INFORMATION TO USERS

This dissertation was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.

2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.

3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again — beginning below the first row and continuing on until complete.

4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.

University Microfilms

300 North Zeeb Road
Ann Arbor, Michigan 48106

A Xerox Education Company

EFFECTS OF OLFACTORY BULBECTOMY ON NURSING AND RELATED BEHAVIORS IN THE WISTAR RAT PUP

by

PAULINE JIRIK SINGH, M.S.

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

February 1, 1973

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy

January 29, 1973
date

Ethel Tobach
Chairman of Examining Committee

January 29, 1973
date

Florence L. Denmark
Executive Officer

Dr. Ethel Tobach

Dr. Jack Orbach

Dr. Gerald Turkewitz
Supervisory Committee

The City University of New York

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. Ethel Tobach for her advice, encouragement, and guidance throughout the course of this study. Appreciation is also expressed for the comments, criticisms, and helpful suggestions of Dr. Jack Orbach and Dr. Gerald Turkewitz and for the interest and consideration shown by Dr. Jeri Sechzer and Dr.H. Philip Zeigler.

Thanks are also due to Dr. Donald Pfaff for consultation and assistance in developing the surgical procedure, to Mrs. Marie Tucker for assistance with histological analyses, to Mr. Michael Maltzman for helping with data analyses, and to Mrs. Sita Bedi for typing the manuscript with patience and skill.

Last, but not least, I wish to thank my husband, Inder Jit, for his unfailing help, advice and moral support.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vii
LIST OF FIGURES	viii
I. INTRODUCTION	1
A. Historical and Theoretical Perspectives	1
B. Evolution of Olfactory System	4
C. Role of Olfactory System in Behavior of Macrosmatic Mammals	5
1. Feeding Behavior	6
a. Immature Rodents	6
b. Adult Rodents	7
c. Complexity of Relationships Between Olfactory System and Feeding Behavior	7
2. Reproductive Behavior	9
3. Maternal Behavior	12
4. Social Bond Formation	13
5. Aggression and Mouse-killing	14
6. Exploratory Behavior	16
7. "Fear" Response	16
8. "Nonolfactory" Behaviors	17
D. Rationale and Purpose	20

Page

II. MATERIALS AND METHODS 23

A. Subjects 23

B. Experimental Design 23

C. Apparatus 26

1. Home Cage 26

2. Observation Cage 26

3. Recording Apparatus 27

D. Procedure 27

1. Maintenance and Handling 27

2. Group Assignment, Marking, and Weighing 29

3. Surgery 30

4. Autopsy 31

5. Histology 32

6. Behavioral Observations and Tests 32

a. Observation Sessions in Observation Cage 33

(1) Pup to Female 33

(2) Pup Alone 34

(3) Pups with Other Pups 34

(4) Female to Pup 35

b. Pup-placement Tests 35

c. Retrieving Tests 36

d. Cage Drawings 37

E. Data Analysis 37

1. Anatomical and Physiological Data 37

2. Data from Observation Sessions in Observation Cage 38

3. Auxiliary Data 38

Page

III. RESULTS 40

A. Anatomical and Physiological Data 40

1. Survival 40

2. Body Weight 43

3. Autopsy 51

4. Histology 51

B. Behavioral Data 57

1. Cross-sectional Data from Observation Sessions in Observation Cage 57

a. Pup to Female 58

b. Pup Alone 62

c. Pup with Other Pups 65

d. Female to Pup 69

2. Longitudinal Data from Observation Sessions in Observation Cage 72

3. Auxiliary Data 74

a. Cage Drawings 74

b. Pup Placement Tests 75

c. Retrieving Tests 77

IV. DISCUSSION 82

A. Anatomical and Physiological Data 84

B. Behavioral Data 88

1. Cross-sectional and Auxiliary 88

2. Longitudinal 96

C. Concluding Remarks 98

APPENDIX 100

BIBLIOGRAPHY 164

LIST OF TABLES

Page

1. Experimental design. Number of pups originally assigned to each treatment 24
2. Number of pups surviving through each day 41
3. Proportion of pups that survived through Day 16 in each treatment groups 42
4. Number of days of survival after treatment of BX, IBX, SC, and HC pups 44
5. Mean body weights (in grams) of pups treated on Day 2 45
6. Mean body weights (in grams) of pups treated on Day 7 46
7. Mean body weights (in grams) of pups treated on Day 11
8. Mean body weights (in grams) of pups from non-treated litters 48
9. Mean last body weights (in grams) recorded before autopsy for BX and IBX pups and of control littermates' body weights recorded on same day 49
10. Amount of milk in stomach at autopsy 53

For additional tables see Appendix p. 100.

LIST OF FIGURES

		Page
1.	Photomicrographs of sections from brain of a typical bulbectomized pup (Day 9)	54
2.	Photomicrographs of sections from brain of a typical incompletely bulbectomized pup (Day 16)	55
3.	Photomicrographs of sections from brain of a typical untreated pup (Day 8)	56
4.	Mean duration (seconds) of suckling for pups treated on Day 2	59
5.	Mean duration (seconds) of suckling for pups treated on Day 7	60
6.	Mean duration (seconds) of suckling for pups treated on Day 11	61
7.	Mean duration (seconds) pups at 13 days of age nosed female	63
8.	Mean duration (seconds) locomotion for pups treated on Day 7	64
9.	Mean duration (seconds) of activity apart from others for pups treated on Day 2	66
10.	Mean duration (seconds) of activity apart from others for pups treated on Day 7	67
11.	Mean duration (seconds) of activity apart from others for pups treated on Day 11	68
12.	Mean number of times female picked up and carried pups treated on Day 7	70
13.	Mean number of times female picked up and carried pups treated on Day 11	71

I. INTRODUCTION

A. Historical and Theoretical Perspectives

The study of sensory systems was one of the earliest branches of psychology to develop. This is not surprising since, whenever one studies behavior, one is automatically dealing with some aspect of sensory processes because an organism receives all information about its environment through or by way of its sensory systems.

Just as the study of sensory processes is an integral part of the study of behavior, the investigation of the evolution of sensory systems and of the chronological development of sensory systems in the individual is a necessary part of research dealing with the phylogeny and ontogeny of behavior. As Schneirla (1949, 1957, and 1966), Tobach (1968 and 1971), Gottlieb (1971), and Kuo (1970) have indicated, the sequence in which sensory systems become functional is important for comparative and evolutionary purposes and should provide fundamental information for basic concepts of the epigenesis of behavior.

Most of the early work on sensory systems dealt with vision, audition, tactile reception, and vestibular reception and most was done on adult animals. The developmental basis of proximal and distal sensory systems and their postnatal integration had not been systematically studied although psychological theories were based on assumptions about sensory development (Hebb, 1949; Helson, 1964; Gibson and Gibson, 1955; and Gibson, 1958).

Complex adult behavioral patterns are most probably integrated on the basis of intersensory relationships formed early in life. Studies on development of orientation in neonatal cats (Rosenblatt, Turkewitz, and Schneirla, 1962), and rats (Turkewitz, 1966) and development of adjustive responses in rats (Tobach, Vroman, Turkewitz, and Schneirla, 1960) and in mice (Tobach, Schneirla, Sang, Gold, Steel, and Wortis, 1958) indicate how non-visual sensory processes may provide a basis for actions such as approaching and following objects. This research with neonatal cats, rats, and mice indicates that pre-visual and pre-auditory processes, namely the proximal sensory systems of chemoreception and tactile reception, are fundamental in the development of complex behavioral patterns such as orientation.

Although chemoreception is now being studied in many species, there is still a paucity of data on the development of chemosensory function and behavior. Volokhov (1968), Scherrer (1968) and Gottlieb (1968 and 1971) have done comparative work, using various species of mammals and birds, on the sequence of sensory development. In their reviews, however, only the developmental sequence of the visual, auditory, vestibular, and cutaneous sensory systems are discussed. Neither olfaction nor gustation are mentioned.

