cords of decerebrate cats produced changes in spinal cord potentials. Sato and associates (15) reported an increase in the amplitudes of the monosynaptic reflex potential and the monosynaptic spike potential immediately following x-ray doses in the 6-20 krad range; spike amplitude also increased with the dose. These changes also correlated well with decreases in the extracellular potential of dorsal horn cells and in the intramedullary spike from the dorsal column. Intracellular potentials did not change, indicating a possible suppression of interneuronal inhibitory pathways. Many of these changes appeared to be related to the gliovascular system (6).

1.3.2.2 Spinal Reflexes. X-irradiation of the spinal cord also resulted in reflex arc effects. A test reflex (S1 ventral root to S1 dorsal root) was used in decerebrate cats to study inhibitory and facilitory effects of conditioning shocks on the L6/17 dorsal roots after x-irradiation of the lumbosacral spinal cord (16). After 3 krad or more, there was a facilitative effect on the S1 ventral root response to L6 stimuli when interstimulus periods were less than 1 msec, the direct opposite of the response seen in non-irradiated cats. Barnes (1) also observed a lack of inhibition after 2.0 krad of x-irradiation in cats. In addition, polysynaptic activity was increased, suggesting a specific effect on the excitatory synapses of the spinal cord by irradiation.

1.3.3 Morphologic Changes.

Structural changes in neural tissue of the spinal cord following irradiation as studied by light microscopy are comparable to those seen in the brain. The patterns of histologic change in the white matter, the primary site of damage in the cervical/thoracic spinal cord, are characterized by vascular damage with hemorrhage followed by edema and glial loss. Neuronal degeneration, when it occurs, is characterized by nodal widening and axonal degeneration followed by cell death. In the lumbar spinal cord, changes consist of a milder version of white matter necrosis plus a severe degeneration of the posterior and anterior roots.

Early studies of radiation damage to the spinal cord, such as Scholz, et al. (17), used localized thoracic spinal cord exposure to 250 rad (180-200 kv x-rays) given daily to rabbits for 12-40 days to study morphologic changes. Animals were euthanized two weeks after clinical signs of paralysis appeared, which varied from 1-8 months. Histopathology revealed damage primarily in the white matter, consisting of vascular wall damage with hemorrhage followed by edema and glial loss. The lowest reported single exposure dose of x-rays was 2 krad producing these alterations at 5 months. Similar lesions of white matter necrosis occurred in the spinal cord of rabbits exposed to 20 krad of 185 Mev proton beam. Lesions

appeared in 9 days when using a 1.5 mm wide beam and in 3 days when using a 10 mm wide beam. Although white matter necrosis was apparent, no neuronal damage was seen. In fact, axons and myelin sheaths remained intact along necrotic beam tracts (9).

Other investigators have since held to the general conclusion that blood vessel involvement predominates in the development of white matter necrosis in the spinal cord (2, 14, 26). Myers, et al. (14) obtained results in the irradiated rat spinal cord that the first pathological change to occur consistently (at the time of appearance of clinical symptoms) was edema and extravasation of red blood cells in the dorsal columns of the white matter and the dorsal horns of the grey matter. These regions have a common blood supply, which has been reported to be quite vulnerable to ischemia (10).

The progression of pathological changes in white matter necrosis has been well described (5, 8, 23, 24, 25). Results from these studies have shown there to be an increase in the number of dividing astrocytes just before the onset of radiation myelopathy. A concurrent increase in oxidative enzyme activity of the glial cells was also observed. At the time clinical symptoms were noticed, vascular damage, hemorrhage, edema and loss of glial cells were evident. In the center of these now necrotic lesions, there was a loss of oligodendroglial cells along with fragmentation of axons and myelin sheaths. Mastaglia, et al. (11) described the axon and myelin degeneration as a breakdown of paranodal myelin and nodal widening which were seen in his study of rat spinal cord as early as 2 weeks after exposure to 0.5 to 6.0 krad doses of 250 kvp x-rays. He also described a random Wallerian-type degeneration of fibers as a separate but concurrent entity.

Van der Kogel (18, 19) and Bradley, et al. (3) have shown changes seen in the irradiated cervical/thoracic spinal cord, primarily those associated with white matter necrosis, to be somewhat different from those seen in the irradiated lumbar spinal cord. After a dose of 3.5 krad of x-rays, the damage seen in the rat lumbar spinal cord was less severe than that in the other areas. However, there was complete degeneration of the anterior and posterior roots, suggesting that the paralysis in these cases of lumbar irradiation was most likely due to a radiculopathy rather than a myelopathy. This myelin loss from the nerve roots was probably due to Schwann cell damage.

Many investigators have shown that there is a time-dependent repair of radiation damage in the spinal cord after x-irradiation (18, 19, 21) and neutron irradiation (22). The first phase of recovery occurs within the first 24 hours after irradiation and is due to repair of sublethal damage. Hornsey, et al. (7) have shown that this repair coincides with the recovery of the proliferative neuroglia from a block in progression to cell division. There was no evidence of increased cell turnover, just a normal cell turnover of surviving neuroglia. The second phase of recovery can be attributable to repopulation. This phase generally occurs approximately 15 days after the first phase, although some incidental strain differences have been seen in rats (20, 21).

1.3.4 Summary: Spinal Cord.

In the species studied (monkey, cat, rabbit, rat), paralysis occurred following localized irradiation of the spinal cord. The latency period between exposure and clinical symptoms was inversely proportional to the total dose, irrespective of the type of radiation or type of exposure. A gradual improvement in clinical symptoms

over an extended time period indicated that a slow repair process did occur. This "repair" phenomenon was not observed during electrophysiology and spinal reflex studies because they were not continued far enough into the recovery period. These studies did produce evidence that radiation exposure, of the magnitude to produce paralysis, resulted in an initial episode of excitation followed by depression and complete loss of function.

Morphologic changes induced by radiation exposure followed a predictable gliovascular pattern. At the time clinical symptoms were seen, vascular damage, hemorrhage, edema, and the loss of glial cells were observed primarily in the white matter. Several investigators reported evidence that the "repair" referred to above does occur in two phases: sublethal damage repair within 24 hours and repopulation after 15 days.

Animal models used to study the localized exposure of the spinal cord to radiation showed similar reactions both clinically and morphologically. Clearly, the non-human primate would best mimic the human simply due to the size and length of the spinal cord. It would not be possible to accurately localize exposures any further than thoracic versus lumbar in the smaller species. If further localization is not an important factor in the study, the basic effects on the spinal cord appear to be equally as apparent in smaller species as in non-human primates.

1.4 BEHAVIOR.

As mentioned in the introduction, alterations in behavior due to exposure to ionizing radiation can result from either direct effects on the nervous system or indirect reactions of an animal to radiation damage of other irradiated sites. It appears that even low doses, which do not produce substantial alterations in physiological measures, do produce alterations in the activity of the animal. With large doses, behavior alterations tend to reflect direct neural damage. In this survey, behavior assessment is broken down into motor functions (performance capacity, general activity, and discrimination performance tasks) and cognitive functions (learning, motivation, and perception discrimination behavior).

1.4.1 Clinical Manifestation: Incapacitation.

There are semantic difficulties in attempting to equate the outcome of various experiments when the endpoint is a complex of clinical symptoms. Investigators do not use standard nomenclature, and terms such as depression, excitation, or convulsive behavior each have degrees of sensitivity depending on the investigator's own point of view. Thus, a number of similar terms, which may or may not be completely synonymous, can be used to describe each complex.

The responses of animals to doses into the supralethal range show species-specific characteristics more clearly than do responses at most other exposure levels. It may be worthwhile to note that some species characteristics are unique and should not lead to "over-interpretation." For example, rats are incapable of vomiting.

1.4.1.1 Non-human Primates. Allen, et al. (1) described studies in more than 100 young adult *Macaca mulatta* exposed to 0.4 to 40 krad (16 whole-body exposure levels) of 1.3 Mev Co^{60} gamma irradiation at 800 rad/min. They described three non-classical syndromes, depending on total dose. Most animals

also shared a common complex of malaise expressed by withdrawing to a remote corner, huddling, and demonstrating disinterest in their surroundings and a disinclination to move about.

At the lowest dose range (400-1000 rad), death occurred after 10-23 days. There were transient mild neural symptoms (nystagmus, ataxia, tremors) and debility, which subsided after 24 hours. Some animals had diarrhea and anorexia beginning on day 5, and evidence of bone marrow injury appeared on day 11. Death was preceded by development of a hemorrhagic phenomenon.

Monkeys in the 1.0-7.5 krad range demonstrated a different pattern of response. In this range, most had transient neural signs, including opisthotonus, as well as debility, which were biphasic. Ten minutes after exposure to 2.5-7.5 krad, the animals became prostrate, a condition which lasted 30-60 minutes, then recovered. Thereafter, some became debilitated again until death, while others recovered again after 10-12 hours only to relapse before death, which occurred in 5-9 days in all of this group.

In the 9-40 krad range, death occurred within 72 hours. Some appeared hyperexcitable even during exposure. All became severely debilitated to comatose by 8-10 minutes of exposure. Many salivated or vomited during exposure and some had nystagmus, ataxia, and convulsive seizures. These signs continued after exposure, along with tremors and a rigid opisthotonoid posture. Severity of signs was dependent upon dose. The animals commonly lost consciousness and had convulsive movements before death.

Haymaker (81) described chimpanzees after whole-body exposure to 5-6 krad (3 Mev x-rays, 0.4-8.2 krad/min). Nystagmus occurred 8 hours after 5 or 10 krad. Convulsions occurred in some animals after 12 hours. They died between 4 and 8 hours post-exposure. With 20 krad, the animals vomited and were debilitated after 30 minutes, weak and incoordinate after 1.5 hours, had nystagmus at 2-3 hours, and were comatose at 9 hours. The first animal died at 4 hours, the last at 72 hours. Those animals receiving 30-60 krad had convulsions and were comatose within the first hour and died within 10 hours.

In his review article, Carpenter (28) suggested that the primary cause of this early transient incapacitation in the monkey, dog, and pig was faintness due to a fall in cerebral blood flow from the direct action of histamine on blood vessel smooth muscle. Others have produced results that support this hypothesis (23, 130).

1.4.1.2 Burros. A series of experiments reported by one group (74, 166, 167, 183) demonstrated the overall radiosensitivity of the nervous system of the burro. The burros (*Equus asinus asinus*) were given whole-body exposure to Co⁶⁰ gamma radiation daily, at 48 rad/hr for total doses of 400, 200, 100, 58, and 25 rad. Clinical signs paralleled the daily doses and were quite uniform. The animals were irritable, kicked, and bit beginning immediately after one exposure to 400 rad, the second exposure to 200 rad, and the eighth exposure to 25 rad. Irritability waned, and was replaced by depressed and lethargic behavior after doses totalling 400 rad were reached. The animals experienced a peculiar "knuckling over" in their fetlock and pastern joints through either weakness or incoordination; they also had excessive lacrimation, hyperesthesia, muscle spasms, and stiff locomotion. These signs were fully expressed in those receiving more than 1000 rad.

Deaths occurred after total doses exceeded 1000 rad, but the earliest deaths were on the 4th day of 400 rad/day and one on the 6th day of 200 rad/day. The authors of the latter study (167) estimated that the LD 50/30 for burros given continuous exposure to Co⁶⁰ at 51 rad/hr was 784 rad. This is not an especially low radiotolerance. The deaths were bimodal, however, over a dose range of 605-945 rad, with peaks at approximately 3 and 26 days. Mean survival time was 14 days. The frequent deaths in the "CNS range" (5 days or less) at dose rates greater than 1 rad/min may indicate a greater sensitivity to higher dose rates. More clearly, the burro does demonstrate neurologic signs at doses lower than those reported for other species (below about 1000 rad), and these signs are associated with early death.

1.4.1.3 Swine. Swine exposed to supralethal doses exhibit an early-death neurological syndrome. Shively, et al. (172) reported total-body exposure to 3.0-3.5 Mev x-ray at 150 rad/min during which the pigs became increasingly restless as exposure progressed past 2.0 krad; by 3.5-4.0 krad, there was salivation, mastication, retching, and profuse emesis. By 10-20 krad, inactivity supervened, with marked depression and prostration by 30 krad and convulsions by 39 krad. When exposure ceased at about 20 krad, there was moderate ataxia along with depression, diarrhea, and vomiting. This was followed after 1-3 hours by marked improvement, until rapid deterioration began and death occurred 10-48 hours later. This differed considerably from those animals given 24 krad or more, where there was minimal improvement before death in the earlier time periods. With 40 krad, there was no recovery, with incapacitation progressing to seizures in 10 minutes to 3 hours, followed by full convulsions and death.

1.4.1.4 Dogs. Head-only exposure of dogs to 23.5 krad of 180 Kvp x-rays at 605 rad/min produced immediate nystagmus, tremors, and disequilibrium. Circling, rolling, ataxia, and clonic convulsions were also described. After 30 minutes, decerebrate rigidity appeared, including excessive thirst, tail erection, tonic neck flexion, and opisthotonus. The rigidity decreased during the terminal 3-4 hours, with death about 20 hours after exposure. At 10 krad exposure, there was no rigidity and less disequilibrium (151).

In a brief report of total-body exposure in the supralethal range to dogs, Bane, et al. (10) described lethargy during the 30-hour survival period. The dogs had received 10 krad of 250 kvp x-rays at 30 rad/min. Muscle twitches, tonic-clonic rigidity, and convulsions preceded death. Retching and vomiting were seen immediately after total body exposures of 1.3-1.8 krad in another study (39) that exposed dogs either to Co⁶⁰ gamma rays or to 2000 kvp x-rays. Again lethargy was noted until 4-8 hours before death, when retching and vomiting recurred and was accompanied by collapse, coma, or death on the third post-exposure day.

Early disequilibrium and prolonged muscular rigidity appear to be characteristic components of the canine "CNS death" syndrome.

1.4.1.5 Rabbits. Gerstner, et al. (73) describe convulsive seizures in rabbits after high doses of head exposure (12.5 krad of 250 kvp x-rays at 520 rad/min). Minutes after exposure, the rabbits became apathetic for about 20 minutes, then began "epileptoid seizures of the grand mal type," each of which lasted 20-30 seconds and was followed by prostration (exhaustion?). This phase was followed by a 3-hour period of somnolence and deep apathy. All animals then became ataxic, with severe impairment of equilibrium and postural reflexes. Death occurred

at about 2.5 days. The epileptiform seizure phase revealed underlying transient neural hyperexcitability that existed; during the interval between seizures, a convulsion could be precipitated by sudden loud noise.

The dose dependency of this seizure phase in rabbits was defined by the same group in another study (72) of head exposure over the range 4.2-9.0 krad. At 4.2 and 5.4 krad, the animals were listless and apathetic but showed no specific neural signs. Doses of 6.6 krad and above repeated the convulsions, severe ataxia, and absent reflexes. Kimeldorf, citing Cheymol, et al. (37), describes seizures in rabbits where heads were exposed to 10.9 krad of Co^{60} gamma radiation at 208 rad/min. Supporting the dose-dependency of this effect is Monnier and Krupp's report (131) of apathy but not convulsions in head-exposed rabbits given 900 rad of Co^{60} gamma radiation.

1.4.1.6 Guinea Pigs. The pattern of lethargy, hyperesthesia, seizures, and ataxia also has been reported in guinea pigs exposed to high doses of radiation. Andrews and co-workers (4, 6, 14) used 2.5-3.0 Mev x-rays at 0.5-2.0 krad/min in some studies and 200 kvp x-rays at 50 rad/min in others. In the 1-5 krad range, animals died after 4-6 days of lethargy. Doses of 7.5-10 krad produced the lethargy together with hyperesthesia and convulsive seizures, and death within 24 hours. Locomotor ataxia, extensor rigidity, and nystagmus were also reported. Henshaw (82) saw muscle spasms and convulsive seizures superimposed on a comatose state. His animals died shortly after 50 krad delivered at 250 rad/min.

1.4.1.7 Hamsters. Hamsters apparently do not display a convulsive phase after heavy irradiation, although apathy, hyperesthesia, and incoordination are evident. Levy and Quastler (117) exposed hamsters to 8-40 krad of x-rays at 1 krad/min. *The animals became somnolent, but within a few hours showed "fits" of rapid circling, backing, and somersaulting, together with disorientation.* The "fits" could be precipitated by any mild stimulus. In the 20-40 krad range, depression was profound, accompanied by fine tremor and occasional violent motor activity. The Andrews compilation (6) described hamsters after angle exposures to 600-100 krad of 2.5-3.0 Mev of x-rays delivered at 0.5-2.0 krad/min, which died within 12 hours but without experiencing convulsions.

1.4.1.8 Rats and Mice. Langham, et al. (115) provided a comprehensive early description of rats and mice heavily irradiated with Co^{60} gamma rays at 4-6 krad/min. Above 5 krad total dose, they saw transient ataxia with spatial disorientation, followed by lethargy and inactivity. The lethargy began within 1 hour at 5 krad but at the end of exposure after 10-200 krad. At 20 krad and above, there was an excitation phase characterized by coarse tremors beginning at 50-60 hours post-exposure; at 30 krad, they were evident at 30 hours and were superseded by convulsions at 36 hours. Between 30-50 krad, "frantic" activity, hyperesthesia, and severe tonic convulsions began before 36 hours. Exposures exceeding 40 krad (head or whole-body) produced fits of running and jumping, violent seizures upon mild stimulation and convulsions. Other workers (82, 132) have reported comparable syndromes with different radiation types and different dose rates.

The sensitivity of specific brain regions was localized in early studies by Hicks and others (83) who delivered 100 krad of 2.5 Mev electrons in 1 second to the brain stem of rats. These animals died in 10-20 seconds. Whole-body exposure with the brain stem shielded permitted survival times of 12-20 hours, with weakness and ataxia in the interim. In a comparable study, Brightman (15) administered a

localized beam of x-rays to the diencephalic region (20-30 krad, 370 krad/min) of rats. These animals died after 1-3 weeks, displaying lethargy, ataxia, and disequilibrium. Appropriately, these rats also refused to eat and drink, behaviors that depend upon intact hypothalamic centers. Control rats for this study were exposed anterodorsally to the diencephalon, in the cerebrum, and they survived many weeks after the exposure.

Similar "dissection" of the brain in early studies in guinea pigs helped to elucidate mechanisms of "CNS death" (2, 80). In these studies, 7.5 krad of x-ray to the cerebellum produced ataxia, convulsions, and nystagmus while similar exposure of the forebrain did not. The authors attributed the deaths during the first 24 hours to cerebellar edema, and prevented the early deaths with cerebellectomy and by internal decompression (hemidecortication of the cerebrum).