Some of the theoretical papers in this area of research (Tobach, 1972; Riss, Halpern and Scalia, 1969) have stressed the evolutionary and developmental significance of chemoreception, but most of the experimentation has dealt with function in mature animals indicating a lack of developmental or longitudinal perspective. The longitudinal method is a special tool for developmental investigations. Although it

has a number of drawbacks such as selective sampling and complex problems relating to the effects of a changing environment, multiple measurements of the same cases remain the best way of learning about development as a process. Developmental psychologists such as Schneirla (1957), Birch (1971), and Harris (1971) have pointed out that one cannot infer longitudinal developmental conclusions from serial cross-sectional data without danger of error, because a stage is just one developmental cross-section or limited interval between turning points in ontogeny. Without adequate longitudinal perspective, misconceptions can arise very easily. Strong a priori convictions in one direction or another might result in drawing conclusions from cross-sectional data as though they were longitudinal data. This, in turn, might result in issues and problems that may have nothing to do with development itself but rather some characteristic of the experimental design and data collection. For example, Kennedy (1966) who in a cross-sectional study found a decline in intelligence with age in Negro children, found no such decline after studying one segment of his population longitudinally rather than cross-sectionally.

This investigation, in a general sense, deals with the ontogeny of behavior in a neonatal, altricial, macro-osmatic mammal (rat) in relation to the olfactory system and has been conducted with a cross-sectional and longitudinal perspective. A more specific description of the rationale and purpose is expressed later. Before going into detail, however, let us review the evolution of the olfactory system and its role in the behavior of macro-osmatic mammals in general, for the purpose of assembling a background of information in

which this study may be better understood and interpreted. (A description of the olfactory system is located in the Appendix.)

B. Evolution of Olfactory System

Olfaction is often considered to be the "oldest" sensory system. Herrick (1921) believed that olfaction was the basis of paleocerebral development and Niewenhuys (1967) and Segaar (1965) both agree with this view. As far back among invertebrates as can be traced, there is evidence of chemosensory input into the anterior end of the neural tube. As multicellular organisms evolved, the first neurons that developed represented specializations of surface ectodermal cells. As evolution proceeded, the nerve cell bodies of most afferent neurons eventually occupied a more central position in cerebrospinal ganglia. However, there was one exception to this general rule and that is the olfactory area where the cell bodies of afferent neurons remained at the surface even though, from insects through fishes to mammals, the receptor surfaces became progressively more buried in the nasal passages behind the turbinates or conchae.

Aronson (1963) pointed out that olfaction actually consists of two physiological processess--one a specific process providing the basis for discrete discriminations, associations, and orientation and the other a diffuse, nonspecific process activating other sensorimotor systems which guide the animal toward or away from a stimulus. In ancestral vertebrates, the center for the olfactory arousal mechanism was the forebrain which projected its impulses downward to the diencephalon, midbrain, and lower centers. This formed the basis of the primitive limbic system (Segaar, 1965; Aronson and Kaplan, 1968).

One school of thought postulated that the olfactory arousal function gradually enlarged and somewhere in early vertebrate history became independent of olfaction. Papez (1937), Brodal (1947), Le Gros Clark and Meyer (1947), and MacLean (1952) favored a clear distinction between olfactory structure and limbic structures. More recently, however, a different point of view has emerged rejecting the extreme position of total separability of the olfactory and limbic systems but rather, leaning toward the view that the systems are related (Berry, Hagamen, and Hinsey, 1952; Powell, Cowan, and Raisman, 1965; and Riss, Halpern, and Scalia, 1969).

Riss et al. (1969) have further postulated that the olfactory system evolved from the limbic system. This is in opposition to the traditional view. Moreover, they have described the limbic system as reponsive to the internal milieu and the olfactory system as responsive to the external chemical milieu.

C. Role of Olfactory System in Behavior of Macro-osmatic Mammals

The olfactory system is of paramount importance in macro-osmatic mammals such as the rat, because olfactory stimuli such as food odors and pheromones play a large role in behaviors such as feeding, reproduction, maternal behavior and social bond formation which are necessary for the survival of the individual and of the species. It appears that the olfactory system is also involved in aggression and mouse-killing, exploration, fear, and so-called "nonolfactory" behaviors. The following review presents material indicating a relationship

between the olfactory system and the above-mentioned behaviors.

1. Feeding Behavior

a. Immature Rodents

Behavioral studies in olfaction were found in the literature as early as 1899 when Small noted the reaction of rat pups to odors. He observed that at 3 or 4 hours of age all odors were "disagreeable," but by the 4th day the pups were able to discriminate food odors which they found "pleasurable" from various other substances such as violet and camphor. Since responses indicating interest in the odors of cheese and milk were often made before they had tasted these substances, Small judged this to be an unlearned behavior. Small's method was simply to expose the animal to the odorant and watch and record its reactions. However, Salas, Schapiro, and Tugman-Flores (1970) reported that electrical activity from the olfactory bulb of a 2-day old rat pup was undetectable and that before 6 days of age there was a slight increase of the average bulb frequency in response to either the odor of the mother or food. They suggested that at this stage the smell reponse is nonspecific and that integrative discriminatory capabilities between different odors are still undeveloped. After 6 days of age the rat pup exhibited a consistent increment in average olfactory frequency in response to maternal odor. Beginning at 9 days of age, food odor produced a slight decrement of this average frequency. When interpreting these results, it must be remembered that the food odor used in this study was powdered Purina lab chow. Perhaps for young rat pups, whose diet consists of mother's milk alone, this is not a

very appropriate olfactory stimulus.

b. Adult Rodents

Using a multiple-choice apparatus, French (1939) trained rats to reach for uncontaminated food in preference to food contaminated with odorants and quinine demonstrating the dependence of food preference upon olfaction. Stone (1941) showed that normal rats could discriminate food by odor in the four corners of the cage while anosmic animals could not. Howard, Marsh and Cole (1968) demonstrated that in deer mice the olfactory sense can be used to detect food in the absence of visual cues. Tapp and Long (1967) studied the reinforcing properties of odors and found that a familiar food odor was more successful in directing a rat's behavior than an unfamiliar odor. They also demonstrated a preference for odorized rather than nonodorized air in rats, the preferred stimuli being food and water odors. (Long and Tapp, 1968).

c. Complexity of Relationship Between Olfactory System and Feeding Behavior

Marks, Seago, and Remley (1971) compared normal and olfactory bulbectomized rats in a single-bottle preference test in regard to the amount of water, sucrose, saccharine, and quinine solutions consumed. Under food deprivation, anosmic rats consumed more water and sucrose and less saccharine and quinine than normal rats. Under water deprivation, the order of these relationships was reversed. This indicates that while the ablation of olfactory bulbs obviously influences taste preferences, the relationship is complex. In interpreting the results of the above-mentioned experiment, it is important to note

that in an ad lib food and water situation, Navakova and Dlouha (1960) found that rats with severed olfactory bulbs drank approximately 60% more water per day and excreted about 60% more urine per day than controls.

Larue and Le Magnen (1970) combined ventro-medial hypothalamic lesions and removal of olfactory bulbs in the rat to clarify olfactory cues in control of food intake. In an animal that had already received a ventro-medial hypothalamic lesion, a bilateral bulbectomy induced a rebound of hyperphagia and weight gain leading to a higher level of the static phase of obesity. They explain this unexpected result in the following way: In intact rats the presence of olfactory sensations is involved in a different manner in the control systems acting to regulate food intake at a constant level. To insure the control of intake at a definite level, they hypothesize that two conditions are required. First, for oral metering, palatibility responses mediating the oral intake have to be controlled by metabolic signals. Secondly, the sensory cues giving rise to these palatability responses must exist acting either (or both) as facilitatory or limiting factors. After a ventro-medial lesion, the oral control seems to escape partially to metabolic influences up to a new equilibrium. The failure of the second condition of this equilibrium due to the lack or suppression of olfactory cues might be the cause of the difficulty to reach this new equilibrium evident by the delayed occurrence of this new level of regulation. It has been shown with intact rats that the sudden removal of an odorous material added to the familiar maintenance diet causes a transient overeating (Le Magnen, 1956).

It is well known that responses of the individual to external food stimuli are mediated by a network in the brain extending through the limbic forebrain areas, the hypothalamus, and the brain stem reticular formation. The lateral hypothalamic area, which is sometimes referred to as an "appetitive center," figures prominently in this system. Lateral hypothalamic neurones can be activated by oral and olfactory stimulation. Scott and Pfaffman (1967) found electrical responses in the lateral hypothalamus when stimulating the olfactory bulbs or the lateral olfactory tract of an anesthetized rat. An electrical response was also seen in the lateral hypothalamus to amyl acetate presented in a stream of filtered air to the rat's nose. Scott and Pfaff (1970) demonstrated similar responses in the female mouse. These electrophysiological responses gave evidence of an olfactory pathway into the lateral hypothalamus by way of the ventrolateral portion of the medial forebrain bundle. These facts and others suggest that olfactory cues are involved in food gathering, in the initiation of food ingestion, and in the control of the daily intake of food at a constant and calorically adjusted level.

2. Reproductive Behavior

It is now known that olfactory-mediated stimuli not only play a large role in the transfer of information that must precede insemination but that odors may also have relatively direct effects on anterior pituitary function itself. Male odors for example, may alter the release of FSH, LH, LTH, ACTH, or prolactin in recipient females (Bruce and Parkes 1960; Dominic, 1966; Chapman, Desjardin, and Whitten, 1970). Thus

olfactory stimuli may also affect the development and maintenance of reproductive organs. Orbach and Kling (1966) found that a delay in reaching puberty occurred in female rats that were made peripherally anosmic and were girdled to prevent them from licking and sniffing the genital region. Reiter, Sorrentino, and Ellison (1970) found hypertrophy of reproductive organs in adult female rats if bulbectomy occurred with blinding. (Neither blinding nor olfactory bulb removal alone appreciably altered the reproductive organs.)

Olfactory-mediated stimuli are called pheromones. The term pheromone has been commonly used for externally-voided, scented, glandular secretions that convey information between two members of the same species (Karlson and Luscher, 1959; Bronson, 1971; Macrides and Chorover, 1972).

Many investigations indicating the existence of a sexual olfactory pheromone have been reported. Donovan (1967, 1969) suggested that secretions from the anal sac of female dogs contain the mechanism for sexual attraction. He also demonstrated that bulls are more interested in fecal matter and secretions from the anal sweat and sebaceous glands of estrous cattle than a similar preparation from anestrous cattle.

Normal mating behavior was eliminated in bilaterally bulbectomized male golden hamsters but not in blinded, unilaterally bulbectomized or sham-operated animals. Testosterone injections restored normal sexual behavior in castrated animals but not in the bilaterally bulbectomized hamsters (Murphy and Schneider, 1970).

Scott and Pfaff (1970) reported that female mice whose estrous cycle can be accelerated by exposure to normal male urine,

spent more time sniffing urine from normal males than from castrated males. Similarly normal sexually experienced male rats spent more time sniffing the urine odor from estrous females than the urine odor of ovariectomized females; however, this was not true of castrated males (Pfaff and Pfaffman, 1969).

In experiments with rats,Carr, Loeb and Dissinger (1965), Carr, Loeb and Wylie (1966) and Le Magnen (1951, 1952) showed that receptive males preferred receptive female odor over nonreceptive female odor. Stern (1970) demonstrated that experienced male rats do not prefer estrous female odor following castration. However, males who were castrated before 11 days of age developed a preference of estrous female odor following injection of testosterone propionate. Experienced females and segregated receptive naive females showed preference for the odor of normal males over the odor of castrated males.

In an experiment by Beach (1942) on the effects of olfactory bulb destruction on copulatory activity, both sexually experienced and virgin male rats showed some decline in responsiveness. The decrease in activity was greater in virgin animals. Heimer and Larsson (1967) confirmed Beach's major results for males that had copulatory ex - perience prior to surgery. Bermant and Taylor (1968) found that bilateral olfactory bulb ablations in male rats with prior copulatory experience produced gross prolongation of first and second series ejaculation latencies. The probability of ejaculation, but not of intromission, was significantly reduced for bilaterally bulbectomized virgin males. Aaron, Roos and Asch (1970) removed the olfactory bulbs in adult,

virgin, female rats and found a decrease in mating frequency in so-called "early mating behavior" (during the night following Day 3 of a 5-day cycle). Thus one can conclude that olfactory cues contribute to the arousal and maintenance of copulatory activity in the rat, but that they are not absolutely necessary for either. Complete disruption of copulatory behavior in the rat appears only when olfactory bulbectomy is combined with the loss of another sensory modality (Beach, 1947).

3. Maternal Behavior

The traditional view of maternal behavior has been that it is under multi-sensory control, that is, no one sensory system is essential for its exhibition (Stone, 1925; Beach, 1942; Beach and Jaynes, 1956). However, recently it has been found that if lactating or virgin female mice are bulbectomized, maternal behavior is completely eliminated and cannibalism of all or a portion of the litter occurs (Gandelman, Zarrow, Deneberg, and Myers, 1971).

Leonard (1971) found that bulbectomized golden hamster females also destroyed their entire litters soon after delivery. Thus exhibition of maternal behavior in this species is largely dependent upon the olfactory system. Fleming and Rosenblatt (1971) bulbectomized virgin female rats and then gave them litters. They found that 58% of the bulbectomized virgin females cannibalized the young, whereas none of the normal virgin females cannibalized the litters. However, Fleming, (personal communication) has pointed out that when virgin rats have zinc sulfate applied to their olfactory mucosa, there is almost no incidence of pup-killing. This result indicates that there is a "non-olfactory" aspect of pup-killing.

Olfactory stimuli have been shown to influence milk ejection in rats. Grosvenor and Mena (1967) found that non-social odors such as oil of peppermint significantly reduced milk ejection in primiparous lactating rats. They also found that whenever the smell of rat pups was present, there was a release of prolactin in the female. However, when the smell of pups was absent, there was no release of prolactin. Bulbectomy of the female interfered with prolactin release and resulted in cannibalism of the litter.

4. Social Bond Formation

Schneirla (1949) proposed that social bond formation results from the process of mutual exchange of stimuli by two or more individuals. Evidence indicates that early olfactory stimuli influence development of social bonds in mammals as pointed out by Tobach and Schneirla (1968) and Schneirla and Rosenblatt (1961).

The results of Leon and Moltz (1971) indicate that one of the cues uniting mobile rat pups with their lactating mother is olfactory in nature. They found that young rats can discriminate the odor of a lactating female from that of a nulliparous female, though each lactating female's odor does not seem to be specific for the attraction of her own litter. Reversal of the direction of the airflow leads to a breakdown of the discrimination. Nyakar and Endroczi (1970) found that olfaction guided approaching behavior of rat pups to their mother in a maze box. They observed that pups went to their mother and to a lesser extent to nonlactating females but not to males. Application of tetracaine on the nasal mucosa of pups resulted in random behavior. Sheppard and

Yoshida (1971) found that olfaction contributed to individual recognition and thus social organization in ground squirrels.

Other experiments have dealt with the connection between early olfactory experience and later social relationships. Marr and Gardner (1965) sprayed rat pups with cologne and found that they later preferred cologne-smelling rats, while pups treated with methyl-salicylate became socially anosmic as adults. Mainardi, Marsen, and Pasquali (1965) treated parent mice with perfume which led to the loss of sex discrimination by their young when adult. Himwich applied aniseed oil to the mammae of lactating bitches whose pups later responded positively to aniseed oil. Thus early exposure to odors has a definite effect on adult response to odors. However, Marr and Lilliston (1969) concluded that exact age was not a critical variable in early learning of species odor in the rat, since they observed learning of species odor from 3 to 29 days of age.

5. Aggression and Mouse-killing

Olfactory bulb function is also apparently involved in the display of aggressive behavior. In male mice, Ropartz (1968a, 1968b) reported less aggression to another male when odors of both mice were masked by a scent and no aggression between male mice when bilaterally bulbectomized. Male golden hamsters also showed a loss of aggression after bulbectomy (Murphy and Schneider, 1970). Murphy (1971) also found that bulbectomized hamsters show a complete loss of territorial defense and territorial discrimination. Leonard (1971) found that female golden hamsters, who typically became more aggressive during pregnan-

cy and lactation, when bulbectomized became less aggressive during these periods. However, as mentioned before, they frequently destroy their entire litters soon after delivery.