1.4.1.9 Summary: Clinical Manifestation: Incapacitation. Lethality following massive radiation doses and occurring within 3-5 days of exposure was preceded in all species examined by clinical signs indicative of neuronal malfunction. Death usually followed cardiorespiratory failure before fatal systemic electrolyte disturbances and infection supervened. These early deaths have been termed "CNS syndrome" or "neurological syndrome". There were species differences in the clinical manifestations of the complex, noted even by the earliest workers and indicated in this review. Non-human primates appeared especially susceptible to early responses from head irradiation; burros had unusual symptoms and may be especially sensitive to dose rate. The syndrome in dogs included prominent muscle rigidity; rabbits showed a peculiar predilection for epileptiform seizures; hamsters appeared not to have a convulsive phase; and rats and mice experienced immediate ataxia. Kimeldorf and Hunt (108) point out that symptoms experienced were a function of time and thresholds of response. If the dose were sufficiently high to exceed thresholds of more than one response, then the second response might occur and obscure the first one, which would have been seen at a dose too low to elicit the second one. Thus, observers may be overlooking a number of potential signs of underlying morbidity until experiments are conducted systematically over a wide range of exposure conditions. They published these observations in 1965, but those gaps in our knowledge base still exist.

Our deficiency in comprehending the biochemical mechanisms and anatomic pathways for primary and secondary neural malfunction cannot be overcome by studies in humans. Progress in understanding will require still more studies in animals to permit careful control of exposure factors, demographic factors, and sample size, as well as to permit examination of discrete anatomic regions at multiple points in time.

That studies conducted to date in animals have contributed to knowledge extrapolatable to humans is documented by the single human patient to be observed medically after massive radiation exposure (171). In this industrial accident, the patient received an estimated 10 krad to the head, as well as 4-5 krad total body (mixed spectrum: gamma/neutron, approximately 1:3). The patient immediately became ataxic and unable to stand. He was in shock and unconscious by 5 minutes, a state that continued for 20-30 minutes. This was followed by a 90-minute phase of semiconsciousness, incoherence, retching, vomiting, hyperventilation, and diarrhea. He also exhibited purposeless movement of his limbs and torso that required restraint. The next 28 hours were characterized by hypotension, anorexia, and circulatory failure, followed by irritability approaching mania in degree. He became comatose and died 35 hours after exposure. This

one case, dominated by neural malfunction, is consistent in its manifestations with even the early work in animals, as reviewed for this report.

1.4.2 General Activity.

Analysis of behavior after radiation exposure includes some system-specific reactions (e.g., convulsions, paralysis-CNS, vomiting, diarrhea-gastrointestinal), as well as a group of "non-specific" reactions amounting to a basic reduction in activity. Kimeldorf and Hunt (108) found this activity reduction to be the most sensitive behavioral manifestation of exposure to ionizing radiation. These disturbances in behavior do not, as yet, have identifiable correlative physiological reactions.

1.4.2.1 Rats. D. J. Jones, et al. (100) used 250 kvp x-rays (HVL, 1.5 mm Cu) at 25 rad/min to study changes in daily volitional activity of rats after whole body irradiation exposure of 200-1000 rad. In general, a biphasic depression in activity was observed. The first phase of depression occurred within the first few days after exposure to all doses. This was followed by a partial recovery in activity. Ten to 25 days after exposures over 400 rad, a second phase of depression occurred whose severity was proportional to the dose. This phase was also followed by a gradual recovery. However animals that died within 9 days after exposure showed an immediate reduction in activity without recovery. Castanera, et al. (30, 31) concluded after further studies that the total activity of rats after irradiation was similar to the volitional activity response, indicating that the quantitation of activity performance was independent of the test used.

Studies have been performed to determine if the initial depression could be directly related to exposure of the abdominal region since the time frame coincided with gastrointestinal symptoms (101). Exposures over 600 rad to the abdomen only did produce the typical depression. The same exposures with the abdomen shielded did not produce depression. These results suggested that the initial decrease in activity following high doses may be due to the gastrointestinal response to irradiation.

Other researchers (102) have produced results indicating the second phase of depression, that occurring 12-15 days after exposure, to be mediated by radiation-induced hematopoietic injury. Fresh bone-marrow suspension was injected intravenously into rats exposed to 650 rad x-rays. The second phase of depression was not seen in these animals. Even though an animal may have enough marrow to survive, a functional hematopoietic deficiency must be present, resulting in depressed activity.

It is also apparent that radiation exposure also affects certain motivational factors, such as food deprivation, which increases activity in normal animals. Food restriction in rats exposed to 360 rad did not increase activity in these animals (54); even 4 months post-irradiation, the extent activity increased in response to food deprivation was significantly less than in normal animals (119).

Later researchers (114) have linked the biphasic activity levels in the rat to biochemical changes in the brain. After exposure to x-rays (800 rad), there was an increase in the hydroproteolytic and MAO activity in the brain, which corresponded to the first phase of activity change. At the same time, there was a decrease of serotonin and noradrenalin content.

1.4.2.2 Hamsters and Guinea Pigs. In addition to their work in rats, Castanera, et al. (30) studied post-irradiation behavior in hamsters and guinea pigs. Results indicated that the initial decrease in activity was small and lasted only 1 day regardless of the dose level, and the second phase of depression was more severe than that seen in rats. Other studies by Newsom (136) and Phillips (155) confirmed the suspicion that these two species were relatively resistant to gastrointestinal radiation damage; therefore, the first phase of depression was not as severe as in rats.

1.4.2.3 Rabbits. Painter, et al. (148) showed a biphasic activity curve just as in other species. After x-ray doses of 500-800 rad, there was an immediate depression followed in 5-15 days by a second more severe depression post-exposure.

1.4.2.4 Mice. Early researchers (13, 113, 141, 142) studied the activity of mice after irradiation exposure. Continuous exposure at 48 rad/min to a total dose of 500-600 rad rendered mice inactive for 5-30 minutes. Specific 1 mm diameter radiolesions of the cerebellar cortex reduced activity in the mice after 1 month post-exposure.

Other studies have shown that exposure to radiation produced a dose-dependent increase in locomotion activity (128). Mickley, et al. (129) irradiated mice with 1000 or 1500 rad of gamma radiation (Co^{60}) to show that endorphins were involved in this radiogenic behavior change. Irradiated mice became hyperactive, which was eliminated if the animal was given naloxone (2 mg/kg intraperitoneally) immediately post-irradiation.

1.4.2.5 Non-human Primates. General activity is depressed in the non-human primate species after radiation exposure. Three to four weeks after total body x-ray exposure to 300-500 rad, random cage activity was reduced (165), as measured by reordering the interruption frequency of photoelectric beam paths in the cage. However, when activity was recorded by an observer, 400 rad total-body exposure produced a reduction in activity and in frequency of various manipulatory activities from days 12-16 post-irradiation (122).

Higher doses (400-800 rad) produced activity decrements prior to the ninth day post-exposure (52). The activity reduction was accompanied by gastrointestinal symptoms which were related to dose. The animals returned to normal activity 1-7 months later. Similar symptoms were seen following whole-body exposure to 150 rad x-irradiation (Co^{60}) at 7-124 rad/min (95).

Direct radiation injury to neural tissue is probably responsible for the reduction in activity of monkeys following head-only exposure to very high doses of x-rays. Doses in the range of 1.5-2.0 krad resulted in reduced activity during week 2, followed by a gradual improvement. The monkeys refused food at 2-4 hours after exposure to 4.5-6.0 krad, which was followed by reduced activity, motionlessness, and death within 3-12 days.

1.4.2.6 Dogs. Pitchford (156) showed a progressive decrease in animal activity after exposure to 1-7 krad of mixed gamma-neutron radiation. Lower dose groups (1-2 krad) showed a longer period of time between exposure and activity changes than did the higher dose groups.

1.4.2.7 Summary: General Activity. Depression of total body activity was reported in several species (rat, hamster, guinea pig, rabbit, mouse, dog, and non-human primate) following exposure to ionizing radiation. This depression could be a result of system-specific reactions (e.g., vomiting, convulsions) or an independent "non-specific" reaction manifested by activity reduction. The biphasic activity depression seen in rats is similar to that seen in humans following exposure. Other species showed a decrease in activity following radiation exposure but that seen in the rat more closely approximated the human reaction.

1.4.3 Discrimination Performance and Physiological Stress.

Although an animal's general activity level appears to reflect phases of underlying physiological damage after radiation exposure, an animal's performance on trained discrimination tasks did not appear to show such a strong change following irradiation. After an initial brief period of early transient incapacitation, most studies showed that the animals were able to perform at or near a normal level until just before death.

1.4.3.1 Non-human Primates. Kaplan (103) showed that after a whole-body exposure to 4000 rad of mixed gamma-neutron radiation, unrestrained rhesus monkeys were capable of performing a learned task of navigating a maze in which a behavioral task operation was also required. Curran, et al. (44, 45) reported similar results following 2000 rad of mixed gamma-neutron radiation in which monkeys were trained to perform cued avoidance tasks. Bruner, et al. (24) found that 300 rad of gamma (Co^{60}) radiation was the minimum effective midbody dose, causing a performance decrement on a delayed match-to-sample task in rhesus monkeys. The same investigators confirmed their results that the threshold dose was 300 rad and further showed that the threshold dose rate was 25 rad/min (23).

Performance of a self-paced, 3-light, 3-lever discrete avoidance behavioral task after neutron radiation exposure was more variable than following gamma-neutron radiation; however, the pattern of performance level was similar. Immediately after whole-body exposure of 8 rhesus monkeys to 1100 rad of neutron radiation (5.8:1 neutron:gamma), all 8 animals showed reduced response accuracy corresponding to early transient incapacitation. This performance degradation was followed by an entire day of performance normalcy, which slowly worsened until death (17, 18). These results indicate that, although eventual performance may return to normal for a period of time, time-critical tasks could be significantly impaired.

1.4.3.2 Pigs. Pigs trained by shock avoidance conditioning to traverse a two-chambered shuttlebox performed at a normal level after a brief time period of early transient incapacitation following radiation exposure (32, 33, 34, 35). After single doses of gamma-neutron radiation of 2400-5000 rad, early transient incapacitation lasted less than 5 minutes, which was followed by performance at normal levels, gradual performance degeneration, and death. Doses of 7600 rad or greater resulted in only a partial recovery from early transient incapacitation before death. Fractionated doses of gamma-neutron radiation to 6800-13,300 rad total dose resulted in a markedly better performance than similar unfractionated doses. Early transient incapacitation was shorter, and a normal baseline level of performance was achieved earlier and lasted longer.

1.4.3.3 Dogs. Chaput, et al. (36) trained dogs by shock avoidance conditioning to work a discrimination problem cued by visual and auditory stimuli. Dogs that received less than 10,000 rad of gamma-neutron radiation in a single dose performed at pre-irradiation levels for several days after a brief period of performance decrement during the first 60 minutes post-irradiation. Afterward, the animals showed a sharp decrease in performance just before death. Doses greater than 10,000 rad produced a shorter time period of normal performance and a shorter survival time overall.

1.4.3.4 Rats. Many studies in rats used conditioned avoidance to study post-irradiation behavior. Haley, et al. (75) found no statistically significant difference between the pre- and post-irradiation responses of the conditioned rats after whole-body exposure to 300-900 rad of x-rays. Performance of a 2-lever shock-avoidance task by rats exposed to 100 Gy of Co^{60} gamma radiation (66 Gy/min) was decreased immediately after exposure. The animals did, however, appear to recover in the 90 minutes following exposure (27). Murphy, et al. (134) did a fairly extensive study of rat activity after exposure to 1000 rad of gamma radiation. Performance in the shuttle avoidance test was not dependent on the time of day of exposure, but performance did seem to differ with the circadian rhythm independent of treatment. Hunt (94) used a footshock to test post-irradiation active avoidance behavior in rats. The rats were trained to avoid footshock by jumping onto a retractable ledge. For the first 24 minutes after exposure to ≤ 200 Gy electrons or ≤ 200 Gy gamma photons, performance was decreased in a dose-dependent pattern. After 24 minutes, however, all animals in all dose/exposure groups recovered.

Early studies by Kimeldorf (107, 110) and Casarett (29) used swimming as a behavioral test in rats to test post-irradiation performance decrements. Results showed a period of early transient incapacitation followed by performance near normal levels. Animals that died soon after irradiation performed at a nearly normal level up to the time of death, while those animals that died later had a gradually decreasing performance level which varied with the length of the post-irradiation survival period.

1.4.3.5 Performance and Physiological Stress. In some situations, an animal may be forced to perform work at a high level after irradiation. These physiological stresses may be too much for the animal to cope with and death occurs. Early studies by Kimeldorf (107, 109) showed that the performance of exhaustive exercise by rats after radiation exposure resulted in an increased mortality. This increase appeared to be proportional to the number of exercise trials during the first 3 weeks after exposure (99); however, swimming exercise performance appeared to reduce post-irradiation mortality (21, 184), while walking a treadmill during the first 3 weeks after exposure failed to shift the survival rate in mice (175).

The physiologic stresses produced by hostile environmental conditions can also alter an animal's response to radiation. The mortality of mice and rats after single x-ray doses of 75 rad was increased by exposure to a low ambient temperature (6° - 10° C) (106, 137, 181). Newsom and Kimeldorf (135, 139) also produced results indicating that acute cold stress tolerance is reduced in guinea pigs and rats following sublethal doses of x-rays and neutrons. These authors attributed this to the suppressed caloric intake that occurs after radiation exposure (138). However, severe hypothermia (0.0° - 0.5° C) in irradiated mice increased the LD50/30 from 620 to 1760 rad (84).

Hibernation causes interesting responses to radiation exposure. High doses of x-rays have been shown to prevent the bat and ground squirrel from entering a dormant state (173). Hibernation induction immediately after radiation exposure markedly increased the survival time of the ground squirrel (51), marmot (174), and bat (143).

1.4.3.6 Summary: Discrimination Performance and Physiological Stress.

Results from these performance task studies consistently showed that the animals did perform at or near a normal baseline level as long as they had the physical capacity to do so. Only when the animals became too weak did they falter in task performance. This occurred only a short time before complete incapacitation and death.

Studies also showed that chronic stress loads can decrease the survival time after irradiation. Physiological stresses, which are normally tolerated, can be overwhelming to an irradiated animal. These changes in the stress tolerance could place limitations on the level of performance possible following irradiation.

1.4.4 Psychological Processes.

The effects of radiation exposure on psychological processes are reflected in an animal's ability to adjust to its environment. These processes are the combination of a stimulus and a response. Motivation, learning, and perception are all functions in this category.

1.4.4.1 Motivation. Kimeldorf and Hunt (108) used three behavioral characteristics to assess motivation: 1) increased activity of the animal, 2) appropriateness of the behavior to the type of motivation, and 3) persistence of the behavior until terminated by a reward or punishment. Radiation exposure can affect the motivational status of an animal as evidenced by any one of these characteristics.

Motivation in rats is commonly initiated by food or water deprivation with a small amount of food or water as the incentive to direct and reward performance. This is commonly tested using a maze. Fields (54) maintained rats on 20.5 hour periods of food deprivation. Hunger-driven activity without food incentives (general activation) was measured by wheel-drum rotations. Hunger-driven activity with food incentives (directed activation) was measured by running speed on a straight path. The animals were trained pre-irradiation so a lack of difference between animals receiving 0, 180, or 360 rad (x-rays) was not surprising. Lever-pressing behavior for food reward after 0, 100, 300, or 500 rad (x-rays) was less affected than was the ad libitum food intake of rats receiving the same doses (96).

Study design constraints made it difficult to assess motivational factors without nutritional or learning factors. McDowell and Brown (119) measured the activity of previously irradiated (1050 rad Co^{60}) rats while the rats were adapting to a food-deprivation schedule and test apparatus. Irradiated animals showed a much smaller increase in activity during daily fasting adaptation than did controls. In animals previously irradiated (2.5-4.5 months) with 550 to 690 rad x-rays and previously adapted to the testing apparatus, food deprivation produced a much smaller increase in activity than in the control animals.

In general, head-only irradiation required higher doses than those to produce similar behavior effects after whole-body irradiation. In one study (7), hunger-driven activity was measured by the frequency with which the animal crossed over a shock-grid barrier to reach food. Normal animals required a food deprivation of 48 hours before crossing one time. Cranial exposure to 2.5 krad of x-rays resulted in a higher number of crossings in days 20-100 post-irradiation. Those animals receiving 5.0 krad crossed fewer times than did the controls.

Several researchers have assessed the effects of radiation exposure on psychological processes by testing the rate of response to positively reinforced electrical stimulation of the brain, self-stimulation. Olds and Milner (140) were probably the earliest to use this test. Their procedure involved the performance of the animal to obtain or stop electrical stimulation delivered through electrodes previously placed in subcortical regions of the brain. These early studies showed that the theories behind self-stimulation behavior were much more complex than first thought (16, 58, 157). Studies by Haley, et al. (76) showed an increase in the rate of response of rats on the day of whole-body exposure to 600 rad (250 kvp) x-rays. By day 17 post-irradiation these rats showed a decrease in the rate of response which continued to the 30-day end of the testing period.

Results from later studies by Christensen, et al. (38) and Bruner (22) showed a similar course of performance decrement of self-stimulation responses as seen with shock-avoidance discrimination tasks. As Bruner suggested, perhaps aversive motivational properties of shock reinforcement are not mediators in the post-radiation performance decrement.

As seen by the results of these studies, the ability to assess motivational factors was extremely limited by the inability to isolate motivation as a singular variable. Although some test results indicated increased/normal responses followed by decreased responses, it was impossible to show that this was strictly a motivational response rather than a physical response. If an animal physically cannot perform or just does not feel like performing, motivation becomes less of a factor in whether or not it responds.

1.4.4.2 Learning. Learning is characterized by the formation of stimulus-response complexes which result from an animal's experience. Historically, learning has been tested by measuring the learning of a task or the change in a learned task instigated by cue variations. Since human performance problems are better studied using complex problems, simple forms of learning such as reflex conditioning will not be discussed here. However, references covering these simple learning topics are included in the "Behavior Reading List."

The maze has been used by many investigators to study complex spatial discrimination behavior. Irradiation of adult rats does not seem to alter the accuracy of maze learning. Furchtgott (56) showed that exposure to 0, 200, or 300 rad (250 kvp) x-rays did not alter swim maze learning in rats. Several other investigators produced similar results (7, 8, 11, 97, 168), and retention of a maze habit does not appear to be affected by radiation (12). Kaplan, et al. (104) did find some decrements in maze learning in partially trained, hunger-motivated rats exposed to 0, 90, 180, 360, or 600 rad (250 kvp) x-rays. Animals in the 360 and 600 rad groups exhibited more errors than did the controls for the week following radiation exposure. Fields (53) demonstrated reduced maze-learning after the first week post-irradiation using a complex 40-unit elevated maze. Control animals learned the maze by trial

16 (1 trial/day), but irradiated animals (100-600 rad x-rays) did not have three consecutive errorless runs until trial 19.