Rowe and Edwards (1971) demonstrated that bilateral removal of the olfactory bulbs of castrated male mice completely prevented the arousal of aggressiveness by exogenous administration of androgen. They concluded that earlier demonstrations of the abolition of inter-male aggressive behavior in mice following olfactory bulbectomy could not be attributed to impairment of pituitary-gonadal function. Although in this experiment, bulbectomy completely prevented the androgenic arousal of inter-male aggression, bulbectomy did not affect the display of aggressive behavior in a competition-for-food situation.

Relatively recent experiments have confirmed the importance of the olfactory system in mouse-killing behavior in the rat. Didiergeorges, Vergnes, and Karli (1966) reported that although only 10 to 20% of normal rats will kill mice, all of their male and female rats, bilaterally bulbectomized at five months, killed mice. However, when the fibers of the anterior pole of the olfactory bulbs were sectioned, only one animal became a mouse killer. Hull (1972) has reported similar results in rats after applying zinc sulfate to the olfactory mucosa. She found almost no incidence of mouse-killing after the zinc sulfate treatment whereas she did find an increase after olfactory bulbectomy. Further experiments (Didiergeorges, Vergnes, and Kali, 1968) showed that it took more imipramine (a mild tranqualizer) to depress mouse-killing in rats who were killers due to bulbectomies than it did in rats who were mouse killers. The authors suggested that

the olfactory afferents have a depressant action on the activity of the amygdala.

The discrepancies among the results of rat, mouse and hamster experiments may be due to the difference in species or due to the difference in measures of aggressive behavior. They may also be due to the length of time intervals between surgery and behavioral tests. In any case, a relationship of olfactory bulb function to aggressive behavior is apparent in all of these studies.

6. Exploratory Behavior

French investigators (Vernet-Maury and Chanel, 1967; Vernet-Maury, Le Magnen, and Chanel, 1968) conducted an experiment with rats to determine the effects of odors from a natural predator (fox), an indifferent animal (lion), another rat, and deodorized air. When exposed to odors from a fox, the rat tended to spend more time in the start box and explored an open field less than when exposed to odors from a lion. The rat also spent less time in the start box and more time exploring when exposed to odors from another rat than if exposed to deodorized air.

It has been observed that,in an open-field situation, both male and female rats spend more time on the side where females were previously placed (Satinder, 1969). Klein and Brown (1969) found that anosmic rats never followed the same path as other rats between sessions in an open-field maze.

7. "Fear" Response

Halliday (1966) suggested that fear may play an important role

in exploratory behavior which may also be due to different odors. The following experiments illustrate that animals emit a differential odor in "fear" situations to which other animals of the same species respond discriminatively. The odor of male mice who had been made the victors of a controlled agonistic encounter was preferred by other mice over the odor of victims of similar encounters (Carr, Martorano, and Kramer, 1970). Furthermore, this preference was shown for odors of mice who had been isolated over the odors of victims indicating that the change in odor was due to the stress which the animal received. Further support was demonstrated by the preference for the odor of unshocked mice over that of shocked mice. House mice avoided the odors from animals exposed to stressors such as blowing or shaking but approached odors from unstressed animals in a choice situation (Mueller-Velton, 1966). This avoidance response appeared to be species-specific since house mice neither avoided nor were attracted by odors from stressed field mice or stressed deermice.

Morrison and Ludvigson (1970) found that after receiving reward and nonreward, rats excreted differential odors perceptible to other rats. Valenta and Rigby (1968) determined that rats on a schedule of conditioned suppression could differentiate between the odors from a rat which had been shocked and an undisturbed rat.

8. "Nonolfactory" Behaviors

Thus far we have been discussing the olfactory system in relation to behaviors that are mediated by olfactory stimuli such as food odors or pheromones. In many of the investigations animals were made

totally anosmic by bilateral olfactory bulbectomy or the olfactory sensitivity of the animals was decreased by damaging part of the olfactory system. It is important to keep in mind that the above-mentioned procedures may affect other behaviors that ordinarily are not thought to be dependent upon the sense of smell. From lesion and ablation studies, extra-olfactory functions of the bulbs appear to be well-established. Zinc sulfate studies have also indicated that some behaviors such as mouse-killing in rats and pup-killing by virgin, female rats are probably "non-olfactory" because they do not occur as nearly as often when there is merely a loss of olfactory sensation (as with the zinc sulfate treatment) as when the olfactory bulbs are removed.

Recent evidence from the albino rat indicates that some mechanism for the detection of radiation is dependent upon an intact olfactory system. Hall, Garcia, Buchwald, Dubrowsky, and Feder (1965) found that X-ray exposure which produced a prompt arousal in control animals had little effect on rats without olfactory bulbs. Cooper (1968) found that electrical impulses from the olfactory bulb of the rat were a linear function of the logarithm of the radiation dose rate which suggests that responses of the olfactory system to X-ray originate at the olfactory receptors.

Another "nonolfactory" effect of olfactory bulbectomy is interference with visual discrimination which Phillips (1970) found in rats. He attributes his findings to a reduction in "arousal" probably mediated by loss of input to the limbic system and suggest that ablation of the olfactory bulbs or transection of the olfactory nerve produces an

organism which reacts slowly and orients poorly.

This interpretation leads us into a discussion of what is perhaps the most widely studied extra-olfactory function of the olfactory bulb—emotional behavior. The hypothesis that the bulbs may mediate emotional behavior is derived from the Papez theory relating emotion to the rhinencephalon (Papez, 1937). The olfactory bulbs were not specifically cited by Papez as part of this system; nevertheless, as mentioned in the previous section,the olfactory system has anatomical connections with many of the structures of the limbic lobe complex.

As early as 1903, Watson observed that rats with olfactory bulb lesions were highly irritable. More recent investigations have found that bilaterally bulbectomized rats are hyperemotional (Kumadaki, Hitomi, and Kumada, 1967) and extremely vicious (Douglas, Isaacson, and Moss, 1969) in comparison with unilaterally bulbectomized rats. Using defecation as a measure of emotionality, Dunn and Kaplan and Tobach (unpublished) found that removal of olfactory bulbs results in an increase of defecation in the standard open-field situation.

It has been suggested that the olfactory bulb has a depressant function on hypothalamic activity associated with emotional states. Lesions in the amygdaloid region restore emotionality to bulbectomized rats, indicating that the amygdaloid region may facilitate hyperemotionality (Kumadaki et al., 1967).

Ventis (1966) found that spontaneous activity in the open field was increased significantly in bulbectomized rats. However, the fact that bulbectomized animals were not hyperactive in an activity wheel

is an indication that they were not made indiscriminately hyperactive by the operation. These results fit in with the above-mentioned studies that olfactory bulbectomy results in hyperemotionality. However, some of Ventis' other results seem to be contradictory to the general consensus. He found that both bulbectomized and smell-deprived animals were less reactive to stimuli such as tail pinching than control animals. The operates were also less vocal than the other groups. Some contradictory evidence has also been reported by Thorne and Linder (1971). Using measures such as response to pencil tap on flank, ease of capture from home cage, amount of vocalization, and amount of urination and defecation in the open field, they found no change in emotionality of rats following bulbectomy. Possible explanations for the contradictory results are the use of different strains of rats, the different testing procedures applied, the different number of measures used in each study, and the extent of removal of olfactory bulb tissue.

D. Rationale and Purpose.

Olfaction is especially important in the early development of an altricial mammal, such as a rat pup, because it, along with other proximal sensory systems, is functional at or within one to three days after birth (Angulo y Gonzales, 1932; Hogg and Bryant, 1969; Bolles and Woods, 1964; Rouger, et al., 1967; Marr and Lilliston, 1969; Salas, et al., 1970). The distal sensory systems of audition and vision do not appear to be functional until 10 days of age (Wada, 1923) and 10 to 12 days of age (Crozier and Pincus, 1937; Detwiler, 1932; and

Rose, 1968) respectively; and they are not fully functional until 12 days of age, when the external auditory meatus opens, and 15 days of age, when the eyes open (Gottlieb, 1971). It is by means of olfaction, along with gustation and thermal and tactile reception, that a neonatal rat pup first orients and adjusts to its environment.