1.4.4.3 Perception. In order to measure perception of stimuli, various discrimination learning tests have been designed. For the most part, these are visual discrimination learning tests. In the rat, visual discrimination learning was reportedly reduced immediately after whole-body exposure to 180, 360, 470, 500, or 575 rad of x-rays (54, 57). This deficiency occurred during the same time period as the early transient incapacitation. Similar results (169) were found in cats following x-irradiation using a T-shaped choice apparatus. Meier, et al. (126, 127) exposed mice to 1 krad of Co^{60} at 1 rad/hr before testing them on a brightness discrimination learning test involving four units of a two-choice discrimination maze. The animals were tested at 3-5 months post-irradiation; at that time, learning was retarded. Studies (49) using dogs showed an accuracy deficit that corresponded to clinical illness. These animals were exposed to 150 or 300 rad (2-Mev) x-rays (whole-body) and tested on a delayed response problem in a T-shaped choice apparatus. The correct path was shown to the animals briefly; then after varying delay times, the dogs were allowed to perform. The performance deficits were seen in those animals receiving the 300 rad dose, which had the longer delay periods.

As an aside, Kimeldorf and Hunt (108) report that Soviet investigators use "serial discrimination behavior" to test perception in non-human primates. In these studies, conditioning involved complex sequencing of interacting conditioned responses (stereotype), which are controlled with a series of quickly presented stimuli. These studies, however, used animal temperament as a variable and most did not include control animals. These problems make it difficult to compare their results with those of Western investigators. The Soviets' results showed wide variations among studies and animals within studies, which they attributed to individual animals' "personality." They contend that those with the "stronger personality" exhibit the greatest resistance to damage from radiation exposure.

Primates have been used in several research programs in the United States to test learned discrimination behavior after radiation exposure (19, 20, 46, 47, 78, 79, 163, 164). Testing procedures typically involve a tray within the animal's reach from which the animal is to select one of the various objects. The "correct" object commonly has a piece of food, the incentive, under it. High doses (6-8 krad range) seemed to produce learning deficits when tested 2-36 months after radiation exposure (77, 120, 121, 123, 164). However, lower doses were less likely to produce deficits (48, 118, 185).

Payne (149) reported that most investigators concluded that no impairment occurred after irradiation. In fact, several studies have shown that radiation exposure facilitates learning discrimination behavior (19, 20, 78, 163). This finding has been attributed to a reduction in the animal's attention span and in distractibility, a conclusion substantiated by extensive work of Brown and McDowell (19, 20).

1.4.4.4 Summary: Psychological Processes. Psychological processes involve a stimulus and a response to that stimulus. Investigators classically used motivation, learning, and perception as endpoints in radiation effect studies. Motivation assessment was difficult because of the inability to show that post-irradiation responses were only due to a motivational effect. Some studies indicated that motivation following irradiation remained normal initially but decreased with time. Learning effects were studied primarily with adult rats in maze-learning studies.

Irradiation did not seem to alter maze-learning significantly. Testing for effects on perception involved the use of discrimination learning tests. High doses resulted in learning deficits, but lower doses did not alter performance significantly. Some investigators showed that irradiation facilitated discrimination behavior by reducing an animal's distractibility.

Although whole-body irradiation does not seem to radically change an animal's capacity for learning, it does appear to affect total activity and manipulative activities, which could affect the results of commonly used testing procedures for psychological behaviors.

1.4.5 Behavioral Activation.

In addition to effects on the behavioral functioning of an animal, radiation exposure also acts as a stimulus to behavior. Apparently, exposure to radiation motivates behavior and acts as a perceptual stimulus.

Early studies (64, 68, 112) measured food and water consumption of rats during exposure to gamma (Co^{60}) radiation. This exposure served as the stimulus and the response was a decrease in food and water consumption.

Extensive studies (67) were then done to investigate radiation-induced motivation by testing a taste-aversion conditioned by radiation exposure. The conditioned stimulus was usually a distinctive taste substance, such as saccharin sodium, added to the drinking water available during irradiation. A single 30 or 57 rad exposure (6 hours) to Co^{60} gamma radiation resulted in a conditioned aversion to the saccharin solution. This aversion continued for 2 months after radiation exposure. The particular taste substance does not seem to be a factor since radiation has successfully conditioned aversion to Kool-Aid (79), chocolate milk (111), NaCl solutions (152), and ethyl alcohol (150), and the aversion does not appear to be species-specific, since mice, rats, cats, and monkeys have all shown radiation conditioned taste aversion (79, 111, 180).

Other studies have investigated radiation-induced motivation using place-avoidance conditioning, which requires the use of location cues as discriminative stimuli. Rats were conditioned by confining them for 5 hrs/day to either of the two end-compartments of a choice-alley and were exposed to radiation (50 or 85 rad Co^{60} gamma) while in one of the compartments. The rats exhibited avoidance of the compartment where they were exposed to radiation (65, 66). Free-choice learning procedures produced results that were interpreted as a conditioned avoidance of the black end of a runway (where they were exposed to x-rays of 360 rad), which is a reversal of the pre-irradiation preference for the black area (145, 146, 147). Andrews, et al. (3, 5) found that mice avoided areas exposed to 3-Mev x-rays at 50, 98, 169, or 196 rad/min but not at 10 rad/min. After investigating several possible reasons for the avoidance such as ozone production and radiation-induced fluorescence of the plastic container, the authors concluded that the mice did discriminate the exposure field. Radiation apparently provides the animal with the differential place-stimulus and the motivation for learning (154).

Radiation factors did play a role in these conditioning behaviors. X-rays, gamma rays, and fast neutrons (63, 182) have produced the conditioned taste aversion. The lowest total exposure reported by Kimeldorf and Hunt (108) were 9.9 rad of x-rays, 10 rad of gamma rays, and 7.5 rad of fast neutrons (all measured

"in air"). But until dosimetry is improved, exact threshold doses and dose rates cannot be established.

The process of radiation-induced aversion-conditioning does not appear to involve direct sensory stimulation. Saccharin aversion was demonstrated in previously bilaterally ophthalmectomized rats (61), and place-avoidance conditioning was demonstrated in previously bilaterally ophthalmectomized mice (105). Exposure of a specific localized area of the body to radiation was not responsible for aversion conditioning since exposures limited to any of several body regions (head, thorax, abdomen, or pelvic) allowed for conditioned saccharin aversion (59).

An important variable involved in conditioning aversions is the time relation between radiation exposure and presentation of the taste solution. Interpretations of study results have been controversial. Garcia and Kimeldorf (60) concluded that the aversion conditioned by rats receiving the saccharin during the first and last 2-hour periods of the 4-hour exposure ("simultaneous" group) was more pronounced than the "trace" and "backward" groups. Studies by Morris and Smith (125, 133) showed that a strong post-radiation (x-ray) aversion to saccharin was produced if the 20-minute saccharin period was initiated within 1 hour after radiation exposure. The aversion could not be produced if saccharin presentation was delayed for 6 hours post-irradiation. Further studies by Smith included an extensive investigation of temporal effects on conditioned aversion (178). Results from this study indicated that significant saccharin aversion was conditioned with delays up to 4 hours after exposure to 100 rad of x-rays or gamma rays. Although McLaurin (124) suggested that his results showed aversion was not conditioning, Smith (180) clearly refuted that suggestion based on the fact that the preference test was presented too soon after x-ray exposure, so the presentation was essentially a continuation of that preceding x-ray exposure. Experiments were then done to confirm this argument (179). Evidence showed that a taste aversion could be conditioned if the distinctive taste solution is presented prior to, during, or following radiation exposure.

Attempts were made to determine if there were specific receptors responsible for radiation-induced motivation. Early hypotheses related aversion to gastrointestinal effects of radiation exposure (59, 66, 112). Garcia and Kimeldorf (61) investigated the possible role of vision, and Dinc and Smith (50) looked into the role of olfaction. Evidence supports the idea that conditioning aversion results more from humoral rather than neural factors (180).

Results by Garcia and Kimeldorf (61) were supportive of the gastrointestinal hypothesis. They found that although whole-body exposure produced the strongest aversion, abdominal exposure produced similar results. Several investigators studied gastrointestinal motility following radiation exposure (40, 41, 87). Although Conard (41) concluded that ionizing radiation acted directly on the cholinergic nerve fibers of the intestine resulting in intestinal contraction, many investigators have produced results indicating that the observed correlation between conditioning and gastrointestinal problems represents a coincidental relationship. Smith and Morris (176, 177) found that atropine had no effect on aversion conditioning at any exposure level. Physostigmine had an augmentative effect with or without radiation exposure. Garcia and Koelling (62) were able to condition taste aversions using such toxic drugs as lithium chloride. In addition, although adrenalectomy attenuated gastric retention (98), it did not affect saccharin aversion conditioning. Hunt and Carroll presented results in which they were able to condition taste aversion in totally gastrectomized rats after an 18 rad whole-body exposure.

Although the olfactory system does appear to be involved in the immediate response of the rat to radiation, it appears unlikely that it mediates conditioned taste aversion. The strongest results refuting its involvement were that taste aversion has been conditioned with a dose rate as low as 0.083 rad/min (67), which is known to be below the exposure rate threshold for olfactory detection of radiation (0.24 rad/min) (180).

Garcia and Kimeldorf (61) have shown that ophthalmectomized rats can be conditioned for saccharin aversion, indicating that the visual system did not play a role in this conditioning.

Early studies designed to investigate direct neural factors involved with conditioned taste aversion exposed the animals to radiation while anesthetized (89). The thought was that this could prevent the visual or olfactory input. Results showed that the rats would still acquire a pronounced saccharin aversion.

Rabin, et al. (158, 159, 160) investigated the involvement of the area postrema in conditioned taste aversion in rats. Their results, along with those of Ossenkopp and Giugno (144), indicated that although area postrema lesions did not affect recall of previously acquired taste aversion, they did appear to attenuate the conditioning of taste aversion especially after body-only exposure. These results suggest a possible role of the area postrema in this process.

So, the final variable in the animal's taste aversion conditioning involves the humoral factors. Probably the most spectacular experiments in this area were done by Hunt, Carroll, and Kimeldorf (90, 91, 92, 93). In the studies, unrestrained parabiont pairs of male rats, which were united by vascular anastomosis at 26 days of age, were tested to see if irradiation of one rat would result in the conditioning of a taste aversion in both rats. A profound aversion to saccharin was found in both rats following whole-body exposure of one. Partial-body exposure did not produce as strong an aversion as did whole-body exposure.

Although evidence suggested that humoral factors mediate the formation of a taste aversion, the actual factor has not been determined. Rabin, et al. (161, 162) investigated the possible role of radiation-induced release of histamine as a mediator in the conditioned taste aversion as suggested by others (116, 170). Rabin's results did not support this hypothesis. And a study of post-irradiation mast cell function by Persinger and Fiss (153) supported Rabin's conclusions. More studies of this type would assist in the understanding of the involvement of humoral factors in conditioned taste aversion.

1.4.5.1 Radiation Detection. There has been reported evidence in support of direct stimulation of animals with ionizing radiation. Hug (85) reported reflex-like responses to x-ray or gamma exposures in invertebrates. A similar type response in mammals was reported by Conard (40) when he observed increased tone and motility in the small intestine within 1 minute post-exposure. Other investigators have tried to explain the perception of radiation by animals.

1.4.5.2 Visual Stimulation. The visibility of x-rays has been documented and results from excitation of the rods (55). The "light" produced by radiation was phosphene and the threshold intensity of x-rays for visibility was around 0.5 mrad. Bachofer and Wittry (9) showed that the electroretinogram (ERG) a, b, c and d waves seen with visible light were also seen after stimulation with radiation. These

results indicated that x-rays function as a stimulus in the same way that "normal" light functions as a stimulus.

Many early investigators reported an immediate response to x-rays through visual mediation (180) if the animal was in a dark-adapted state. Visual detection of x-rays and gamma rays (180) was demonstrated in dark-adapted rhesus monkeys following bilateral interruption of the olfactory tracts. Evidence showed that visual detection of radiation was possible if the animals were tested in a dark-adapted state. So, it was concluded that visual mediation played an insignificant role in behavior studies since testing generally occurred in sufficient light to preclude radiation-induced visual stimulation.

Hunt and Kimeldorf (88) found that exposure to x-rays could immediately arouse a sleeping rat and increase its heart rate even in blinded rats, indicating that vision was not singularly involved. In addition, this detection appeared to be dependent on exposure rate, not total dose, unlike conditioned aversions where exposure rates were not critical. Garcia, et al. (26, 69, 70) demonstrated conditioned suppression with only 10-sec x-ray exposures (no subsequent shock). Responses were reported to exposure rates ≥ 50 mrad/sec and occurred even in blinded rats.

Dinc and Smith (50), in a conditioned suppression study, conditioned rats to suppress then removed their olfactory bulbs. Olfactory bulb removal resulted in a loss of x-ray sensitivity. Brust-Carmona, et al. (25) corroborated these results in a similar experiment, and Hull, et al. (86) demonstrated that animals with their olfactory bulbs removed were not aroused from sleep by radiation exposure. Electrophysiological data reported by Cooper and Kimeldorf (42, 43) involved the use of microelectrodes in the olfactory bulbs. Extracellular potentials were reported after x-ray exposure at 1500 mrad/sec. When ethyl alcohol was flushed through the nasal cavity, which obliterated the olfactory receptors, no potentials were recorded. Other evidence in support of x-ray stimulation of olfactory receptors rather than olfactory brain area stimulation was found after the nasal cavities of rats were perfused with air, oxygen, argon, or nitrogen. Extracellular potentials were depressed in animals after ozone or nitrogen perfusion following exposure to x-rays. Gasteiger and Helling (71) were able to obliterate the immediate response to x-rays using ambient ozone.

Smith (180) reported results from his laboratory involving olfactory stimulation by x-rays in monkeys. Conditioned suppression was achieved in these animals until the olfactory tracts were severed. At that time, suppression could not be demonstrated.

The actual method of olfactory detection was not clear. The possibility existed that an odor was formed in the nasal mucosa, such as ozone, making radiation detection a secondary effect from normal olfactory processes. It was thought that an odor could be formed when air next to the nasal mucosa ionizes. However, the radiation detection could arise from a direct effect on mucosal receptors or the olfactory nerve or bulbs.

1.4.5.3 Summary: Behavioral Activation. It is clear that under certain conditions, radiation, specifically x-rays, is visible and can act on olfactory receptors (directly or indirectly). It also appears that this detection can be transferred humorally. The taste aversion and conditioned suppression test results also support the theory that animals are able to perceive radiation even at very low doses and dose rates.

1.5 CONCLUSION.

Clearly, radiation effects on neural function and behavior can result from direct neuronal damage and/or indirectly through damage to surrounding supporting structures. Functional alterations can also affect animals' reactions to stimuli from noninjured systems or from radiation-damaged systems. Behavioral manifestations of radiation exposure can arise from any of the above processes. It is thus understandable that interpretation of behavioral study results is a difficult task. There are simply so many variables in the dynamic systems of an animal that precise measurements of individual functions are impossible.

"Measurable" items used to assess radiation damage include EEG results, histopathology of morphological changes and various behavioral "tests." EEG and morphological changes are probably the most obvious ways to detect damage. Results reported in this review demonstrate that there are morphologic and EEG changes after radiation exposure. However, behavioral changes are observed in animals without concurrent changes in their EEG or cellular morphology. General activity of an animal appears to be the most sensitive measure of radiation exposure. Irradiation is capable of altering the performance of animals in a predictable manner. With high doses, performance changes tend to correlate with some phases of systemic damage. Massive doses appear to result from direct neuronal damage. Psychological processes, such as learning, memory, motivation, and perception, are also assessed in behavior tests. Animals show a loss of distractibility and smaller attention span.

Previous theories on neurological radioresistance were based on the fact that very large doses of radiation were required to cause morphologic alterations in neural tissue. But the immediate EEG and behavioral responses to low doses of radiation suggest that these radiation-induced responses are at least mediated through neural pathways.

SECTION 2

RADIATION EFFECTS ON THE CARDIOVASCULAR, GASTROINTESTINAL, AND ENDOCRINE SYSTEMS

2.1 CARDIOVASCULAR SYSTEM.

2.1.1 Introduction.

The cardiovascular system is an integral part of every major functional activity of the body. Structurally, it consists of components to pump, transport, and distribute oxygen and nutrients to cells and tissues of the body. In addition, it provides the mechanism for specialized tasks such as filtration by the renal glomerulus. Clearly, damage to any or all of the components of the cardiovascular system will subsequently affect, whether directly or indirectly, the functioning of cells, tissues, and organs.

Pathologists have noted for over 50 years (49, 27) that ionizing radiation structurally damages the heart and blood vessels. More recently, studies have shown that the structural damage can also result in functional deficits (4, 29). Changes can be produced by interference with myocardial metabolic processes and vascular functions. The difficulty in studying these responses to radiation exposure is, at least in part, due to the vascular system's being structurally interwoven into other organ systems. The ability to attribute an observed response to cardiovascular damage alone is clouded by the intermixed parenchymal damage. However, significant progress has been made in recent years primarily because of renewed interest in understanding damage to the cardiovascular system induced by higher energy therapeutic irradiations.

2.1.2 Heart.

2.1.2.1 Morphologic Changes. Historically, the heart has been thought to be a radioresistant organ; in fact, fairly heavy doses of radiation are necessary to produce gross lesions in the heart (4). Rabbits have been found to require a local dose of over 1,000 rad to induce cardiac lesions (15-17, 30-32, 57). Since the morphologic response of the heart in rabbits follows the exact pattern seen in humans (17), the morphologic description to follow is that of the rabbit heart. The severity of the post-irradiation lesions appears to be dose-related. Initial gross findings (<6 hrs post-exposure) included only a small increase in the amount of pericardial fluid. Histopathology revealed no microscopic changes at 3 minutes post-exposure. After 6 hours, acute inflammation occurred as an accumulation of heterophils in the pericardium, epicardium, myocardium, parietal endocardium, and valves. This pancarditis continued through 24 hours with only the addition of small numbers of lymphocytes and foamy histiocytes at the 12-hour mark. Microscopically, the parietal endocardium appeared to be the most severely affected during this phase. Electron microscopy typically revealed some focal cytoplasmic degenerative changes in the endothelial cells, the presence of a few capillary thrombi, prominent contraction bands, disruption of intercalated discs, myofibrillar degeneration, and disorganization with myofibrillolysis. Animals usually did not show clinical disease during this time.

By 48 hours post-exposure, gross lesions disappear, and histopathology revealed only small focal areas of myocardial fibrosis. However, electron microscopy of cardiac myocytes during this time revealed advanced myofibrillar degeneration, the loss of whole sarcomeres in groups of myofibrils, mitochondrial alteration and loss of cristae, Z-band destruction, and disruption of the intercalated discs. In addition, alterations in the capillary endothelial cells included cytoplasmic swelling, dense bodies, and interruption of the capillary wall. Fibrin and platelet thrombi are also seen in the later phases.

Although gross lesions are the most prominent after 70 days post-exposure, electron microscopic examination of the myocardium at various times between the 48-hour and 70-day time points revealed a progression of ultrastructural changes. Architectural disorganization of myofibrils, focal cytoplasmic degeneration, and subplasmalemmal vacuolation characterize the changes at day 8. By day 22 post-exposure, myofibrillolysis became less prominent, but many fibers showed thicker Z-lines, dilated sarcoplasmic reticulum, mineralization of mitochondria, focal accumulations of glycogen granules between myofibrils and sarcolemmal membranes, and slight pericellular fibrosis. Endothelial cell changes included basement membrane thickening, platelet sequestering, abnormal endothelial cell phagocytic activity, widening of the junctional gaps, complete obstruction of the lumen of the capillaries by cytoplasmic swelling, and rupture of the capillary wall. Fibrosis of the myofibers and perivascular areas characterized the changes at 70 days post-exposure. At this time, gross lesions included pericardial thickening and a fibrinous to sanguinous effusion. In some cases, the effusion was severe enough to cause cardiac tamponade and heart failure. Histopathology revealed replacement of the pericardial adipose tissue by collagen with subsequent pericardial fibrosis, diffuse myocardial fibrosis, and atherosclerosis with thrombi in the subepicardial vessels.