The importance of olfactory bulb function in the early development of a rat pup is demonstrated by the fact that Kling(1964) found a 50% mortality rate in pups which were deprived of some aspect of rhinencephalic function from 3 to 19 days of age. More specifically Rouger et al. (1967) found that if rat pups are bilaterally bulbectomized at less than 10 days of age, they do not survive. The surgical controls in this study survived indicating that mortality was not due to effects of surgery. In pups bulbectomized at 10 days of age, the survival rate improved, and about 60% of the pups bulbectomized at 13 days of age survived to maturity.

A possible explanation for these results is that pups bulbectomized at earlier ages may not develop normal nursing behavior, whereas those bulbectomized at 10 days of age or later may do so. Removal of the olfactory bulbs could disrupt nursing behavior by affecting the orientation of the pup towards the mother because of the loss of olfaction even though one could expect that the integration of the remaining functional sensory systems would partially compensate for this loss. Removal of the olfactory bulbs could also disrupt nursing behavior by affecting gustation and the so-called "appetitive center" and "satiety center" in the lateral and medial portions

of the hypothalamus respectively. Because of the relationship between the olfactory bulbs and the limbic system, bulbectomy most probably also affects development of emotional behavior in the pup. These changes in responsiveness of the pup without olfactory bulbs might elicit changes in the behavior of the female toward this pup or toward the entire litter. The interaction of this pup with other pups might also be altered. Thus social behavior other than nursing would also be affected.

Olfactory bulbectomy would also decrease the level of early stimulation that the pup receives because of decreased input to developing limbic and hypothalamic systems and in this way might interfer with the normal development of the brain. Thompson (1967) suggests that stimulation may have an arousal function by producing an alertness that allows for neural organization to be built up via specific sensory pathways.

The general purpose of this investigation is to try to answer the question about the relative importance of the olfactory system in the development of behavior salient in an altricial, macro-osmatic animal. A part of this question can be answered by specifically studying the effect of bilateral olfactory bulbectomy on the development of nursing behavior and related behaviors in a neonatal rat pup. Related to this purpose is observing the above-mentioned behaviors in intact rat pups to determine normal developmental patterns for comparative purposes.

II. MATERIALS AND METHODS

This investigation was a cross-sectional and longitudinal study done with laboratory rat pups. It was both observational and experimental using quantified behavioral data-taking methods and surgical and histological techniques. Detailed observations of the behavior of pups assigned to different types of treatment were made in the home cage and in a special apparatus. The behavior of the nursing female was recorded during undisturbed situations designed to elicit retrieving of pups. Physiological variables such as body weight of pups, amount of milk in the stomach of the pups at autopsy, and conditions of mammary glands in the female at the conclusion of the observation were studied.

A. Subjects

The subjects were Wistar random-bred rat pups of primiparous females. A total of 17 litters was used. Each litter was culled to seven pups to keep litter conditions as similar as possible and to make observation of individual pups feasible when all were aggregated in the nest area. Male and female pups were equally represented as nearly as possible in all litters (three or four males and females in each).

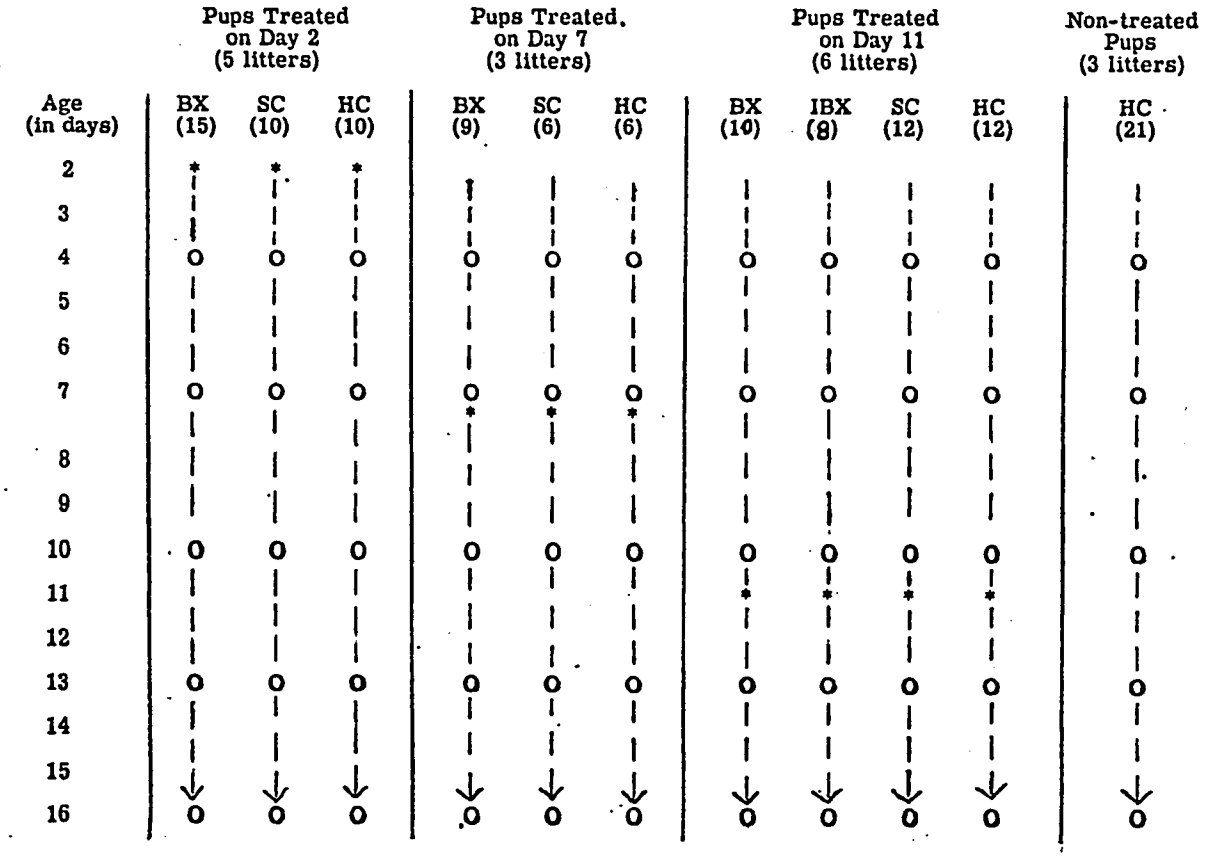
B. Experimental Design

The experimental design is summarized in Table 1. Pups were bulbectomized on one of the following days:

TABLE 1

EXPERIMENTAL DESIGN

NUMBER OF PUPS ORIGINALLY ASSIGNED TO EACH TREATMENT GROUP



BX : Bulbectomy
IBX : Incomplete Bulbectomy
SC : Surgical Control
HC : Handling Control
* : Day of Treatment
O : Age when observed in special apparatus

Arrow indicates that the same pups were observed throughout the experiment.

Day 2, Day 7, or Day 11 (counting the day of birth as Day 1). There were five litters in the group treated on Day 2, three litters in the group treated on Day 7, six litters in the group treated on Day 11, and three litters in the non-treated handling control group. All litters were culled to seven pups on Day 2.

Previous work (Rouger, Tobach, and Schneirla, 1967) had shown that most of the bulbectomized pups die within five days after treatment. As it was important to maintain the nursing level in the female so that non-surgically treated pups would be able to nurse, only three pups in each litter were bulbectomized. Also, because it was only possible to determine whether the bulbectomy had been successful upon histological analysis, the number of pups assigned to be bulbectomized was made larger than the number assigned to be surgical controls or handling controls. Thus in the groups treated on Days 2 and 7, each litter originally consisted of three bulbectomized pups, two surgical control pups, and two handling control pups. This was also the case for the first four of the six litters treated on Day 11; however, because it was found that four of the pups supposedly bulbectomized on Day 11 were inadvertently incompletely bulbectomized, four additional pups (two of the three assigned to be bulbectomized in each of the last two litters) were intentionally incompletely bulbectomized to make a total of eight incompletely bulbectomized pups. This subgroup was added to the other subgroups (bulbectomy, surgical control, handling control) of the litters treated on Day 11 to determine what effect removal of a portion of the olfactory bulbs has on the behavioral development of the pups.