In monkeys, exposure of the heart to 6,000 rad of x-irradiation results in grossly thickened, fibrous pericardia and infarctive fibrotic myocardial lesions (46) at five months. Histopathological examination of the myocardial lesions revealed a spectrum of changes from hemorrhagic necrosis to hyaline degeneration, fatty infiltration, and replacement of myocytes. Vascular changes in these areas were prominent. Cytoplasmic swelling was severe and, in some cases, obliterated the lumen of the vessel. The basement membrane of the vessels thicken and perivascular collagen loses its cross-striations. Some vessels were completely fibrotic.

In mice, histopathological and ultrastructural evidence of myocardial damage has been reported following 400-2,000 rad of x-irradiation (7, 17, 33, 57), 240 rad of neutrons, and 788 rad of 60-Co gamma rays (64). In general, cardiac muscle showed degenerative changes such as myofibrillolysis, lipid bodies, partially vacuolated mitochondria, and dissociation of the intercalated discs. Vascular changes included cytoplasmic swelling, cytoplasmic blebs, vacuolated mitochondria, and thrombi. These changes appeared to be the most severe between 4 and 12 weeks post-exposure.

In rats, radiation-induced changes in the myocardium and its vasculature occurred after 500-2,000 rad of x-irradiation (11, 36, 48) and 500 rad of 60-Co gamma rays (44). Animals developed life-threatening symptoms within four to ten months after irradiation. These animals had similar changes in the myocardium at that time; however, the degree of degeneration within the myocardium varied within the same heart. Areas of severe degeneration were interspersed among areas of normal

myocardium. Severity of the lesions did not vary with the dose. The clinical endpoint was always associated with the same degree of myocardial change. Vascular damage appeared to be associated only with the myocardial lesions. Ultrastructurally, the myocardial mitochondria were markedly altered within 12 hours of irradiation with only 500 rad of gamma rays. Other myocardial cell elements and myocardial vascular elements were not affected at this time. At 24 hours post-exposure, most of the myocardial cells showed mitochondrial lesions, Z-lines became disorganized, and sometimes myofibrils were completely degenerate. Endothelial changes were seen only in areas where myocardial cell damage was severe.

In dogs, 750-8,000 rad of x-irradiation resulted in an initial myocarditis followed by myocardial destruction and fibrosis (47, 56, 60). Hyalin degeneration in the myocardial vessels was prominent. The severity of the lesions appeared to be dose-related. Like the rat, the degree of degeneration within the myocardium varied within the same heart and did not appear to be related to vascular distribution.

2.1.2.2 Functional Changes - Electrocardiography. As discussed previously, large doses of ionizing radiation are required to produce histologic changes in the heart but electrocardiographic (ECG) changes are reported to occur at lower dose levels. Radiation-induced changes in the electrocardiographic response of the heart to radiation have been studied in the dog (2, 13, 47, 60), rabbit (4), hamster (18), rat (10, 36), and monkey (46). It appears that the functional myocardial damage, as measured by the electrocardiogram, is due to a direct action of irradiation on the myocardial cells whereas the later effects, such as those demonstrated by light microscopy, are multifactorial and depend on the radiation dose. Some researchers (18) believe that the radiation-induced electrocardiographic changes are at least partially due to a change in the potassium concentration in the serum. However, after doses of less than 1,000 rad, the ECG changes occurred in the absence of any alteration in plasma potassium level (11). There is evidence that the heart undergoes some changes in its chemical composition, most notably a decrease in actomyosin (10).

In dogs, exposure to 750-6,000 rad of gamma rays resulted in ECG pattern alterations and changes in aspartate aminotransferase (AST/SGOT) levels (60). Regardless of dose, ECG pattern alterations included ST segment elevation, prolongation of the Q-Tc interval, and signs of myocardial infarction. ST segment elevation, which indicates an alteration in the rate of polarization, occurred only during irradiation and never post-exposure. Prolongation of the Q-Tc interval, an indication of delayed polarization, occurred during exposure and then several (greater than ten) weeks after exposure. During irradiation, this interval reached its maximum at the end of exposure and then disappeared. At this time, there were no other ECG changes and the AST levels remained normal, indicating functional damage to the myocardium. The time of onset of the second episode of Q-Tc interval prolongation was dose-related. The AST levels rose two to three weeks prior to the onset of this second episode. These factors support structural myocardial damage as the cause of the second episode. Badran, et al. (2) reported inversion of the T-wave in dogs after exposure to greater than 2,000 rad of x-irradiation, the severity of which was dose-related. They did not observe any Q-wave alterations and concluded that no myocardial infarction had occurred. Moss, et al. (42) observed inverted T-waves, along with Q deflections and S-T elevations, which were associated with focal areas of myocardial necrosis. Similar results obtained by Phillips, et al. (47) were also indicative of focal areas of myocardial necrosis.

Electrocardiographic changes were seen in monkeys exposed to 6,000 rad of x-irradiation to the heart (46). Histopathology revealed significant damage to the cardiac conduction tissue such as the sinoatrial node region and the atrioventricular node region. ECG changes, such as a complete lack of P waves and prolongation of the A-V interval, corresponded with this observation. Another investigator (34, 35) using proton and gamma radiation sources observed no consistent changes in the ECG. Some of the animals showed inverted or peaked T-waves. One animal developed elevation of the S-T segment during irradiation, which subsided after exposure ended much like that reported in the dog (60).

Radiation-induced electrocardiographic changes have also been noted in the rat (11, 36). The most frequent findings included atrioventricular blocks and bundle branch blocks post-exposure, which subsequently reversed to normal. From days 2 through 6 post-exposure, there were cyclic variations in the R-R interval length and R-wave amplitude. A marked arrhythmia occurred concurrently with these alterations during days 8 through 10. Alterations in the T-wave, as described in other species, cannot be documented in the rat since the normal rat ECG has no isoelectric segment between the QRS-complex and the T-wave.

Fulton and Sudak (18) reported similar radiation-induced changes in the ECG of hamsters exposed to x-irradiation. After 600 rad, ECG changes included a depression of the T-wave, variation of the R-wave amplitude, and marked arrhythmia. Depression of the P-wave, T-wave inversion, S-T segment depression, and prolongation of the Q-T interval were observed in hamsters after 1,000 rad of x-irradiation.

2.1.2.3 Functional Changes - Cardiac Output. Another measurement of the functional capacity of the heart is cardiac output. Radiation-induced alterations in cardiac output have been observed in the dog (5, 13, 58, 59) and monkey (8, 34, 35). Investigators have reported only slight changes in the cardiac output except just before death. During the first two days after 1,000 rad of whole-body x-irradiation, the cardiac output in dogs was altered only slightly. However, 65 to 70 hours after irradiation, the cardiac output decreased rapidly until death occurred (usually 15 to 20 hours later). Stone, et al. (58) determined that the maximum ability of the canine heart to pump blood decreased to one-half the normal amount post-exposure, but the cardiac output remained close to normal until just before death. Apparently, the myocardial functional capacity has enough reserve to handle this decrease in ventricular pumping ability until the animal is close to death. Stress could be the trigger for this inability to compensate. Myers, et al. (43) demonstrated that the monkeys exposed to 250-1,000 rad of gamma radiation maintained cardiac output until the animals were stressed by three transient bleeding episodes post-exposure. The animals then showed a reduction in cardiac output and stroke volume. Kundel (34, 35) reported that monkeys exposed to gamma radiation (3,900-6,600 rad) showed a decrease in cardiac output by 18 hours post-exposure. However, proton irradiation did not produce the same effect. Similar results were obtained by Bruner (8) after gamma radiation exposure of monkeys; however, the decrease in cardiac output was seen only 6 minutes post-exposure and followed a temporary slight increase in cardiac output.

Possible explanations for the fall in cardiac output following radiation exposure have been proposed. In fact, this functional alteration is most probably the result of a combination of factors. These include 1) a reduction of pressure-receptor sympathetic drive to the heart due to a reduction in heart rate, 2) a reduction in return volume of blood to the heart due to venous pooling and reduced venous tone, 3) a

decrease in responsiveness of the baroreceptor reflex arc, and 4) a loss in cardiac compensating ability.

2.1.3 Blood Vasculature.

2.1.3.1 Morphologic Changes. Exposure to radiation results in widespread vascular changes including degeneration and necrosis of endothelial cells and proliferation of the endothelium with edema, fibrosis, thickening, and infiltration of the vascular wall. Investigators attempting to measure endothelial cell survival have used an assay method involving the irradiation of a selected vascular area, initiation of endothelial cell proliferation by physical or chemical stimuli, and then counting the subsequent numbers of capillary sprouts or neovascularization network density (21). Animal models used in these studies were primarily in the rat (52, 53). Results indicated that the radiosensitivity of endothelial cells is similar to cell survival values for both epithelial and connective tissue cells.

Histopathologic examination of blood vessels after exposure to radiation revealed a variety of morphologic changes in the vessel wall. Historical data from clinical reports provide good descriptions of structural changes, but many fail to provide the dose and/or time between exposure to radiation and tissue sampling. Therefore, the possible progression of morphologic changes with time post-exposure was obscured by these reports (50). Experimental studies do suggest that such a progression of lesions does exist; and the type of lesion can be categorized with respect to time post-exposure: 1) early changes, 2) intermediate changes, and 3) late changes (21).

Early changes are those occurring within the first few days to weeks post-exposure. At this time, endothelial cell death is probably not the main factor causing disturbances in microcirculation (51). Ultrastructural studies (39), using the lung capillary system as a model, reveal immediate changes (three hours after exposure to 2,000 rad of x-rays) in the endothelial cells consisting of dilated cisternae of the endoplasmic reticulum, lysosomal-like bodies, widening of the perinuclear space, and a segregation of the nucleolar components. At 6 hours post-exposure, endothelial cells exhibit lipid droplets and osmiophilic precipitations in the cytoplasm, alterations in the cell membrane, the apposition of platelet groups, and associated fibrin to the basement membrane, and the hypertrophy of nuclei. In some areas, the nuclei are hypertrophied to the point of capillary lumen obstruction. No histopathologic changes can be detected at this time. From 1 to 7 days post-exposure, the endothelial cell lesions are more severe. Endothelial cells are separated from the basement membrane and, in some cases, the endothelium sloughs, leaving the basement membrane exposed. The most consistent histopathologic change at this time is capillary vasodilation. This would correspond to the erythema seen in the skin and mucous membranes after exposure to irradiation. Hopewell (22) suggests that this vasodilation is an inflammatory response to epithelial cell death.

Lesions associated with the intermediate time period, that of 1 to 9 months post-exposure to radiation, are directly related to endothelial cell death. Ultrastructurally, at 1 to 2 months post-exposure, aggregates of abnormally shaped platelets can be found close to damaged endothelium. In addition, other capillary lumens are obstructed by lipid inclusions and/or collagen fibers. From 3 to 7 months post-irradiation, endothelial cell cytoplasm shows definitive evidence of degenerative changes: osmiophilic precipitations; autophagic vacuoles; dilated, agranular, and rough endoplasmic reticulum; and large numbers of free ribosomes. Capillary

lumens are filled with platelets, collagen, fibrin, or lipid inclusions. Basement membrane folding and edema are seen in the later portion of this time period. Histopathologic examination of several different tissues, including lung, brain, heart, kidney, and skin, during the intermediate time period reveals irregularly spaced constrictions of the capillaries which are thought to represent localized thickening of the intima, the presence of thrombi, and capillary necrosis (15, 22, 23, 25, 37). The cells in these thickened and/or occlusive lesions have been found to be synthesizing DNA (21), but the exact cell type has not been identified. The pooling of blood around the occluded vessels contributes to intravascular deposition of fibrin and collagenous material.

Late changes (those occurring nine months and longer post-exposure) in the capillaries are primarily degenerative changes. Ultrastructurally, the capillary lesions consist of basement membrane thickening, basement membrane edema, lumen occlusion by collagen and recanalization. Histological examination of the vessels reveals an acellular hyaline, fibrinoid, and collagenous thickening of the vessel wall, which is sometimes severe enough to obstruct the lumen. These lesions appear to be more severe in the arteries/arterioles than in the veins/venules. In addition, thrombi and teleangiectasia are other types of changes seen in the irradiated vessels of various tissues (54). Severely damaged blood vessels, those with thrombosis or occlusion, can produce marked changes in tissues dependent on them for blood supply.

In summary, irradiation produces changes in vessels including degeneration and proliferation. Severe damage to vasculature compromises the dependent tissues. The endothelium is the most sensitive component of the blood vessel, and changes are more severe in capillaries within organs than in the arterial trunks. Although the endothelium seems to be the most sensitive to radiation injury, the connective tissue cells and muscle cells in the vessel wall are all involved to some extent in the changes seen in the vasculature of various tissues.

2.1.3.2 Blood Pressure/Vascular Resistance. Hypotension following radiation exposure has been observed in the rat (1, 11, 19, 20, 40, 45, 65), rabbit (6, 41), cat (55), dog (5, 14, 41, 55), monkey (9, 12, 34, 35), pig (3), sheep (3), and burro (3, 63). Various explanations and pathogeneses for this reduction in post-exposure hypotension have been proposed, including increased histamine levels (61), CNS depression (40), neurohormone release (55), and direct effect or lack of end-organ response (35).

Blood pressure in the rat has been studied by chemical and physiologic methods. Caster, et al. (11) reported significant increases in venous blood pressure at 3 hours and from five to 12 days after a single dose of 700 rad of total-body x-irradiation. Arterial pressures remained stable throughout the experiment. Phillips and Kimeldorf (45) measured aortic blood pressure and peripheral blood pressure (tail) simultaneously during and after exposure to 485 rad of x-irradiation. Peripheral pressure decreased markedly eight hours after exposure and returned to control levels by day 3 post-exposure. Aortic blood pressure was not altered at this dose. After 970 rad, there was a mild decrease in aortic pressure at 24 and 48 hours; after 1,940 rad, there was a marked decrease in aortic pressure at 8 and 24 hours post-exposure. These results suggest that a reduction in peripheral blood pressure after a sublethal dose of radiation reflects a response in peripheral circulation rather than central effects. Haley, et al. (19) demonstrated that the decrease in peripheral blood pressure was mediated by the release of vasoactive material into circulation rather than through a direct effect of the radiation on the precapillary sphincter and terminal

arterioles. This vasopressor material was released by the liver of rats during the first week after exposure to 600 rad of whole body x-irradiation.

Decreases in peripheral blood pressure without a fall in central pressure following certain doses of total body x-irradiation (e.g., 600 rad) suggested that compensatory mechanisms were involved, allowing for a wider pressure gradient from central to peripheral sites. The fall in aortic blood pressure observed by Phillips and Kimeldorf (45) following a higher total body dose (e.g., 970 rad) probably resulted from a different mechanism of action, such as through changes in the autonomic nervous system. As described in the previous section concerning cardiac output, the force of myocardial contraction is sufficient to maintain a normal cardiac output until just before death. This reduces the possibility that the decrease in pressure is due to a direct effect of irradiation on the heart.

Epinephrin-responsive cardiovascular changes were also investigated in the rat (62). The rats exposed to 700 rad of fast neutrons showed a 48-hour decrease in the maximum systemic pressure response (as measured by direct cannulation of the carotid artery) and an inability to maintain the pressure response to epinephrine (e.g., incapacitation of the adrenergic smooth muscle of blood vessels). The adrenergic motor endplates appeared to be intact and slightly more sensitive than in the control animals. In addition, there were no differences between the blood pressure response curves of irradiated versus control rats to acetylcholine, indicating that the radiation-induced central hypotension was not due to activation of the cholinergic portion of the vasomotor system. It follows that this central hypotension must be due at least in part to radiation effects on the adrenergic vascular smooth muscle of blood vessels. Wykoff (63) proposed that this damage to adrenergic muscles could be due to a direct effect, to intracellular damage, or to decreased blood flow through the vasa vasorum.

Post-irradiation hemodynamic studies in the dog have had similar results. Kabal and co-workers (28) observed that at 48 hours after 1,500 rad of mixed gamma-neutron radiation exposure, major cardiovascular parameters were within normal limits. However, the cardiovascular response (alpha and beta adrenergic activity) following epinephrine injection was altered. At 72 hours post-exposure, the epinephrine response was more severely altered and peripheral blood pressure deteriorated. Central blood pressure remained within normal limits. Once again, this study demonstrated that the cardiovascular deterioration at these dose levels appears to be peripheral rather than central in origin.

The monkey has also been the subject of studies involving radiation-induced cardiovascular effects. Kundel (34) reported a dose-dependent decrease in aortic blood pressure after whole-body 60-Co gamma rays. Total peripheral resistance decreased only slightly in the irradiated animals, indicating that vascular tone was either normal or slightly decreased. In addition, the irradiated animals exhibited a diminished response of the mean arterial pressure to norepinephrine within the first hour after irradiation. This response returned to normal by 24 hours in all animals except those in the highest dose group (6,600 rad) in which it remained depressed. Clearly, the loss of response to norepinephrine suggests that an effect on the smooth muscle of the vessel walls is important in the production of post-irradiation hypotension.

The obvious complexity of radiation-induced changes in blood pressure results in difficulty in ascertaining the exact mechanism(s) responsible for the fall in blood pressure, whether central or peripheral. A number of possibilities have been ruled

out based on studies directed toward these entities. One such proposal was a reduction in blood volume. Several investigators (38, 40) have shown that the decrease in red blood cell mass observed after irradiation is adequately compensated for by an increase in plasma volume. Cardiac output, as described earlier, is maintained at a reasonable level so direct myocardial effects are unlikely at least within the first nine months post-exposure. Some investigators suggest that the hypotension is due to an effect of the central nervous system (CNS). This hypothesis does not take into account the results indicating that focal irradiation of the head requires doses far greater than the whole-body doses to result in decreased blood pressure. As described above, evidence points toward an effect on peripheral vasculature as the causative factor resulting in post-irradiation hypotension. Several researchers have found histamine and/ or other vasodepressor materials in the blood of rats, rabbits, and dogs after exposure to radiation (19, 34, 61). Further support for this hypothesis was gained from exchange studies in rabbits which show that replacement of 50 percent of an unexposed rabbit's blood volume with blood from an irradiated animal produced a mild hypotension in the unexposed rabbit. However, definitive evidence for the post-irradiation induction of hypotension by vasopressor and/or vasodepressor materials has not been procured. In fact, irradiation could have a direct effect on the peripheral vasculature. Support for this theory involves the lack of a "normal" response of mean arterial pressure to norepinephrine after exposure to radiation. The mechanism(s) responsible for this effect have not been completely worked out but probably involve one or more of the following: 1) endogenous norepinephrine release, resulting in overstimulation of the vascular beds and a superimposition of exogenous norepinephrine on already constricted vessels; 2) endogenous norepinephrine release of brief duration (maximal stimulation) in response to an early fall in blood pressure, resulting in a state of decreased vascular sensitivity; 3) a drop in blood pH; 4) rapid inactivation of the exogenous epinephrine after injection; and 5) direct effect on the smooth muscle of vessel walls.

2.2 GASTROINTESTINAL SYSTEM.

2.2.1 Introduction.

Documentation on radiation injury to the gastrointestinal system is extensive. Researchers began recognizing the association between radiation exposure and gastrointestinal lesions as early as 1909 (44). Early degenerative changes appearing in the intestinal epithelium of the duodenum after whole-body or abdominal exposure to doses as low as 80 to 100 rad reflect the severe radiosensitivity of the small intestine.

Damage to the intestine at higher doses appears to be dose related. Observations of symptoms, gross lesions, and microscopic lesions following x-ray exposure of dogs were documented by 1912. Despite these and subsequent efforts by numerous investigators, the actual mechanisms involved in producing the "gastrointestinal syndrome" and its symptoms are not completely known. It is evident that there is not one single cause but a combination of changes that results in the syndrome. These gastrointestinal changes, along with damage to other organ systems, such as the hematopoietic system, can so severely impair an animal that death will occur. Most investigators recognize the gastrointestinal syndrome as a critical, early post-exposure event that can result in the death of an animal within the first week after exposure.

2.2.2 Gastrointestinal Syndrome.

The gastrointestinal syndrome was first described by Quastler (59) in animals following doses of 10-1000 Gy of x-ray or gamma rays. Although the survival and early symptoms differ from species to species and even from strain to strain, all mammals exhibit similar symptoms, including vomiting (in animals capable of vomiting such as dogs and monkeys), anorexia, delayed gastric evacuation, diarrhea, dehydration, lethargy, and weight loss. The symptoms become progressively more severe, and death occurs 3 to 5 days post-exposure in mice, rats, dogs, and several other species. The survival time is longer for guinea pigs, monkeys, and humans. The progression of symptoms in humans appears to be most like that in monkeys.

The majority of symptoms observed in the gastrointestinal syndrome are primarily a consequence of radiation damage to the intestinal epithelial stem cell. This damage results in mucosal denudation, fluid and electrolyte loss, and subsequent bacteremia. Vomiting, fatigue, and anorexia have been reported in animals with the abdomen shielded. In these cases, the symptoms probably result from shock induced by the destruction of cells and liberation of their products.

2.2.3 Morphologic Changes.

2.2.3.1 Stomach. Since the most prominent gastrointestinal lesion appears to be in the small intestine, few investigators have studied changes in the stomach. Pierce (58) found that mitotic activity in the stomach of rabbits exposed to 800 rad of x-rays dropped within 40 minutes after exposure. The zymogenic glands showed a loss of granulations after two hours which persisted for five days. Granulations, though abnormal, began to increase between the fifth and ninth days. By day 14, the granulations returned to normal. Mitosis was greatly reduced in the mucous cells immediately after exposure. The number of mitoses did not return to normal until day 5. Parietal cells appeared to be fairly resistant. From 2 hours to 5 days after exposure, a few cells showed pyknosis of their nuclei and cytoplasmic vacuolation, but the majority of cells remained normal.

After 550 rad of whole-body x-irradiation in rabbits, the stomach showed similar changes but were less severe and more quickly resolved. After 1 hour, mitoses had stopped. The zymogenic cells were pyknotic, and the parietal cells had swollen nuclei at 3 hours post-exposure. The mucous and parietal glands returned to normal within 24 and 48 hours, respectively, but, the zymogenic cells were not considered normal for 5 days post-exposure. Clearly, the zymogenic cells are the most radiosensitive cells in the stomach.

Early reports (44) showed that increasing the dose can lead to atrophy of the gastric glands with subsequent mucosal thinning, and excessive doses can produce gastric ulcers with subsequent perforation.

2.2.3.2 Small Intestine. Many of the clinical signs associated with the gastrointestinal syndrome can be traced to damage of one or more specific cell types in the small intestinal mucosa. These different epithelial cells perform different functions, which include proliferation of the intestinal mucosa (crypt stem cells), secretion of various substances (e.g., goblet cells, Paneth cells, Argentaffin cells), and absorption of material from the lumen (columnar villus epithelial cells). After irradiation, the intestinal mucosa becomes denuded due to the loss of the radiosensitive crypt stem cells' ability to proliferate. Therefore, as the villus epithelial

cells migrate to the tips of the villi and slough into the lumen, there are no cells to take their place on the villus. The villus becomes shortened and denuded; and thus, the integrity of the intestinal mucosa is lost. In addition, radiation appears to inhibit absorption, stimulate secretion, and affect intestinal motility. The effects of radiation on these different cells of the small intestinal mucosa have been studied in great detail.

The sequence of histologic changes in mice and rats is the same for most species with only slight variations. Studies involving radiation effects on the mouse intestine have provided a basis for understanding the sequence of events in radiation injury (52, 53, 55). Mice receiving 1000 rad of x-irradiation died within 4 to 7 days. Histopathologic examination of the small intestine of these mice at death revealed denuded villi with mostly restored crypts of Lieberkuhn (crypt stem cells). Time sequence studies of the post-exposure radiation lesions revealed a progression of changes. The earliest changes seen histopathologically occurred 30 minutes after irradiation. At this time, the nuclei of the crypt stem cells were slightly enlarged, with a thin, less basophilic nuclear membrane and contained residual karyolysis materials. After 2 hours, the nuclei of the crypt stem cells were larger, vacuolated, and contained karyolytic bodies. The cytoplasm was less basophilic (indicative of a loss of rough and smooth endoplasmic reticulum). Four hours post-exposure, the nuclei were huge and vesicular, and no cytoplasm could be seen. Abnormal mitoses were seen in the crypt stem cells after 12 hours; and 24 hours after exposure, mitoses increased in number but were still abnormal, while karyolysis and karyorrhexis continued. At this time, a nuclear enlargement was seen in a few of the Paneth cells, and the structures required for granule synthesis were not seen.

The cells at the base of the villi began to show damage by 48 hours after exposure to x-rays. These cells had enlarged nuclei with some karyolysis. At this time, the degenerative processes were decreasing in the crypt stem cells and intense mitotic activity began to repopulate some of the crypts. Although the Paneth cells still retained their characteristic appearance, they had a decreased number of granules. After 72 hours, villus cells had vacuolated cytoplasm and enlarged to pyknotic nuclei. The crypts were still shallow, although many cells had densely staining nuclei and dark basophilic cytoplasm. A few crypts were completely collapsed. In addition, many of the Paneth cells were degenerative, with a significant decrease in the number and density of zymogen granules. Many crypts regained a moderate length and appeared normal after 96 hours after exposure. The cells had ovoid nuclei and basophilic cytoplasm, and normal mitotic figures were seen. The Paneth cells returned to a normal appearance even though there was a loss of ribosomes. However, the villus mucosa was severely destroyed, and most of the villi were denuded and collapsed. The cytoplasm of surviving villus cells was no longer basophilic.

Denudation of the villi results from the extreme radiosensitivity of the crypt stem cell. The time between radiation exposure and denudation of the mucosa correlates with the amount of time required for the cells to migrate up the villus from the crypt region. The association between the stage of crypt stem cell cycle and the result of its exposure to radiation has been studied (2-4, 30, 31, 41, 42, 44). The great majority of stem cells in G2 phase or prophase are destroyed by supralethal irradiation. Cells in the G1, M, or S phase can survive and, although damaged, continue their migration toward the villi. Cells irradiated during mitosis are unable to divide. The progression from G1 into S phase is slowed. Cells irradiated in S phase are blocked there. During recovery, the surviving cells resume mitosis; and

with each cell cycle, severely damaged cells are eliminated and the proliferative compartment expands. Studies of the long-term effects of radiation exposure indicate that, although the cells proliferate, their progeny may not be capable of functioning in the same way as in non-irradiated animals. This indicates that radiation is capable of causing a non-lethal alteration in the stem cell DNA.

Histopathologic examination of the small intestine mucosa after repeated exposures to radiation documents the ability of the intestine to recover and adapt to this type of exposure at sublethal doses. In mice continuously exposed to ¹³⁷-Cs gamma radiation, the mitoses are partially blocked in G2 after one day of exposure. After 12 days of exposure, mitoses occur, but the generation cycle is 20 percent shorter (43). The generation cycle subsequently increases to control values by 35 days of exposure. This shortening of cycle length has been proposed as being a compensatory reaction of the mucosal cells to try to maintain a sufficient number of cells to cover the villi.

Electron microscopic examination of the small intestine after exposure to radiation have shown changes that follow those seen by light microscopy (16, 32-36, 44). Mitochondria are the first organelles to show changes. Fifteen minutes after radiation exposure, mitochondria exhibit considerable swelling. The number of swollen mitochondria increases over three to six hours and is accompanied by a clarification of their matrix, rupture of the cristae, and a break of the limiting membrane. After three hours, the swollen mitochondria appear to be separated from the normal mitochondria by a network of fine fibrils or surrounded by small ergastroplastic sacks. The mitochondrial surface has a maximum at six hours after irradiation and returns to normal by 24 hours. Mitochondria become progressively more dense even though of normal size. After 96 hours, membrane-bound vacuoles appear between the cristae.

Other cytoplasmic organelles also show changes. From 30 to 90 minutes post-exposure, the Golgi apparatus is dilated and the number of dense bodies decreases. Also, after 30 minutes, some microvilli show a dissociation of the triple-layered membrane along with a swelling of the apex. This lesion increases in severity until the entire border atrophies 24 hours after irradiation. After 90 minutes, dense lysosome-like bodies and multivesicular bodies appear in large numbers in the cytoplasm. At three hours, these cytolysosomes (karyolytic bodies) are observed migrating within all the cells along the crypt and are eliminated into the gut lumen. Cytolysosomes, also called autophagic vacuoles, contain hydrolytic enzymes, including acid phosphatase, arylsulfatase, glycuronidase, ribonuclease, and cathepsin.

Nuclear changes are seen in one-third to one-half of the cells between 30 minutes and 3 hours after a dose of 1350 rad of x-rays. Early changes (30 to 90 minutes) are characterized by the formation of two or three clearly demarcated zones in the nucleoli. One zone is formed by the aggregation of dark granules embedded in an amorphous material. A second zone is formed by very dense material with scattered small granules and fibrils. The third zone contains more electron-lucent material with fibrillar areas. At 90 minutes post-exposure, blebs can be seen on some nuclei. These probably represent an evagination of the nuclear membrane and grow progressively to form a large electron-lucent vacuole extruding from the nuclear membrane. These vacuoles may even become completely separated from the nucleus. In other nuclei, degeneration occurs much more rapidly. These early nuclear lesions seen ultrastructurally appear to occur independently from

the cytoplasmic changes seen, and do not seem to correlate with the increase of detectable enzyme activity.

After 48 hours, the nuclei still present show further changes. The chromatin material appears to decrease in amount and form a thin layer along the nuclear membrane. Giant multilobated nuclei increase in number by 72 hours post-exposure. These cells may even contain several micronuclei. Nucleoli swell and become opaque, lining themselves up against the nuclear membrane.

A pathogenesis for the production of these changes in the cytoplasmic organelles and the nucleus has been postulated by Maisin (44). The dense bodies (lysosomes) coming in close contact with cytoplasmic organelles leak their hydrolytic enzymes (possibly due to radiation-induced increased membrane permeability), resulting in damage to the mitochondria or other organelles including the nucleus. Cytolysosomes develop by segregating the necrotic foci within the cell from the rest of the cytoplasm. They are surrounded by a double membrane probably derived from the fusion of smooth ergastoplasmic reticulum with isolated vesicles from the Golgi apparatus. Clusters of ribosomes form and are also surrounded by a double membrane. The inner layer of the double membrane disappears and the cytolysosomes fill with necrotic material within 90 minutes after irradiation and continue for 2 to 3 hours. Heterophagosomes contain phagocytized membranes from degenerative leukocytes and dying stem cells. They may be difficult to distinguish from the cytolysosomes. The cytolysosome, heterophagosome, nuclear debris or a combination of all three could result in the formation of the karyolytic bodies described by many investigators.

2.2.4 Physiologic Changes.

2.2.4.1 Intestinal Transport. Many investigators have studied the relationship of intestinal transport deficiencies to the gastrointestinal syndrome. Early studies involving the effects of radiation on the transport capability of the small intestine were done prior to the elucidation of the transport mechanisms in the normal intestine (7). Glucose transport was one of the first substrates studied (57). After 6 Gy, the transport of glucose across everted sacs of small intestine was increased by 1 day post-exposure and depressed by 3 days post-exposure. This transport was back to normal by day 6. Later studies by Perris (56) investigated the transport of glucose, galactose, 3-o-methyl glucose, sorbose and histidine in the irradiated rat intestine (650 rad of x-ray or gamma ray). In these studies, the intestinal transport of glucose, galactose, and 3-o-methyl glucose was depressed 3 days after irradiation. Galactose transport was depressed only if low levels of glucose were also present, and sorbose transport was elevated. Proline uptake was demonstrated to be depressed not only at day 3 after 7 Gy of x-ray radiation in rat small intestine, but also at day 30 (54).

The capacity of intestinal epithelial cells to transport electrolytes is also altered after exposure to radiation. The sequence of alterations involving electrolyte movement (particularly sodium and potassium) post-exposure have been documented (12, 38, 45). After exposure to 1500 rad of x-rays, the concentration of potassium in the small intestine wall of mice decreases during day 1 to day 4. By day 4, the potassium level in the small intestine wall is only 50 percent of that in control mice. At the same time, the sodium concentration increases to 50 percent above that of control mice. Sodium concentrations in the colon of irradiated mice remained within normal limits, but the potassium concentration decreased over days 1 to 3. The potassium and sodium concentrations in the contents of the small

intestine was significantly higher in the irradiated animals as compared to controls. By day 3 post-exposure, the potassium concentration in irradiated animals was almost two times as high as in the controls, and the sodium concentration was three times as high as in the controls. Similar values were seen in the stomach and colon. Although alterations are seen in the sodium and potassium concentrations in the intestinal wall and intestinal contents, serum concentrations for these two elements are not significantly altered in the irradiated mice.

Despite these and other animal studies demonstrating alteration of the transport capacity of the small intestine after radiation exposure, the mechanisms responsible for the changes in absorption are not completely known. Perris and co-workers (56, 57) proposed that the reduced absorption of glucose is due to an impairment of the active transport process resulting from the severely damaged intestinal epithelium. Other investigators have postulated that this phenomenon is a result of the lowered epithelial cell population seen histologically with the denudation and atrophy of intestinal villi (5, 17, 61). However, Detrick and co-workers (15) showed that alterations in absorption occurred even after complete histopathological recovery, while later studies by Cheeseman et al. (7) showed that the changes in transport are not a simple matter of reduced numbers of intestinal epithelial cells. The overall observable results of the exposure of the intestine to radiation is an impairment of the absorption of substrates. However, these studies with isolated cells suggest that the intestinal epithelial cells are able to compensate for the reduced cell population by increasing their individual cellular capacity to take up hexose and dipeptide for up to 7 days post-exposure. In addition, substrate transport in the small intestine does not appear to be uniform among substrates.

Possible mechanisms for the loss of fluids and electrolytes after exposure to radiation, as described above, have been investigated (6, 14, 21, 23, 28, 63). Sullivan (63) reported both a marked decrease in water and sodium insorption from the lumen of the small intestine and a decrease of the exsorption of water and sodium from the blood stream. His results, and those of other investigators (14, 45), supported the hypothesis that the excessive loss of fluid and electrolytes after radiation exposure is due to an impairment of the reabsorption. In addition, studies (e.g. short-circuit technique, radioisotope fluxes) involving the ileum of rabbits exposed to 5 to 12 Gy of whole-body gamma radiation have shown that radiation alters active ileal electrolyte transport by stimulating chloride secretion (28).

The secretion of fluids and electrolytes is also influenced by a variety of factors occurring in response to radiation exposure. One such factor is the release of several different agents after radiation exposure. These include serotonin (13, 49), prostaglandins (6, 21), and histamine (9, 46). The action of bile and bile salts comprise another possible factor. Early studies suggested that post-exposure diarrhea was a result of some direct effect on the intestinal mucosa from bile salts (23, 25, 37, 62, 64). However, recent studies do not support this hypothesis (29). Alterations in intestinal blood flow have also been proposed as a factor in the post-exposure loss of fluids and electrolytes. Some researchers have reported decreased intestinal blood flow at 72 hours post-exposure (20, 39), while others have demonstrated an increase in intestinal blood flow beginning 10 minutes post-exposure (9, 10). Although ischemia can result in necrosis and loss of intestinal epithelial cell and thus the loss of fluids, the true role of intestinal blood flow in the loss of fluid and electrolytes after irradiation has not been demonstrated. Another factor in the loss of fluids and electrolytes is the presence of enteric bacteria and/or their products. Enteric bacteria are thought to contribute to the deleterious effects of radiation on the gastrointestinal tract because of studies that demonstrate that

treatment of irradiated animals with electrolytes only (no antibiotics) is ineffective (68) and that the onset of gastrointestinal signs after irradiation is delayed in germ-free animals (50, 51, 69). Studies have shown that the germ-free mice have an increased post-exposure survival time because of an increase in transit time and cell life span of their intestinal mucosal cells. This change in cell transit time and cell life span has been proposed as being due to the absence of free bile acids in the intestine (47, 48). This free bile acid is normally produced by bacterial action on conjugated bile acids in the intestine. However, Geraci and co-workers (26) demonstrated that overt sepsis and endotoxemia did not play a significant role in the intestinal radiation syndrome in rats exposed to neutrons or ¹³⁷Cs gamma rays. Bacteremia and/or endotoxemia did not appear to be correlated with the breakdown and recovery of the mucosa after irradiation.

Clearly, the radiation-induced alterations in the intestinal transport capacity resulting in the loss of fluids and electrolytes are multifactorial in origin. Although the mechanisms are not completely understood, such things as the denuded intestinal mucosa, decreased reabsorption, increased secretion, release of various agents from damaged cells, activity of bile and bile salts, changes in intestinal blood flow, and the presence of enteric microflora all contribute to the loss of fluids and electrolytes and the gastrointestinal syndrome in general.

2.2.4.2 Intestinal Motility. Exposure to ionizing radiation produces gastrointestinal injury, including mucosal dysfunction, as described previously, and abnormal gastrointestinal motility. Early studies investigating the effect of radiation exposure on gastrointestinal motility reported increased intestinal tone (12). Intestinal tone and contractions in the rat and rabbit showed an immediate increase after x-ray doses from 100 to 1,000 rad (12). In this same study, Conard also described an increase in propulsive motility in rats after 800 rad. This reaction was followed by a depression in motility for about 4 days post-exposure. Other investigators demonstrated conflicting results, namely a decrease in motility. Goodman and co-workers (27) reported that the transit time for materials through the small intestine was not altered significantly in rats exposed to 450 rad of whole-body x-irradiation. Baker and Hunter (1) reported antiperistaltic activity in the intestine of rats after exposure to 100 to 700 rad.