In the three non-treated handling control litters, the entire litter consisted of handling controls only. The number of males and females in each subgroup was balanced as nearly as possible.

C. Apparatus

1. Home Cage

The dimensions of the home cage were as follows: width, 24"; length, 12"; and height, 12". The two sides and back of the home cage were made up of gray, acrylic panels; the front was made of transparent, acrylic panels; the top consisted of wire mesh panels. The gray panels had red marks spaced 3" apart to aid in describing the location of the pups and female. The home cage rested on a metal tray covered with sawdust. The sawdust was never changed but was periodically replenished when necessary. Each cage was located in a three-sided, gray cabinet which aided in buffering outside sounds and odors.

2. Observation Cage

The home cage of each litter was used as its observation cage with the exception of the metal tray which was replaced by a transparent, acrylic tray with no sawdust on it. The observation cage was located in a three-sided chamber with off-white walls which again aided in buffering outside sounds and odors. The observation cage was elevated on a metal stand and a mirror approximately the size of the acrylic tray was placed underneath the transparent bottom of the cage so that the pups could be observed even when under the female or under other pups.

3. Recording Apparatus

Data from the observation sessions were recorded by the experimenter on a data-taking apparatus called an ATSL (Tobach, Schneirla, Aronson, and Laupheimer, 1962). It consisted of a custom-made keyboard which had 20 keys and a built-in timer accurate to 1 sec. (for timing duration of behavioral items and duration of observation period) and of a paper-tape punch (Model 2110R, Mohawk Data Sciences Corp.). The depression of keys and time of depression were recorded on paper tape which was subsequently processed for computer analysis.

D. Procedure

1. Maintenance and Handling

Litters were born and housed in individual, identical home cages. The female was placed in the home cage at least five days before parturition, and this same home cage was used for the female and her litter throughout the experiment.

The litters were maintained on a reversed light-dark cycle (the dark portion of the cycle occurring from 7:00 AM to 7:00 PM). Since rats are more active during the dark period of the day, they were observed during their active period. A dim (30W) incandescent lumiline light bulb was situated above the top of each litter's home cage to enable the experimenter to observe the litter during the dark period. A similar dim light from a small lamp near the front of the observation cage enabled the experimenter to see the inside of the observation cage during the dark period. During the light period, in addition to the dim incandescent lights, bright fluorescent lights were

turned on in the rooms. The lack of complete darkness during the dark period was considered acceptable because Munn (1950) pointed out that the rat responds not to specific brightnesses, but to the relation between them; that is, "brighter than or darker than." Sample incident light readings taken with a Lunasix Electric Exposure Meter in the home and observation cages about 3-4" above the tray were as follows:

Light period - in the observation cage: approximately 12 ft.-c.
in the home cage: approximately 16 ft.-c.

Dark period - in the observation cage: approximately 5 ft.-c.
in the home cage: approximately 4 ft. -c.

The home cages and the observation cage were located in thermostatically-controlled rooms ($70^{o} \pm 1^{o}F$). Special attention was paid to monitoring the temperature within the observation cage. Sample temperature readings within the observation cage were taken during the course of the experiment with a telethermometer (manufactured by Yellow-Springs Instrument Company, Inc.) using surface and air thermisters. The surface temperature of the floor of the cage ranged from 71.5^{o} to 73^{o} F. The air temperature taken about 3" to 4" above the floor of the cage ranged from 71^{o} to $73.5^{o}F$.

All females were given food (Purina rat chow) and water ad lib. Whenever a litter was being weighed, marked, or surgically treated, the female was taken out of the home cage with an opaque cup and placed in a wire-mesh holding cage with sawdust on the bottom and food and water ad lib. Each female had the same holding cage throughout the course of the experiment. The sawdust in the cage was never

changed but was periodically replenished when necessary.

2. Group Assignment, Marking, and Weighing

On Day 2, pups were sexed and marked a particular color (red, orange, yellow, green, blue, olive, or violet). The pups were taken at random from different areas of the nest. This procedure was used because individual differences in growth, development and temperament may be related to the location of pups in the litter or cage thus making some pups more accessible for removal from the cage than others. In adult rats, it has been noted that the more emotional animals are likely to be found at the back of the cage rather than at the front (Maier, 1939).

After removing each pup from the home cage, it was randomly placed in a labelled, white plastic cup (3" in diameter). The color of the pup was assigned according to the label of the cup. The assignment of pups to particular treatment groups (bulbectomy, surgical control, handling control) was pre-determined by counter-balanced Latin Square sequences of colors and treatments.

The sex of the pups was determined during the group assignment procedure. If five males or females were found out of the seven pups randomly chosen from the litter, the fifth male or female would be replaced with the first pup of the opposite sex picked randomly from those remaining in the home cage.

In addition to being marked on Day 2, each pup was repeatedly marked, beginning with Day 3, every three days in conjunction with transferring the litter from the home cage to the observation cage

(Days 3, 6, 9, 12 and 15).

Food-grade dyes were used to insure against any toxic effects upon either the pups or the females. The dye was spread with a cotton swab on the pup's entire body with the exception of the head and the ano-genital area. The pup was then placed under an incandescent (60W) lamp (about 12" from the pup) until the dye dried (for approximately 2 hours).

All pups were weighed when they were marked on Day 2, when they were transferred from the home cage to the observation cage (Days 3, 6, 9, 12, and 15) and when they were transferred from the observation cage to the home cage (Days 4, 7, 10, 13 and 16). The pups were weighed on an Ohaus scale, accurate to one-tenth of a gram, in their respective white plastic cups which had been tared.

3. Surgery

Complete bilateral olfactory bulbectomy was performed in the late afternoon on pups at one of the following ages: Day 2, Day 7, or Day 11. For anesthesia, the pup was placed in chipped ice until it stopped moving. A transverse incision was made in the skin overlying the frontal bone at the level of the superior orbital margins. The skin was reflected; two adjacent openings were made in the frontal bone with a sharp, pointed scalpel; and the olfactory bulbs were exposed. The bulbs were aspirated with a glass pipette. The incision was closed by pushing the two ends of skin together. Sulfa pow der was sprinkled on the incision to help seal it and also to help combat infection. The pup was held in the experimenter's hand until it

started squirming and moving its appendages. At that time it was placed in its white plastic cup and put under an incandescent (60W) lamp (about 12" from the pup) for approximately 2 hours. It was then returned to the home cage and sprinkled with a little home-cage sawdust. The female was returned to the home cage 15 minutes later.

The procedure for an incomplete bulbectomy was identical to that described above except that bulbs were not aspirated entirely. The surgical control procedure also was identical to that described above except that the bulbs were not aspirated at all. The handling controls in the treated litters simply had sulfa powder sprinkled on their heads and were placed immediately in their white plastic cups under the lamp. From that point on, their handling procedure was the same as the bulbectomized and surgical control pups. The handling controls in the non-treated litters were not subjected to any part of the surgical procedure.

4. Autopsy

Autopsies were done on pups on Day 16 or at the time of imminent death, whichever occurred first. The stomach of each pup was checked for presence of milk. The amount of milk in the stomach was rated on a five-point scale as follows:

4 - full stomach

3 - between 2 and 4

2 - 1/2 full stomach

1 - between 0 and 2

0 - empty stomach

The sex of the pup was verified by inspecting the gonads. The lactating females were also killed on Day 16 and the nipples and mammary glands were inspected for state of activity.

5. Histology

The brains of all of the surgically treated pups and the brains of a few non-treated pups were prepared for histological analysis using an *in situ* method developed by Tucker and Shapiro (1971). At autopsy, the head of each pup was removed and the mandible, anterior portion of the snout, and fur (if any) were cut off and discarded. The head with the brain *in situ* was then fixed in 10% formalin, decalcified in a nitric acidphloroglucin solution, dehydrated, cleared in xylene, and paraffin-embedded. Specimens were serially cut in cross-section at 10μm thickness. Every tenth section was mounted on an albuminized glass slide and stained with gallocyanin.