Many studies have demonstrated delayed gastric emptying in animals after radiation exposure (8, 12, 18, 19, 22, 24, 67). This gastric retention can complicate the study of gastrointestinal motility since the gastric emptying can be so severe, especially in rodents, that small intestine transit may appear normal or delayed if a marker technique is used to monitor transit through the gastrointestinal system and the marker is placed into the stomach. Summers, et al. (65) demonstrated that if the marker is placed into the duodenum after irradiation, the transit rate is actually increased. The issue is further clouded by the fact that measurements of transit times do not necessarily correlate with the actual motor activity (66).

The most extensive study of intestinal myoelectric activity after radiation exposure was done by Summers and co-workers (66). A dose of 938 cGy of x-rays produced an acute intestinal radiation syndrome in dogs. Jejunal slow waves, which normally have a regular rhythm, uniform morphology, and tight coupling, were greatly altered. They showed an irregular rhythm, variable morphology and were uncoupled. Although no changes were seen in the smooth muscle by light microscopic examination, their myoelectric abnormalities were significant and suggested functional problems in these cells. The interdigestive myoelectric complex was uniformly disrupted. After the introduction of food into the

gastrointestinal tract at 24 to 72 hours, jejunal myoelectric activity showed progressively fewer and shorter spike bursts. There were also abnormal clusters of migrating spike bursts. On days 3 and 4, spike bursts decreased in number and length. These results are similar to those seen in rodents where an initial increase in motility is followed by a decrease in motility (11, 40, 60). These alterations in motility patterns are probably due to multiple mechanisms including altered cellular metabolism, altered membrane ion transport, impaired cell-to-cell communication, enhanced inhibitory or reduced stimulatory nerve transmission, and altered humoral substances (e.g., prostaglandins, lipoxygenase products, catecholamines).

2.3 ENDOCRINE SYSTEM.

2.3.1 Introduction.

The effects of external sources of ionizing radiation on the endocrine glands can be discussed in terms of direct effects on the individual glands and in terms of indirect effects mediated by various endocrine glands. The study of the direct effects on individual glands is complex since it is almost impossible to isolate a gland completely due to the functional interrelationships between the glands and other organs. Radiation effects on the thyroid and pituitary have been the most extensively studied endocrine glands of the body. Indirect consequences of endocrine-gland radiation include systemic alterations that are mediated by hormones and biogenic amines, such as blood pressure, water excretion, and gastrointestinal motility. These effects involve so many factors that interpretation of the exact effect of radiation-induced alterations of endocrine glands is almost impossible.

With these considerations in mind, the following describes radiation effects on the pituitary gland, thyroid glands, parathyroid glands, adrenal glands, and pancreas (Islets of Langerhans). The thymus, considered to be part of both the endocrine system and the immune system, will be covered in detail in the Phase III section of this report. The ovary and testis will not be discussed in this text due to the scope of work delineated by the AFRRI technical advisors. However, pertinent articles on these topics have been included in the Endocrine Reading List.

2.3.2 Pituitary Gland.

The pituitary has been recognized as a fairly radioresistant organ. Histopathologic examination of the adult rat pituitary following irradiation with 3400 rad of x-rays revealed degranulated acidophils of the anterior lobe and signet ring castration cell degeneration at 80 days post-exposure (25). Single doses of 5000 rad of deuterons or protons resulted in progressive morphologic changes and functional deterioration. These increased in severity with time; the larger the dose, the earlier the morphologic changes were observed (8). Mateyko and Charriper (17) demonstrated that acute changes after 10,000 RFP cathode-ray particle irradiation included increased basophils after one hour and increased acidophils after 24 hours. However, doses of only 2000 rad were necessary to produce histological damage in immature rats (12). This difference in sensitivity between adult and immature rats appears to be due to the difference in the mitotic index of the cells in the anterior pituitary. The normal anterior pituitary lobe mitoses are more frequent in immature than in mature animals. In addition, the neural elements of the pituitary appear to be more resistant to radiation than the epithelial elements (8).

Alterations in pituitary-gland function do occur even without evidence of histologic changes. Mateyko and Edelmann (18) demonstrated that sublethal doses to the head of a rat resulted in early increase in adrenocorticotrophic hormone (ACTH) and thyroid-stimulating hormone (TSH). Furthermore, higher doses resulted in a decrease in ACTH, TSH, somatotrophic hormone (STH), and gonadotropin (27). These hormonal deficiencies were accompanied by growth retardation, infertility, and decreased steroid hormones (23, 27).

Radiation-induced changes in the hypothalamus as a whole are observed at doses of 200 rad or more. The earliest change seen at lower dose levels was the disappearance of neurosecretory granules (1). After doses of 3000 rad, histopathologic examination revealed multifocal necrotic lesions (2). Since the hypothalamus-pituitary axis provides control over the majority of hormonal activity in the body, destruction of the hypothalamus or its link to the pituitary will cause a multitude of systemic effects.

2.3.3 Thyroid Gland.

The effects of ionizing radiation on the thyroid glands have been studied extensively (10, 15, 16, 25). However, a great deal of the work has been done with radioisotopes. The following discussion includes only studies using external sources of radiation.

Like the pituitary, the thyroid gland is the most sensitive to radiation in immature animals (25). Sommers observed that the rat thyroid gland exposed to 50 to 4500 rad of x-irradiation showed no histological alterations. In addition, the basal metabolic rates remained normal. No changes were noted histologically except after 9000 rad. At that dose level, some epithelial damage was observed (3). Michaelson, et al. (19) demonstrated that dogs developed hypothyroidism two to four years after exposure of the upper body to 970 to 2125 rad. At necropsy, the thyroid glands were small and fibrotic. Histological examination revealed follicular epithelial atrophy and very little colloid storage.

Whole-body irradiation appears to affect the thyroid gland function more than local irradiation (12). Within a week after whole-body irradiation, the morphology and function of the thyroid gland are altered indirectly from the radiation effects on the pituitary (10, 16). Within 48 hours after whole-body irradiation, thyroid function in the mouse decreased concurrently with a decreased TSH output and an increased ACTH secretion by the pituitary (4, 18, 26). Gray et al. (10) demonstrated that a single whole-body dose of 800 rad of x-rays caused a reduction of thyroxine (T4) levels in rats, and a dose of 750 rad resulted in a reduction in triiodothyronine (T3) levels. Kinetic studies of these thyroid hormones in control and irradiated rats revealed an early slight decrease in both hormones in the control animals due to a decreased production. The significant decrease in the hormone levels in irradiated rats was attributed to a change in the distribution of the hormones. Results indicated that early after exposure, the thyroid hormones were diverted to the tissues and their utilization was increased. The continuing reduction in thyroid hormones of irradiated rats was due to decreased production.

The radiation-associated development of tumors in the thyroid is also well documented. These tumors are considered to be a late effect (>2 years post-exposure) and will not be discussed.

2.3.4 Parathyroid Gland.

The parathyroid glands are considered to be fairly radioresistant based on the limited amount of information available (12). A study done by Sommers (25) demonstrated that the parathyroid glands of parabiont rats exposed to 1200 rad showed no changes. Parathyroid destruction in mice has been reported, however, following treatment with radioisotopes (25), and radiation-associated carcinogenesis has been reported in parabiont rats exposed to 1200 rad doses two to three years after exposure (24).

2.3.5 Adrenal Gland.

The adrenal glands are considered to be radioresistant (12). The adrenocortical activity is increased after irradiation probably as part of the stress response in the body. The adrenal gland weights increased 30 percent 48 hours after irradiation of the rat abdomen with 3680 rad or of the head and neck with 2800 rad (25). Histopathologic examination of the adrenal glands in these animals revealed zona fasciculata hypertrophy and cortical lipid depletion. Adrenal gland weights increased 100 percent in rats exposed to 900 rad of whole-body x-irradiation, and these animals died of radiation sickness. Edelmann demonstrated that lead shielding of the adrenals increased the survival of rats given 600 to 850 rad (7, 32). Corticosterone synthesis and secretion increased in rats after whole-body exposure to 800 rad when the adrenal glands were lead shielded. Increased synthesis of the corticosterone was seen 2.5 hours after exposure, while increased secretion of the corticosterone was observed 72 hours after exposure (6). Rat adrenocortical cholesterol decreased significantly at 24 hours after exposure to 900 rad of x-irradiation (5).

At the same time, cortical acid lipids were increased and ascorbic acid was decreased. Six to eight days post-exposure, however, the adrenocortical cholesterol increased beyond normal value. At that time, cortical phospholipids had decreased, and medullary venous thrombi/medullary atrophy were observed. Kovacs (14) reported that, after exposure to ionizing radiation, the blood levels of rat adrenocortical hormones and their cortical lipid content were inversely related. Then 24 hours following 1500 rad of whole-body irradiation, rat adrenal lipids had an increased proportion of highly unsaturated fatty acids (25). The arachadonic acid content of phosphatides increased to three times normal. This caused the arachadonic acid content to constitute 40 percent of the total fatty acids. These rats died 60 hours after exposure; and at that time, the tetraenonic acid values of cholesterol esters were two times normal. In addition, triglyceride arachidonic acid also increased.

Similar findings were obtained in other species. In monkeys, 17-hydroxycorticosteroid synthesis and secretion occurred four hours after whole-body exposure to 200 rad of x-rays (33). Few morphologic changes were seen in calf adrenal glands after exposure to low doses of 60-Co gamma radiation, but functional alterations were observed. After ACTH-stimulation, the irradiated adrenal glands secreted significantly less hydrocortisone, cortisone, and Porter-Silber chromogens than did the non-irradiated controls (28). However, the calf adrenal glands became significantly hypertrophied after exposure to 600 rad, and total 17-hydroxycorticoids were increased (20). Cortical lipid depletion was observed in guinea pigs after local or whole-body exposure to 400 rad (25). This depletion was proportional to the severity of the radiation sickness observed clinically. In addition, the adrenal nonspecific esterases showed a decrease in activity, while the acid

phosphatase had an increase in activity. This seemed to correlate with lysosomal damage. Possible proteolytic activity was implicated in the increases in the adrenal E-600 resistant esterase. The increase in adrenocortical cytoplasmic granules (possible chromidia of Selye) was attributed to degeneration.

Morphologically, few changes have been noted in the adrenal gland exposed to ionizing radiation. As described above, the adrenal gland hypertrophies initially and then later atrophies. The number of mitoses in the mouse adrenal cortical cells was shown to be depressed after doses of up to 325 rad of x-rays (13). Severe morphologic radiation-induced damage to the adrenal glands did not occur until higher doses were used. Exposure to doses of 2000 to 3000 rad resulted in adrenal cortical atrophy (9). Post-irradiation neoplasms of the adrenal gland have been reported. These are seen as a late effect of radiation exposure (>2 years) and will not be discussed.

2.3.6 Pancreas.

The exocrine and endocrine parts of the pancreas are considered to be radioresistant (12, 25). Heinkel and Bergethal (11) demonstrated that enzyme changes usually associated with pancreatic damage (e.g., pancreatitis) were not present in rats exposed to doses up to 2250 rad of x-rays. Multiple repeated doses of ionizing radiation did result in a decrease in serum lipase. Rabbits irradiated with doses of 200 to 1000 rad had temporary degenerative and retrogressive changes in the exocrine and endocrine portions of the pancreas (21).

Light microscopic and electron microscopic changes in the exteriorized canine pancreas following exposure to 5000 to 9000 rad doses of x-rays were studied extensively by Volk and associates (29, 30). Histopathologic examination revealed focal necrosis and leukocyte infiltration of the exocrine pancreas during the 7 days after exposure. After two to three months, acinar cells were moderately basophilic, and their nucleoli were large, dense, and multiple. The endocrine portion of the pancreas did not have any changes demonstrable by light microscopy.

Electron microscopic examination revealed three phases of ultrastructural changes in the pancreas. The first phase (weeks 3 to 4) involved extensive cellular damage with degradation and sequestration of the areas of the cytoplasm. This cellular change has been described in other organ systems such as the gastrointestinal system. The acinar cell microsome lesions were most severe at 5 to 8 days after exposure. Pleomorphic alterations were still evident at 12 to 21 days post-exposure. The size and number of zymogen granules decreased over time. Morphologic alterations in the A and B cells of the islets of Langerhans were similar but less severe, and the function of these cells remained normal. The second phase (months 2 to 6) was characterized by endoplasmic reticulum alterations, including dilatation and vesiculation of the cisternae. These changes corresponded with the cytoplasmic basophilia seen by light microscopy. The number and size of zymogen granules began to return to normal. The third phase (months 6 to 9) was characterized by the return to normal of the cellular appearance. Volk (29) proposed that since the mitotic rate in the pancreas is virtually zero, the recovery of the pancreas must be due to a recovery of the injured but surviving cells rather than the proliferation of new cells.

These phases of morphologic changes are accompanied by marked decreases in the pancreatic amylase, leucine aminopeptidase, and lipase activities. There is a moderate amount of fibrosis after recovery of the pancreas. This appears to be a

response to a mild inflammatory reaction. Fractionated exposure of the canine pancreas to larger total doses (e.g., 4500 to 5000 rad) results in severe late fibrosis. The canine model for studying the cellular effects of ionizing radiation on the pancreas is the most extensively studied and appears to approximate the effects seen in humans.

SECTION 3

RADIATION EFFECTS ON THE HEMATOPOIETIC AND IMMUNE SYSTEMS

3.1 HEMATOPOIETIC SYSTEM.

3.1.1 Introduction.

The effects of ionizing radiation on hematopoietic tissues have been described extensively. Considerable emphasis has been placed on the effects of radiation on the hematopoietic system since the discovery of x-rays and the observation that exposure to x-rays resulted in hematopoietic derangement. Indeed, hematopoietic cells are among the most radiosensitive. Scientific literature covers many aspects of hematopoietic damage, including peripheral blood response, stem cell damage, late effects on specific bone marrow compartments, and late bone marrow stromal damage. Early work focused on static parameters, such as peripheral blood cell counts and histopathologic changes in bone marrow and spleen. More recent studies use newly developed techniques to expand knowledge of the pathogenesis of hematopoietic responses to ionizing radiation. This allows for a more dynamic and quantitative approach to the problem by providing a means of observing the events that occur after exposure to radiation, from cell killing to cell regeneration during hematopoietic recovery.

As with other organ systems, the effects of radiation exposure on the hematopoietic system may vary with the total area and site exposed, radiation type, total dose, dose rate, species and strain of animal exposed, age of the animal exposed, presence or absence of other stressors (internal and/or external), and combined radiation injuries. These variables and their relationships to the effects of acute exposure to ionizing radiation on the hematopoietic stem cell compartment and peripheral blood cell compartment are described.

3.1.2 Hematopoietic Stem Cells.

3.1.2.1 Survival of Stem Cells. The "stem cell" is a cell that is capable of extensive self-replication, as well as progressive differentiation to one or more mature cell types. Till and McCullough (30) were among the first to use the spleen colony assay to evaluate the mammalian cell survival curve after exposure to radiation. This assay measures the production of hematopoietic colonies after injection of syngeneic bone marrow into irradiated recipient mice. The colonies are thought to be the progeny of single cells that are able to differentiate into (1) erythrocytic, (2) thrombocytic, or (3) granulocytic series cells (13, 33). Several investigators (3, 5, 13) have reported that the stem cell compartment has a radiation survival curve similar to those described for other mammalian cells, although the radiation survival of stem cells does vary. The dose-response curve is exponential after single doses of whole-body radiation with x-rays or gamma rays (20, 21, 22).

Studies have shown an age-dependent variation in radiation sensitivity of stem cells, with 6-week old mice demonstrating a greater sensitivity than 30-week old mice (9, 24 25). In addition, the type of radiation has an effect on stem cell survival.

Neutron irradiation results in a higher relative biological effectiveness (RBE) than does Co⁶⁰ gamma ray or x-ray irradiation (27, 31).

To expand on the information gained from the spleen colony assay, investigators utilize the erythrocytic repopulation assay and the granulocytic repopulation assay to measure the repopulating ability of transplanted progenitor cells to form specific mature progeny (7, 14, 16). Using the two repopulation assays, Hellman, et al. (15) demonstrated a difference between the erythrocytic and granulocytic repopulation assays, namely that the erythrocytic is more sensitive to radiation. Further studies in mice irradiated with 300 rad of x-rays revealed that the colonies produced from cells that survive irradiation are different from unirradiated cells. The colonies from cells that survive irradiation are smaller, primarily due to the loss of erythropoietic differentiation. This repopulation data, along with the spleen colony assay, indicate that erythrocytic differentiation is selectively impaired.

To summarize, the radiation survival curve for hematopoietic stem cells is similar to that of other mammalian cells, and the differentiation potential of the surviving stem cells is altered by radiation exposure. The spleen colony assay and the two repopulation assays provide suitable endpoints for the evaluation of stem cell damage.

3.1.2.2 Stem Cell Compartment Recovery. In response to the cell depletion caused by radiation, the stem cell population markedly increases its proliferative rate. Chervenick and Boggs (4) suggested that, because the process of differentiation into blood cells is suppressed after a heavy dose of radiation, the stem cells can increase their number without the added burden of supplying blood cells. This may explain the initial exponential growth of the number of stem cells. Cronkite, et al. (8) and von Wangenheim, et al. (32) have demonstrated that the number of stem cells does not return to pre-irradiation values after high doses of radiation.

The repopulation assays previously described have also been used to evaluate the recovery of the stem cell compartment after radiation exposure. Hellman, et al. (15) demonstrated that erythrocytic and granulocytic series recover at different rates, with the erythrocytic series repopulating more rapidly. This suggests another alteration in the differentiation of stem cells after radiation exposure. As described earlier, the granulocytic pathway, favored initially, is preserved at the expense of erythropoiesis. By day 3 post-irradiation, this trend reverses so that erythrocytic production is favored. Eventually, both curves return to the pre-irradiated state. These alterations appear to be due to a direct effect on the stem cell. The proliferating stem cells vary in their response to radiation exposure, depending on their position in the cell cycle at the time of radiation exposure. The synthetic phase appears to be the most resistant aspect of the cell cycle of proliferating stem cells.

In addition, there is evidence of cellular repair in stem cells after sublethal exposure to radiation (29). After two doses of 200 rad spaced by time intervals from 0 to 24 hours, the repair in mouse bone marrow appears to occur in cycles. The recovery reaches a maximum after 5 hours, a minimum after 10 hours, and a maximum again after 24 hours. The cycles are considered to represent intracellular recovery coupled with synchrony in the cell population produced by the first fraction of dose.

3.1.2.3 Histologic Changes of Stem Cell Compartment. Histologic changes of the stem cell compartment following radiation exposure have been described

extensively (1, 11, 23, 26, 28, 34). The first few days after radiation exposure reflect a depopulation of the hematopoietic cells. Initially, bone marrow has an excess number of red cells and a disruption of the vascular structure. At three to four days post-irradiation, the bone marrow is aplastic and filled with red cells, and the number of nucleated cells also drops to its lowest level. Depopulation of nucleated cells is most severe in the erythroid precursors. The bone marrow attempts to compensate for the decrease in cellularity by dilation of vascular sinusoids. This is followed by an extravasation of red blood cells—hemorrhage—which is not attributed to any derangement of the platelet population. Later, local regenerative foci do appear, but some may arise from abortive clones. True regenerative foci continue to grow, but an animal may not survive despite this activity.

Initially after radiation exposure, the spleen begins to collect nuclear debris and hemosiderin. The foci of erythropoiesis normally found in the spleen decrease in number and size. By day 14 after radiation exposure, the size and weight of the spleen return to normal. Erythrocytes and lymphocytes appear to be the most affected cells in the spleen. Other cells, such as macrophages, megakaryocytes, and fibroblasts, are relatively resistant to radiation exposure (18).

3.1.3 Peripheral Blood Cells.

The effects of radiation exposure on peripheral blood cells has been described extensively in the literature (2, 5, 10, 12, 17, 19). Bond, et al. (2) has produced one of the most complete discussions of the effects of radiation on peripheral blood cells. The following description presents only a small portion of the volumes of information available on the subject.

3.1.3.1 Red Blood Cells. Immediately after midlethal doses of radiation, the numbers of red cells are not altered significantly. Any slight decrease might be due to loss from hemorrhage or direct cell wall injury. Very high doses of radiation (several kilorads) are needed to show direct red cell destruction. However, morphologically, damage is evident within the first day after doses of 1000 rad or more. Damage consists of a loss of normal shape, sometimes with five or more protuberances (5). Later during post-irradiation, the number of red cells decreases significantly. Reticulocytes do not appear until the stem cell compartment recovers, which results in a non-regenerative anemia. This anemia converts to a regenerative anemia in those animals which survive. In one study (10), for example, after midlethal doses of radiation, the packed cell volume (PCV) in rhesus monkeys decreased until the end of the third week. At that time, the PCV was 50% of normal. At week three, the PCV began a progressive increase in the surviving animals. It appears from the work reported in the literature that the non-human primate and the dog most closely mimic the red cell response seen in humans.

3.1.3.2 White Blood Cells (Granulocytes). The response of the white blood cell compartment is somewhat different from that of the red blood cell compartment. The number of circulating white blood cells does not decrease as rapidly as does that of red blood cells. Jacobson, et al. (17) showed that, in rabbits, the decrease in granulocyte numbers was dose-dependent during the first few days post-irradiation. A higher dose resulted in a more rapid decrease in the granulocyte number. As presented earlier, initially after irradiation, the surviving stem cells preferentially differentiate to granulocytes. This would confirm the observation that the decrease in granulocyte numbers is initially protracted as compared with the decrease in erythrocyte numbers. As the surviving stem cells switch to favor erythrocyte differentiation, the white blood cell numbers reach a minimum. With time, stem cell

differentiation and recovery allow the circulating numbers of both series to return to normal in animals that survive.

3.1.3.3 Thrombocytes. Circulating platelets are not radiosensitive (12). There is a dose-dependent decrease in the circulating numbers of platelets after irradiation. This is considered to be a result of the effects of radiation on the megakaryocytes in the bone marrow.

3.1.3.4 Lymphocytes. Lymphocytes are markedly affected by exposure to radiation, with their number decreasing significantly after relatively low doses. The lymphocyte is described in greater detail in Section 2.0, Immune System.

3.2 IMMUNE SYSTEM.

3.2.1 Introduction.

As with the hematopoietic system, the effects of ionizing radiation on the immune system have been described extensively in the literature. Many investigators have shown that lymphocytes are among the most radiosensitive mammalian cells (9, 13, 28, 32, 42). Of all of the histopathologic changes observed in mammals following exposure to ionizing radiation, the most striking change is the rapid death of lymphocytes in the lymphoid tissues. Effects on the immune system can be seen within two hours of a single short exposure at dose levels which are insufficient to kill any other cells of the body. Recently, investigators have begun to use knowledge gained by cellular biologists and immunologists to reexamine the responses of the immune system with respect to both morphology and function. Better techniques have been developed to identify and characterize distinct populations of lymphocytes. Now the radiobiologist must take into account the precise population and subpopulation of lymphocytes under investigation before drawing any conclusions.

Radiation-induced injury to the cells of the immune system occurs through a variety of mechanisms, both direct and indirect. Variables, such as radiation type, total dose, dose rate, total area and site of exposure, time of exposure with respect to the cell cycle, and time interval between exposure and antigen presentation, all affect the results of the investigation. These variables and their effects on lymphocyte populations, cell-mediated immunity, and humoral immunity are described.

3.2.2 Lymphocyte Populations.

Both circulating lymphocytes and organized lymphoid tissues are radiosensitive. Advanced morphologic damage appears rapidly in lymphoid tissues after exposure. A rapid decrease in the size of lymphoid organs, including lymph nodes, thymus, and spleen, is also observed. Suter (39) showed that, with whole-body exposure to 25 r of x-rays, a significant decrease occurs in absolute lymphocyte counts in the peripheral blood. In rats, 100 R of x-rays reduces the lymphocyte counts to 25% of normal values within four hours post-exposure (32). Histopathologic evaluation reveals that necrosis of lymphoid tissues is evident within one hour after exposure to an LD₅₀(30) dose of x-rays (4, 8, 18). Necrotic lymphocytes are phagocytized and nuclear debris accumulates rapidly, reaching a maximum within three hours post-irradiation.

The rapidity of the observable effect in lymphoid tissue can be explained by the timing of radiation-induced cell death. Unlike other mammalian cells, radiation-induced cell death of lymphocytes occurs in interphase. Most cells exposed to 50-100 r do not die until the first or second mitosis after exposure—mitotic death. Small lymphocytes are killed without entering mitosis—interphase death.

As radiation-induced depletion of lymphocytes is somewhat dose-dependent up to the lethal range, so is the time required for lymphoid tissue recovery. Regeneration generally appears to occur with collections of cortical lymphocytes appearing first followed by germinal center formation. Several investigators (15, 22, 24) have shown that an intact thymus must be present for lymphoid recovery to occur in sublethally irradiated mice. Whole-body irradiation results in a protracted recovery period in comparison to local irradiation of the spleen or lymph nodes (5). Future progress in understanding the mechanisms involved in interphase death will assist investigators in their studies of lymphocyte population repair and recovery following irradiation.

There does appear to be a certain subpopulation of T lymphocytes that can function after exposure to radiation (19, 38). Results show that this population of T cells is able to survive interphase death; but when the cells are stimulated to proliferate by exposure to an antigen, they die soon after entering mitosis. In addition, activated T cells of all populations are less sensitive to radiation-induced interphase death than are nonactivated T cells (2, 7, 8).

B lymphocytes appear to be more radiosensitive than T lymphocytes. Several studies (3, 36) utilizing computer-assisted cytometric analysis have shown that radiation-induced abnormalities of the nuclei of B cells are more pronounced than they are in T cells. B cell changes include redistribution and rearrangement of the nuclear chromatin immediately after irradiation. There may be a difference in the radiosensitivity of populations of B cells as there is with T cells; but, clearly, a change in radiosensitivity occurs with B cell maturation.

The thymus and lymph nodes are primary lymphoid organs, and their response to radiation exposure follows expected trends based on their cellular populations. The spleen, however, contains only 60%-70% lymphocytes, and the other cellular elements (macrophages, plasma cells, and hematopoietic cells) are less radiosensitive than are lymphocytes. As one would expect, necrosis is most pronounced in the germinal centers. Necrosis is also marked in the nonthymic-dependent follicular areas (B cell area) of the spleen (1). Recovery of the spleen develops earlier than in the thymus (14).

Cell migration of T and B lymphocytes is also affected by radiation exposure. Anderson, et al. (2) showed that irradiated small T lymphocytes homed normally to the lymphoid tissues within four hours of injection (primary migration). This migration was decreased or abolished when the irradiated small lymphocytes were held *in vitro* for one to seven hours before injection (secondary migration). Anderson suggested that cell damage affecting migration ability develops over several hours. Activated T cells, which are more radioresistant, have only a reduced secondary migration. B cells, which are more radiosensitive, have significantly reduced primary migration and an abolished secondary migration.

3.2.3 Cell-Mediated Immunity.

The effects of radiation exposure on delayed hypersensitivity and graft-versus-host reactions are difficult to assess. Studies utilizing guinea pigs and rabbits have shown that the delayed hypersensitivity reactions are more radioresistant than are antibody responses (31, 33, 43). The graft-versus-host reaction has been studied by irradiation of the parental-strain lymphocytes prior to their injection into F₁ hybrids or irradiation of the hybrid recipients prior to injection of parental-strain lymphocytes (1). Irradiation inhibits the capacity of parental cells to elicit a graft-versus-host response in F₁ hybrids.

Studies have demonstrated that a majority of activated cytotoxic lymphocytes, effector cells that mediate cellular immunity, are extremely resistant (1, 10, 37). They are not sensitive to interphase death and can still function even after relatively high doses of radiation. Grant, et al. (16) have shown some evidence that stimulation by an antigen renders cytotoxic lymphocytes more radioresistant.

3.2.4 Humoral Immunity.

The initiation and persistence of an antibody response involves many different cell types, including macrophages, T and B lymphocytes, and others. Therefore, the well-documented suppressive effect of radiation exposure on the humoral antibody response may involve alterations of one or all of these cell types (6, 21, 41). Presentation of the antigen involves polymorphonuclear leukocytes, primary lymphoid follicles in the spleen, and lymph nodes and macrophages. The effects of radiation exposure on polymorphonuclear leukocytes varies depending on the timing of the exposure. Whole-body irradiation does not impair their ability to phagocytose bacteria. Radiation exposure at the time of or after phagocytosis increases their bactericidal activity (25, 26, 27). Radiation exposure prior to phagocytosis decreases their bactericidal activity (29).

As noted in the discussion on the hematopoietic system, radiation exposure destroys bone marrow stem cells responsible for polymorphonuclear leukocytes production. Primary lymphoid follicles in the spleen and lymph nodes contain specialized reticular cells, which retain antigen on their processes. This retention is suppressed by doses of 450 R and higher (17, 44). This mechanism of follicular antigen localization is probably more important in immunological memory since an antibody response can occur even without follicular localization of antigen. Macrophage migratory activity and phagocytic function are relatively radioresistant (1). With doses in the kilorad range, their catabolism of ingested antigens is variably reduced. There are increases in macrophage intracellular biochemical activities and increased levels of membrane-bound antigen post-exposure. Clearly, the immune depression after irradiation with doses below the kilorad level is not due to macrophage dysfunction for most antigens.

The type of effect that radiation exposure has on the primary antibody response (lymphocyte involvement) depends, in part, on the timing of the exposure. If antigenic challenge is given at the time of or closely after irradiation, the primary antibody response is inhibited since lymphocytes are unable to proliferate in response to antigen presentation. Antigenic challenge given later after irradiation results in an enhanced primary antibody response since suppressor T cells, which are very radiosensitive, have been destroyed (41). Several possible mechanisms of radiation enhancement of antibody production have been proposed:

disproportionate repopulation of depleted lymphoid tissues by rapidly dividing antigen-stimulated cells (12); endotoxin release from radiation damaged gut (34, 35); local cellular destruction, creating an environment for proliferation of more immunocompetent cells than would normally respond (20); selective inhibition of IgG-mediated feedback control (11); and preferential inhibition of regulatory cells (40).

Like the antibody molecules themselves, the cells that produce them are extremely radioresistant (23, 30). Although the primary antibody response is fairly radioresistant, the secondary antibody response is even more so. The cells involved in these responses are similar, so the actual expression of immunity is influenced by cell kinetics and the role of germinal centers. As discussed previously, the timing of the antigen challenge relative to the time of exposure determines the alteration of the antibody response, both primary and secondary.

Clearly, the lymphocyte is the prime target of radiation-induced inhibition of humoral antibody formation.

SECTION 4

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APPENDIX A

BIBLIOGRAPHY

APPENDIX A

BIBLIOGRAPHY

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A.8 READING LIST: IMMUNE SYSTEM.

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APPENDIX B

TABLES

Table B-1. Brain references: burro*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			MIXED GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY							214			215		
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY		38 150										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-2. Brain references: cat*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			ALPHA PARTICLE RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	999	19										
	57											
BLOOD-BRAIN BARRIER		182									41	
ELECTROPHYSIOLOGY	17, 24	203			14, 36				76		167	
	184, 201											
	16, 48											
	78, 89											
	53											
	77											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-3. Brain references: dog*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			ELECTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	33, 49	74, 75, 196	161	151	227	206	23	227			113	
	23, 57 64, 130 185											
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY					35							
					145							

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-4. Brain references: guinea pig*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	127	19										
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY		2, 7, 8, 25										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-5. Brain references: hamster*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			ALPHA PARTICLE RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY		23, 50 88, 186	23, 50 88, 186									
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-6. Brain references: mouse*.

MANIFESTATION	X - RAY RADIATION (r)			DEUTERON RADIATION (r)			ELECTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	117, 118	120, 221, 222	222	57	39	40			95			
	178, 222		223	156 229	156	156 158 179						
BLOOD-BRAIN BARRIER	22	22										
ELECTROPHYSIOLOGY	86	86										
		6 24		156	156	156						

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-7. Brain references: non-human primate*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	10, 11	3, 11, 14, 25	150		25	25				93	93	100
	16, 35	9, 10, 11, 19, 38			52, 90, 92	95, 208						
	43, 84	39, 40, 42, 44			95, 150,**							
BLOOD-BRAIN BARRIER		50, 51, 64, 90			202**							
		92, 95, 152										
ELECTROPHYSIOLOGY		11										
		51										
	15	9, 10, 29, 46		1	1	1						
	71	27, 37, 41, 110										
		176										

*Cited references are underlined. Others may be found in the reading List in Appendix A.

**Gamma-neutron radiation.

Table B-8. Brain references: rabbit*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			ALPHA PARTICLE RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	142	19, 47 17, 19, 57, 81 89, 123, 130, 176, 178	123	142**	17, 86, 89 130, 212	206		135			124 135	124 135
		20, 21										
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY	56	2, 20, 21	58	5, 30, 34								
	105 223	8, 82, 83		35, 36 15, 112, 142 145, 146, 154								

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

**Gamma-neutron radiation.

MANIFESTATION	X - RAY RADIATION (r)			NEUTRON RADIATION (r)			MIXED GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY	4, 30, 31, 46 47, 48, 70, 102 115, 116, 117 127, 133, 140 145, 159, 163 165, 185, 191 210, 211	2, 3, 32 47, 60, 61 80, 96, 97 98, 99, 114 115, 131 133, 143 145, 169 170, 189 190, 209 210, 211 225	65, 66, 98 143	47, 216					33, 34, 62, 70
BLOOD-BRAIN BARRIER				0					43 169
ELECTROPHYSIOLOGY	13, 13, 18, 27 44, 45 29, 55, 56, 104, 105, 147, 149, 162, 172, 174, 175, 187, 197	52, 37, 51							

MANIFESTATION	PROTON RADIATION (r)			ELECTRON RADIATION (r)			ALPHA PARTICLE RADIATION (r)			GAMMA RAY RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY		28	31			54, 67, 107 108, 112		119, 134	134	110, 160, 199 200, 201, 210	210	153 213
BLOOD-BRAIN BARRIER	32 129	42, 32 129, 168										
ELECTROPHYSIOLOGY	187	187	187									

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-10. Brain referenes: swine*.

MANIFESTATION	X - RAY RADIATION (r)			ELECTRON RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
MORPHOLOGY					45							
BLOOD-BRAIN BARRIER												
ELECTROPHYSIOLOGY												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-11. Spinal cord references*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL	22, 31	2, 3, 4, 9 13, 19, 21 2, 3, 4, 10 13, 19, 20, 22, 23, 25, 31, 33 36, 44, 45, 48 49	13		12 22, 32		13, 22	13, 22, 41 48				9 19
ELECTROPHYSIOLOGY		6, 15 9, 10, 27										
SPINAL REFLEXES		1, 16 1, 28										
MORPHOLOGY	11, 20	2, 3, 5, 7, 8	5		8, 32		13, 22	22 13, 22, 37 41				9 19
	21, 22	11, 14, 17, 18	5									
	35, 42	19, 22, 23, 24 25, 26, 29 2, 3, 5, 10, 12 14, 15, 17, 19 20, 21, 22, 24 32, 33, 36, 37 39, 40, 41, 42										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-12. Behavior references: burro*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL				74, 167 183	166, 167 259, 260	167 260						
GENERAL ACTIVITY				118, 260 288								
BEHAVIORAL ACTIVATION				219								

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-13. Behavior references: dog*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			MIXED GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL		39 57	10, 151 12, 243		39 57							
GENERAL ACTIVITY		178, 149									156 248	
DISCRIMINATION											36 51	36 51
PSYCHOLOGICAL	49 76											
BEHAVIORAL ACTIVATION	42 59											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-14. Behavior references: guinea pig*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL		2, 4, 6	4, 6, 14, 82									
		14, 80	5, 7, 19, 128									
		3, 5, 7, 19, 125										
GENERAL ACTIVITY	30, 31							155				
	136, 155							247				
	45, 46, 225, 247											
DISCRIMINATION								135, 139				
								138				

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-15. Behavior references: hamster*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL		117	6, 117									
		177	7, 177									
GENERAL ACTIVITY	30, 31, 136											
	45, 46, 225											
BEHAVIORAL ACTIVATION												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-16. Behavior references: mouse*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			DEUTERON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL					115, 132 174, 216							
	13 16				129, 128 210, 213		171 266				141, 142 231, 233	141, 142 231, 233
DISCRIMINATION	84, 106, 7 75, 181	84 130		209								
	130, 162, 226 270, 276											
PSYCHOLOGICAL				209	126, 127 202, 204							
BEHAVIORAL ACTIVATION	3, 5, 111, 154 4, 6, 167, 246			105 161								

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-17. Behavior references: non-human primate*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			MIXED GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CLINICAL		81 127		1 2, 179	1, 28, 23 2, 33, 42 159, 204	1, 28 2, 42, 258 284					130 81, 85 259, 298	259
GENERAL ACTIVITY	165 122 52			95 146, 296	158						85	
DISCRIMINATION	68, 69 70	73, 188		24, 23 33, 34			297	17, 18 26, 27		191, 194	44, 45, 103 25, 62, 63, 64, 79, 109, 110, 181 182, 190, 194, 195 196, 280, 281 286, 298, 299	64, 111, 300
PSYCHOLOGICAL	67, 68 69, 70 173	46, 47, 48, 78 79, 118, 120 121, 123, 183 184, 185 66, 71, 72, 83 123, 124, 157 182, 188, 189 190, 192, 255 256, 294	203	182	77 35, 122						108, 19, 20 25, 28, 29, 64 74, 75, 195 280, 281	64
BEHAVIORAL ACTIVATION	180 275, 278											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-18. Behavior references: rabbit*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	> 10K	100-1K	1K-10K	> 10K	100-1K	1K-10K	> 10K	100-1K	1K-10K	> 10K
CLINICAL		72	73	131		37						
		114, 115, 140	115	215		52						
GENERAL ACTIVITY	148	115, 140										
	239											
BEHAVIORAL ACTIVATION	42											
	59, 140											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-19. Behavior references: rat*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)				ELECTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K		100-1K	1K-10K	>10K
CLINICAL					81, 115 128, 174	15, 83 20, 129							208
	30, 31, 54 100, 101, 102 45, 46, 85 154, 155, 156 172, 183							43					206, 208
	21, 75, 99 106, 107, 109 110, 137, 181 184	31, 292		40, 288	27, 134 39, 40, 144 220, 293	54 85, 144		135, 139 138 292, 43	29		292		205, 206
	30, 36, 199 153, 162, 163 165, 166, 226 276, 291												
PSYCHOLOGICAL	8, 11, 12, 38 53, 54, 56 76, 96, 104 168	7, 108 9, 164		22, 97, 119 32, 41, 141 149, 183, 288	119 8, 183								
	10, 14, 15, 36 53, 84, 85 90, 92, 120 149, 216, 261												

Table B-19. Behavior references: rat* (continued).