Beginning at the nasal area where the olfactory nerves originate and proceeding caudally toward the frontal cortex, serial sections of the specimens were independently examined at X40 by three examiners to determine the extent of bulbectomy. The absence of organized bulb tissue in any section anterior to the first section where frontal cortex tissue appeared indicated a complete bulbectomy.

6. Behavioral Observations and Tests

Repeated observations were made of each female and her litter when the pups were 4, 7, 10, 13 and 16 days of age. On each of the five observation days there were two observation sessions, one in the first half of the dark cycle and one in the second half of the dark

cycle. Each session included a complete nursing period.

In addition to the data obtained from these observation sessions, whenever a litter was being transferred from one cage to another, auxiliary data were obtained from pup placement tests and retrieving tests. Home cage drawings showing location and type of nest arrangement and location and orientation of pups and female were made twice during the morning and twice during the afternoon. Drawings of the location and orientation of the female and pups in the observation cage were made before and after each nursing period observation.

a. Observation Sessions in Observation Cage

The litter and female were placed in the observation cage the night before the observation so that they spent at least 12 hours in the observation cage before the observation session began. Each pup was observed individually for three minutes at a time at the beginning, middle, and end period of each session making a total of nine minutes during the morning session and nine minutes during the afternoon session. A counter-balanced Latin Square design was used to determine the sequence in which pups of each litter were observed.

The frequency and duration of the following behavioral items were recorded.

(1) Pup to Female

Suckling: pup attached to nipple with rhythmic movement of pup's abdomen.

Nosing female: pup's nose in contact with and moving on female's body.

Switching to anterior nipple: pup moving from one nipple to more anterior one, either on same or opposite side.

Switching to posterior nipple: pup moving from one nipple to more posterior one, either on same or opposite side.

Switching to lateral nipple: pup moving from one nipple to another one on the opposite side at the same level.

(2) Pup Alone

Locomoting: pup moving from one location to another (excludes rolling or being pushed to a different location).

Activity apart from others: pup moving without changing location and without being in contact with the female or other pups.

Self-grooming: pup's nose, mouth, or limbs moving over other parts of its body.

Twitching: very rapid spasms in pup's body.

Nosing substrate: pup's nose in contact with and moving on substrate.

(3) Pup with Other Pups

Weaving in clump: pup moving and changing its location within a heap of pups.

Active in clump: pup moving in a heap of pups without changing its location.

Nosing other pups: pup's nose in contact with and moving on the body of another pup.

(4) Female to Pup

Licking pup: female's tongue in contact with and moving over pup's body. The following areas of the pup's body were differentiated: ano-genital, head, and any other part of the body.

Picking up pup: female picking pup up in jaws from substrate or out of heap of pups.

Carrying pup: female locomoting with pup between her jaws.

Nosing pup: female's nose in contact with and moving on pup's body.

b. Pup-placement Tests

Pup-placement tests were carried out in both the home cage and the observation cage. They occurred whenever a litter was being transferred from the home cage to the observation cage or vice versa. Pups were placed in various locations around the wall of the cage, each pup being placed in each location at least once throughout the entire experiment. Locations were defined in relation to the nest corner. The pups were placed in their locations one at a time. The time each pup was placed in its assigned location was noted, and the location of each pup already in the cage was also recorded. The data from this test were used as measures of activity of the pups and of movement of the pups in relation to litter-mates and (when done in the home cage)

in relation to the nest.

c. Retrieving Tests

The retrieving tests were also carried out in both the observation cage and the home cage whenever the litter was being transferred from one to another. These tests occurred immediately after the pup placement tests. At this time the female was placed in the center of the cage and retrieving behavior was recorded for 10 minutes. Whenever the female picked up a pup, the identification of the pup, the locations in the cage where it was picked up and put down, and the time were recorded. Other behavior patterns of the female were also observed. In each 30 second interval, the following activities of the female were recorded.

Rising: changing from a quadruped to a biped position with forelimbs raised.

Climbing: locomoting (movement of all four legs resulting in a change of location) on a vertical wall.

Chasing tail: circular movement of body with head facing the tail.

Digging: alternate movement of forepaws on substrate towards the body.

Self-grooming: nose, mouth, tongue, or limbs moving over other parts of the body.

d. Cage Drawings

Cage drawings were made during the dark period before and after the morning observation (first half of dark cycle) and before and after the afternoon observation (second half of dark cycle). All litters had the same number of cage drawings done during each day. The following items were checked: 1) nest location, 2) identification and number of pups in the nest, 3) identification, number, and location of pups out of the nest, and 4) location of the female.

E. Data Analysis

All non-parametric tests used in the data analysis were conducted according to Siegel (1956). The analyses of variance were performed according to Winer (1962).

1. Anatomical and Physiological Data

The survival data were analyzed with non-parametric statistics in terms of number of pups surviving and actual number of days survived. Litter differences in number of pups surviving and litter and treatment differences in actual number of days survived were evaluated with Kruskal-Wallis one-way analyses of variance. If significance was indicated in any of these analyses, the Mann-Whitney U test was employed to determine which two groups were significantly different from each other. The Fisher exact probability test was used to determine whether or not there were treatment differences in number of pups that survived. To evaluate pup body-weight data, simple one-way analyses of variance were used.

2. Data from Observation Sessions in Observation Cage

The data obtained from the observation sessions in the observation cage were analyzed cross-sectionally and longtitudinally. For the cross-sectional comparison, one-way analyses of variance were performed comparing all thirteen treatment groups for each of the nineteen behavioral items on each of the five observation days. In addition, one-way analyses of variance for repeated measures were done on the data for longitudinal comparisons. For each treatment group and for each behavioral item, data obtained on the five days of observations were compared. Since this was a repeated-measures design, only pups within each treatment group which survived through Day 16 could be used. Whenever an analysis of variance indicated an over-all significance, the Newman-Keuls method was used for making post-hoc comparisons to evaluate exactly which treatment groups were significantly different from each other.

3. Auxiliary Data

The data obtained from the cage drawings, the pup-placement tests, and the retrieving tests were analyzed using nonparametric methods. When the number of subjects in each group was equal, Friedman two-way analyses of variance were employed and, if significant, were followed by the Wilcoxen matched-pairs signed ranks test to determine which groups were significantly different from one another. If the number of subjects in each group was not equal, Kruskal-Wallis one-way analyses of variance were done and, if significant, were followed by the Mann-Whitney U test for two-sample comparisons. The

details about the application of these nonparametric tests are discussed in the Results.

III. RESULTS

In this section the anatomical and physiological data obtained are presented first, followed by the behavioral data. The interpretation of these findings as well as some of their interrelationships will be considered in the Discussion.

A. Anatomical and Physiological Data.

1. Survival

The survival results of this experiment are similar to the survival statistics from previous work (Rouger, Tobach, and Schneirla, 1967; Kling, 1964). (See Table 2) Using survival through Day 16 as a criterion, a Kruskal-Wallis one-way analysis of variance on number of pups that survived indicated no significant differences among the three main groups of treated litters (litters treated on Day 2, litters treated on Day 7, and litters treated on Day 11). However, there were treatment differences within each of these three main groups. Fisher exact probability tests revealed that a greater proportion of surgical control (SC) pups, handling control (HC) pups, and incompletely bulbectomized (IBX) pups survived through Day 16 than bulbectomized (BX) pups. (See Table 3.)