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			ELECTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
BEHAVIORAL ACTIVATION	25, 26, 40, 43	133		59, 60, 64, 65			63, 108 102, 164					
	50, 59, 61, 62			66, 67, 68, 108								
	69, 70, 71, 79			112, 116, 124								
	86, 87, 88, 89			144, 153, 158								
	90, 91, 92, 93			159, 160, 161								
	108, 111, 124			162, 170, 180								
	125, 133, 145			182								
	146, 147, 150			96, 97, 101								
	153, 176, 177			102, 103, 104								
	178, 179, 180			105, 164, 168								
	36, 38, 55, 60			176, 200, 235								
	77, 96, 98, 99			245, 250, 251								
	107, 108, 124			252, 253, 254								
	132, 133, 134			264, 273, 275								
	135, 137, 138			278								
	139, 140, 141											
	164, 167, 200											
	201, 217, 236											
	237, 238, 241											
	244, 271, 272											
	273, 274, 275											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-20. Behavior references: swine*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			MIXED GAMMA-NEUTRON RADIATION (r)			
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	
CLINICAL		172	172	107	107	107	24						
		267	267										
GENERAL ACTIVITY							24						
DISCRIMINATION				107	107	107		108	108		32, 33, 34 47, 48, 49 50, 283	283	

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-21. Cardiovascular references: burro*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			PROTON RADIATION (r)			DEUTERON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY												
BLOOD PRESSURE/ BLOOD FLOW				3	3		63					
CAPILLARY PERMEATION				11	11		260					

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-22. Cardiovascular references: cat*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			ALPHA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY		18, 68, 70										
BLOOD PRESSURE/		55										
BLOOD FLOW		209										
CAPILLARY PERMEATION		67									202	

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-23. Cardiovascular references: dog*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY	217	56 53, 79, 186, 217	53, 171 53, 171	60 181	56, 60 17, 63	17						
ECG		2, 49 10, 186, 216		4 233	4 63, 233							
CARDIAC OUTPUT		44			17, 63	228, 17, 229					124	
VASCULAR MORPHOLOGY	6, 14, 82	14, 23, 44, 75, 166				228					123	
BLOOD PRESSURE/ BLOOD FLOW	55 86, 209	13, 39 53, 86, 166		48	4 17, 40	4 17, 40 46, 225					29 123, 124, 180	242
CAPILLARY PERMEATION	7	7			16							

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-24. Cardiovascular references: guinea pig*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY	14	14, 120, 258										
BLOOD PRESSURE/ BLOOD FLOW												
CAPILLARY PERMEATION		258								220	220, 221	

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-25. Cardiovascular references: hamster*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG	78											
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY	87	106, 150										
BLOOD PRESSURE/ BLOOD FLOW	104	104										
CAPILLARY PERMEATION												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-26. Cardiovascular references: mouse*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY	31	7		262			262					
	136	28										
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY	1, 25, 54, 87, 152, 219	1, 54, 57, 152, 158, 159, 213, 232, 235		67, 126	7							211
BLOOD PRESSURE/ BLOOD FLOW	77, 81	29, 77, 81, 89, 110, 212			142	142						
CAPILLARY PERMEATION	25	57, 98, 114, 158	56, 126									

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-27. Cardiovascular references: non-human primate*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			ELECTRON RADIATION (r)			GAMMA-NEUTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY		50 186	186	44 172								
ECG												
CARDIAC OUTPUT				32	9 139, 140							
VASCULAR MORPHOLOGY	2, 14	14, 95			27, 95, 96			162				
BLOOD PRESSURE/ BLOOD FLOW	2, 153	50 180, 234		43 30, 31, 32 33, 34, 35 36, 177	3, 8, 9, 12 31, 35, 39 41, 42, 93 139, 140, 142, 165	39, 49, 142		162			33 60, 164, 169 180	
CAPILLARY PERMEATION	64, 65, 91	20, 64, 65, 91, 174, 205										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-28. Cardiovascular references: pig*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			ALPHA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY	26	24, 26										
	105	102, 105, 108										
BLOOD PRESSURE/ BLOOD FLOW		24		3	3	3						
		175, 183		11	11	11						
CAPILLARY PERMEATION		175										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-29. Cardiovascular references: rabbit*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			BETA RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY	53, 187	15, 16, 17, 30 35, 36, 57 72, 73, 74, 131 132, 133, 141 224, 225, 239	72									
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY	58, 59, 134 214, 243	16, 36, 42, 57 92, 120, 134, 141, 154, 214, 224, 242			92	58, 59 228, 229		179			163	163
BLOOD PRESSURE/ BLOOD FLOW	28, 119, 214, 243	19, 20, 155, 172, 214, 242						179			163	163
CAPILLARY PERMEATION	64, 65, 91	20, 64, 65, 91, 174, 205										

*Cited references are underlined. Other may be found in the Reading List in Appendix A.

Table B-30. Cardiovascular references: rat*.

MANIFESTATION	X - RAY RADIATION (r)				GAMMA RAY RADIATION (r)			PROTON RADIATION (r)			ELECTRON RADIATION (r)		
	100-1K	1K-10K	>10K		100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY	48	34, 48											
	99, 149	144, 178											
ECG	10, 11												
	41, 49												
CARDIAC OUTPUT		116, 130										4	4
VASCULAR MORPHOLOGY	48, 53	48, 52, 53, 54			115, 126, 182					143		123	
	14, 87, 188 195, 247	1, 12, 13, 14, 38, 37, 65 80, 83, 97, 111, 106 101, 118, 145, 188 189, 195, 201, 241											
BLOOD PRESSURE/ BLOOD FLOW	11, 19, 45, 61, 65	48, 52, 53, 54			248	142	142	62			4, 167, 166		20
	41, 88, 113, 135 176, 184, 185 230, 247, 252 257, 263, 264	8, 9, 13, 66, 101, 116 127, 129, 145, 155 170, 176, 185, 218 237, 238, 247, 250 251						261					4, 93, 125
CAPILLARY PERMEATION	55, 90, 31, 244, 256, 255	90, 114, 145, 241, 255 254			126	71	88			143	88		

*Cited references are underlined. Other may be found in the Reading List in Appendix A.

Table B-31. Cardiovascular references: sheep*.

MANIFESTATION	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			PROTON RADIATION (r)			DEUTERON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
HEART MORPHOLOGY												
ECG												
CARDIAC OUTPUT												
VASCULAR MORPHOLOGY												
BLOOD PRESSURE/ BLOOD FLOW				3	1, 3							
				11	3, 11							
CAPILLARY PERMEATION												

*Cited references are underlined. Other may be found in the Reading List in Appendix A.

Table B-32. Gastrointestinal references: cell survival*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	30, 31 87, 128, 129, 131, 132, 133, 134, 199, 349	49, 87, 92, 152, 154, 163, 164, 266, 271, 278, 283, 314, 315, 341, 349		41, 42, 43 62, 97, 176, 177, 204, 207, 257, 261, 352	62, 154, 283, 343, 349, 352		125, 154, 163, 348, 349, 352	49, 163, 283, 349				
Rat				3, 4, 43 13, 14, 16, 17, 18, 207	16, 18							
Rabbit												
Dog												
Hamster												
Pig												
Non-Human Primate												
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-33. Gastrointestinal references: Intestinal repair*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	128, 129, 131 238	130, 136, 314, 315, 340	130	41, 42 175, 185, 186, 204, 205, 206, 258, 259, 260, 316,	259, 342		185			186		
Rat	332, 334	146, 147, 148, 332		18	18, 273							
Rabbit												
Dog												
Hamster												
Pig												
Non-Human Primate				96								
Cat												
Guinea Pig												
Gerbil	238											

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-34. Gastrointestinal references: Infection*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	69	48, 50, 51, 69	221	177	47			284				
	84, 115, 231	221, 223, 224,			220, 245							
	338	284, 338										
Rat	68			26	28		28					
Rabbit	303, 304			117	117, 255		117					
Dog		12			12							
Hamster		72, 287			72							
Pig												
Non-Human Primate												
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-35. Gastrointestinal references: Intestinal blood flow*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	42, 109, 321	109, 321			101			321				
Rat	80, 197, 335, 336	20 98, 145, 182, 183, 312, 335									39 190, 191, 192	
Rabbit												
Dog		40			9, 10 65, 67	9 65, 66						
Hamster												
Pig		37										
Non-Human Primate												
Cat												
Guinea Pig		105, 106, 107										

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-36. Gastrointestinal references: morphology*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	21, 52, 53, 55 48, 52, 56, 74, 89, 102, 140, 166, 227, 228, 233, 267	32, 33, 34, 35, 36 9, 48, 52, 54, 56, 88, 89, 118, 119, 137, 138, 141, 142, 143, 150, 166, 167, 168, 169, 170, 248		52, 56, 139, 174, 327, 330	48, 52, 53, 55, 56, 139, 327, 345		48, 52, 56, 118, 119, 140, 156, 161, 174, 242, 327	48, 52, 56, 119, 139, 327				
Rat	13, 15 30, 45, 50, 73, 85, 320, 334, 347	3, 32, 46, 83, 114, 149, 165, 208, 296, 319		5 17, 19, 22, 24, 195, 256	4, 203							
Rabbit	104			63								
Dog	43, 121	66			45, 135							
Hamster		45										
Pig				203	188		51, 188			79		
Non-Human Primate					339							
Cat		108, 277										
Guinea Pig	333				203		333					
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-37. Gastrointestinal references: motility*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	6, 8, 22 39, 61, 70, 111, 285	70		24 70, 113	24 113							
Rat	1, 8, 11, 27, 67 8, 41, 61, 68, 69, 123, 171, 172, 284, 270, 285, 300 323, 324, 346	40, 65 187, 193, 194, 297, 346										
Rabbit		49 222										
Dog		66 298										
Hamster												
Pig												
Non-Human Primate	1			18, 19 93, 94, 95, 201								
Cat												
Guinea Pig	285		60 288									
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-38. Gastrointestinal references: transport capacity*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			GAMMA/NEUTRON RAD. (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	17 29, 33, 90, 229, 321	216, 321										
Rat	16, 23, 27, 54, 56, 57	2, 14, 23, 37, 38, 61, 62, 63, 64		7, 56 11, 20, 21, 23, 25, 26, 27, 56, 251, 308, 311, 325	10, 15, 23, 180, 307		321				91, 196	
	26, 33, 66, 99, 112, 123, 124, 232, 235, 251, 252	12, 33, 78, 91, 110, 112, 120, 124, 179, 161, 196, 235, 244, 291, 292, 293, 294, 295, 351					180					
				28 126	28 126							
Rabbit												
Dog	33											
Hamster												
Pig												
Non-Human Primate	1			2, 6, 7, 260	2	2						
Cat												
Guinea Pig	33											
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-39. Endocrine references: adrenal gland*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	13											
	32, 76											
Rat	4, 7, 24, 31	1, 5, 6, 14										
	5, 6, 7, 18, 38, 46	3, 20, 30, 77,										
	54, 62, 66, 71, 99,	136, 143										
	103, 106, 119, 140											
Rabbit		9										
		43, 54										
Dog	78, 97, 117, 146,	97, 144										
	147											
Hamster												
Pig	22											
Non-Human Primate	32											
Cat	142											
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-40. Endocrine references: pancreas*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse												
Rat	21	11 69, 121		137			109					
Rabbit		122										
Dog	107	28, 29, 30 2, 132, 133, 136, 139								36, 37		
Hamster												
Pig												
Non-Human Primate												
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-41. Endocrine references: parathyroid*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	13	13										
Rat	13	13										
Rabbit												
Dog	13	13										
Hamster												
Pig												
Non-Human Primate	13	13										
Cat												
Guinea Pig	13	13										
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-42. Endocrine references: pituitary gland*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			ELECTRON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	35, 49, 50, 55	49, 50, 94										
Rat	4	17, 18			17		49, 50			89	18	
		84, 88, 89, 128			88							89
Rabbit												
Dog	113, 145											
Hamster												
Pig												
Non-Human Primate		24										
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-43. Endocrine references: testis/ovary*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	27	91			141							
Rat	8, 27, 31, 40 41, 63, 72, 74	1, 15, 45, 83		29, 64	64							
Rabbit		122										
Dog	78											
Hamster												
Pig												
Non-Human Primate	70	70										
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-44. Endocrine references: thyroid gland*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			PROTON RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
Mouse	26 120, 124, 134, 135	135										
Rat	3, 10 10, 16, 28, 34, 52, 53, 56, 65, 87, 104, 105	3 10, 28, 32, 47, 52, 57, 73, 80, 98, 105		67, 86	86		86					
Rabbit	131											
Dog	82, 114	19 48, 82, 92, 93										
Hamster												
Pig												
Non-Human Primate												
Cat												
Guinea Pig												
Gerbil												

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-45. Hematopoietic references: stem cell*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CAT	416											
DOG	11 1, 21, 25, 27, 58, 299, 302, 308, 309, 310	74, 86, 87, 145, 308		25,** 27,** 122, 311, 380		47	28, 58					
GOAT				108	108							
GUINEA PIG	46, 71			46, 184, 185, 186, 187			46					
MOUSE	13, 16, 18, 22, 24, 29, 30 7, 17, 34, 36, 37, 42, 43, 44, 45, 48, 52, 53, 54, 64, 68, 77, 81, 84, 85, 95, 99, 104, 106, 107, 121, 130, 131, 141, 146, 152, 157, 158, 171, 173, 174, 178, 181, 182, 183, 197, 198, 199, 200, 202, 209, 219, 222, 227, 233, 240, 241, 242, 243, 244, 272, 277, 279, 280, 283, 294, 314, 317, 322, 347, 353, 359, 366, 377, 402, 403											
NON-HUMAN PRIMATE	112			88, 89, 188**	88							
PIG				108	108							
RABBIT	17 45, 46, 71, 218, 271, 377	30		17 46, 218			45, 46					
RAT	28 13, 19, 20, 21, 22, 23, 24, 32, 33, 45, 71, 103, 167, 204, 212, 211, 213, 232, 305, 306			28** 29, 30,** 32,** 40, 73, 91, 143, 144, 289, 380	6 30, 60, 97, 103		45					

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

**Gamma-neutron radiation.

Table B-46. Hematopoietic references: peripheral blood*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
CAT	416											
DOG	11 1, 21, 25, 27, 58, 299, 302, 308, 309, 310	74, 86, 87, 145, 308		25, * 27, * 122, 311, 390		47	28, 58					
GOAT				108	108							
GUINEA PIG	46, 71			46, 184, 185, 186, 187			46					
MOUSE	13, 16, 18, 22, 24, 29, 30 7, 17, 34, 36, 37, 42, 43, 44, 45, 48, 52, 53, 54, 64, 68, 77, 81, 84, 85, 95, 99, 104, 106, 107, 121, 130, 131, 141, 146, 152, 157, 158, 171, 173, 174, 178, 181, 182, 183, 197, 198, 199, 200, 202, 209, 219, 222, 227, 233, 240, 241, 242, 243, 244, 272, 277, 279, 280, 283, 294, 314, 317, 322, 347, 353, 359, 366, 377, 402, 403											
NON-HUMAN PRIMATE	112			88, 89, 188*	88							
PIG				108	108							
RABBIT	17 45, 46, 71, 218, 271, 377	30		17 46, 218			45, 46					
RAT	26 13, 19, 20, 21, 22, 23, 24, 32, 33, 45, 71, 103, 167, 204, 212, 211, 213, 232, 305, 306			26* 29, 30, * 32, * 40, 73, 91, 143, 144, 289, 380	6 30, 60, 97, 103		45					

*Cited references are underlined. Other may be found in the Reading List in Appendix A.

**Gamma-neutron radiation.

Table B-47. Immune references: lymphocytes*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
COW	48, 199	48										
DOG				138, 156, 167, 183			156					
GUINEA PIG	33, 79			109, 110								
MOUSE	5, 23, 36, 38, 44	32, 40, 41, 106, 165, 188, 202, 278		39, 85, 90, 192, 201, 259	130, 192		122, 123, 124, 273					
	14, 16, 20, 21, 22, 23, 28, 40, 41, 45, 46, 52, 53, 59, 84, 104, 105, 106, 107, 116, 117, 122, 123, 136, 140, 141, 169, 170, 190, 201, 202, 208, 209, 210, 227, 230, 247, 249, 250, 273, 274, 285											
NON-HUMAN PRIMATE												
PIG	263											
RABBIT	12 33, 66, 244											
RAT	4, 23, 12, 33, 36, 51, 78, 95, 125, 170, 186, 261, 262, 270	10, 36, 37, 95, 102, 280, 281, 289	262, 270	14, 80, 162	27							

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-48. Immune references: cell-mediated immunity*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
COW												
DOG												
GUINEA PIG	33											
	135, 215, 266											
MOUSE	17, 24, 34,	278										
	35, 44											
	6, 7, 25, 52, 104, 128, 169, 190, 224, 225, 231, 248, 270, 275, 285											
NON-HUMAN PRIMATE	47, 73, 179	179										
PIG												
RABBIT	30, 61	30										
RAT						88						

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

Table B-49. Immune references: humoral immunity*.

SPECIES	X - RAY RADIATION (r)			GAMMA RAY RADIATION (r)			NEUTRON RADIATION (r)			BETA RADIATION (r)		
	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K	100-1K	1K-10K	>10K
COW												
DOG												
GUINEA PIG	33, 43			183								
	135, 215, 285											
MOUSE	17, 24, 34,			31, 34, 69,	34, 89, 92							
	35, 44			149, 204								
	13, 25, 41, 52, 84, 94, 104, 128, 160 169, 190, 224, 225, 231, 248, 270, 275, 285											
NON-HUMAN PRIMATE	47, 73											
PIG												
RABBIT	12	30										
	30, 61, 67, 253, 254											
RAT	26					88						

*Cited references are underlined. Others may be found in the Reading List in Appendix A.

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