In addition to comparisons made for number of pups surviving, comparisons were also made for actual number of days of survival. Kruskal-Wallis analyses of variance indicated that there were no litter differences, within the three main groups of treated litters, in actual

TABLE 2

NUMBER OF PUPS SURVIVING THROUGH EACH DAY

Age (in days)	Pups Treated on Day 2 (5 litters)			Pups Treated on Day 7 (3 litters)			Pups Treated on Day 11 (6 litters)				Non-treated Pups (3 litters)
	BX	SC	HC	BX	SC	HC	BX	IBX	SC	HC	HC
2	10*	10*	10*	8	6	6	8	8	12	12	21
3	10	10	10	8	6	6	8	8	12	12	21
4	9	10	10	8	6	6	8	8	12	12	21
5	8	10	10	8	6	6	8	8	12	12	21
6	2	10	10	8	6	6	8	8	12	12	21
7	2	10	10	8*	6*	6*	8	8	12	12	21
8	2	10	10	8	6	6	8	8	12	12	21
9	2	10	10	8	6	6	8	8	12	12	21
10	2	10	10	7	6	6	8	8	12	12	21
11	2	10	10	6	6	6	8*	8*	12*	12*	21
12	2	9	10	4	6	6	8	8	12	12	21
13	2	9	10	3	6	6	8	8	12	12	21
14	2	9	10	3	6	6	8	8	12	12	21
15	2	9	10	2	6	6	6	8	12	12	21
16	2	7	10	1	6	6	1	8	12	12	21

BX : Bulbectomy
IBX : Incomplete Bulbectomy
SC : Surgical Control
HC : Handling Control
* : Day of Treatment

Number of pups shown on Day 2 in each group represents total number of subjects originally assigned to groups, except in the case of BX pups where only those satisfying histological criteria were used.

TABLE 3

PROPORTION OF PUPS THAT SURVIVED THROUGH DAY 16 IN EACH TREATMENT GROUP. RESULTS OF FISHER EXACT PROBABILITY TESTS.

	Pups Treated on Day 2		
	BX	SC	HC
Survived	2	7	10
Died	8	3	0

BX and SC, p = .05; BX and HC, p = .01, SC and HC, N.S.

	Pups Treated on Day 7		
	BX	SC	HC
Survived	1	6	6
Died	7	0	0

BX and SC, p = .01; BX and HC, p = .01, SC and HC, N.S.

	Pups Treated on Day 11			
	BX	IBX	SC	HC
Survived	1	8	12	12
Died	7	0	0	0

BX and SC, p = .005, BX and HC, p = .005; BX and IBX, p = .005
SC and HC, N.S.; SC and IBX, N.S.; HC and IBX, N.S.

N.S. Not Significant

number of days of survival but that there were treatment differences. (For litters treated on Day 2: $H = 20.29$; $df = 2$, $p < .001$. For litters treated on Day 7 : $H = 15.49$; $df = 2$, $p < .001$. For litters treated on Day 11: $H = 16.03$; $df = 2$, $p < .001$.) Mann-Whitney U tests indicated that the BX pups survived a smaller number of days than the IBX, SC, or HC pups. (See Table 4.) BX-2 pups, BX-7 pups, and BX-11 pups were also compared, using a Kruskal-Wallis one-way analysis of variance for number of days of survival after surgery. Since BX-11 pups could survive no more than five days (to Day 16), five days were used as a cut-off point for BX-2 pups and BX-7 pups when making the comparison. A significant difference was indicated ($H = 800$, d.f. = 2, $p < .02$). Mann-Whitney U tests showed that the BX-2 pups survived a significantly smaller number of days than the BX-7 pups ($U = 15$, $n_1 = 10$, $n_2 = 8$, $p < .01$) or the BX-11 pups ($U = 16.5$, $n_1 = 10$, $n_2 = 8$, $p < .05$). There were no significant differences between the BX-7 pups and BX-11 pups in regard to number of days survived.

2. Body Weight

Inspection of Tables 5 - 8 indicates that BX pups weighed less than SC pups or HC pups within one or two days after bulbectomy. The IBX pups also began to weigh less within one or two days after surgery. The last body weights of the BX pups recorded before autopsy were always lower than body weights of the control pups recorded on the same day. Table 9 lists the mean of last body weights recorded before autopsy for BX and IBX pups and the mean control weights for the same day. By Day 16 the mean body weight of the BX pups that survived

TABLE 4

NUMBER OF DAYS OF SURVIVAL AFTER TREATMENT OF BX, IBX, SC, AND HC PUPS.

RESULTS OF MANN-WHITNEY U TESTS

Pups Treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			
BX	SC	HC	BX	SC	HC	BX	IBX	SC	HC
2	9	15	3	10	10	3	6	6	6
3	12	15	4	10	10	4	6	6	6
3	12	15	5	10	10	4	6	6	6
3	15	15	5	10	10	5	6	6	6
3	15	15	5	10	10	5	6	6	6
3	15	15	8	10	10	5	6	6	6
3	15	15	9			5	6	6	6
4	15	15	10			6	6	6	6
15	15	15						6	6
15	15	15						6	6
								6	6

BX and SC: $U = 6$, $n_1 = n_2 = 10$, $p<.001$
BX and HC: $U = 0$, $n_1 = n_2 = 10$, $p<.001$
SC and HC: N.S.

BX and SC: $U = 0$, $n_1 = 9$, $n_2 = 6$, $p<.001$
BX and HC: $U = 0$, $n_1 = 9$, $n_2 = 7$, $p<.001$
SC and HC: N.S.

BX and IBX: $U = 0$, $n_1 = 8$, $n_2 = 8$, $p<.001$
BX and SC : $U = 0$, $n_1 = 8$, $n_2 = 12$, $p<.001$
BX and HC : $U = 0$, $n_1 = 8$, $n_2 = 12$, $p<.001$
IBX and SC : N.S.
IBX and HC : N.S.
SC and HC : N.S.

TABLE 5

MEAN BODY WEIGHTS (IN GRAMS) OF PUPS TREATED ON DAY 2

Age (in days)	BX Pups			SC Pups			HC Pups		
	N	X	S.D.	N	X	S.D.	N	X	S.D.
2	10	6.2	1.5	10	5.7	.8	10	5.6	.8
3	10	5.0	.8	10	6.1	.9	10	6.0	1.1
4	9	5.6	1.2	10	6.6	1.3	10	6.8	1.4
6	2	7.7	.6	10	8.5	2.0	10	9.1	2.2
7	2	8.8	.2	10	9.1	1.9	10	10.0	2.7
9	2	10.0	.5	10	11.8	3.6	10	13.4	3.5
10	2	11.2	.3	10	13.0	4.4	10	15.2	4.2
12	2	13.2	.7	9	17.0	6.6	10	19.6	5.4
13	2	13.2	1.0	9	16.4	8.9	10	21.7	5.6
15	2	16.3	.8	9	26.4	4.2	10	26.6	5.9
16	2	16.8	.1	7	28.8	4.0	10	28.9	6.2

TABLE 6

MEAN BODY WEIGHTS (IN GRAMS) OF PUPS TREATED ON DAY 7

Age (in days)	BX Pups			SC Pups			HC Pups		
	N	X	S.D.	N	X	S.D.	N	X	S.D.
2	8	6.2	.7	6	6.2	.4	6	6.1	.7
3	8	7.2	.9	6	7.4	.4	6	7.2	.8
4	8	7.8	.9	6	8.0	.4	6	7.9	1.0
6	8	10.4	1.2	6	10.8	.9	6	10.5	1.2
7	8	11.3	1.4	6	11.8	1.0	6	11.4	1.2
9	8	9.8	1.6	6	16.2	1.1	6	16.0	1.2
10	7	10.2	1.6	6	18.6	1.4	6	18.0	1.2
12	4	12.2	2.8	6	24.0	1.3	6	23.4	1.4
13	3	13.7	1.2	6	26.7	1.4	6	25.5	1.6
15	2	14.5	.3	6	31.1	1.3	6	29.9	3.0
16	1	12.5	-	6	32.8	1.0	6	31.3	2.6

TABLE 7

MEAN BODY WEIGHTS (IN GRAMS) OF PUPS TREATED ON DAY 11

Age (in days)	BX Pups			IBX Pups			SC Pups			HC Pups		
	N	X	S.D.	N	X	S.D.	N	X	S.D.	N	X	S.D.
2	8	5.7	.3	8	6.3	.7	12	5.8	.4	12	5.8	.6
3	8	6.2	.6	8	7.4	1.1	12	6.7	.8	12	6.6	1.0
4	8	7.0	.7	8	7.5	.8	10	7.2	.6	10	7.0	.7
6	8	8.9	1.2	8	10.6	1.4	12	9.4	1.3	12	9.1	1.1
7	8	10.4	.9	8	11.7	1.3	12	10.9	1.2	12	10.4	1.1
9	8	13.3	1.0	8	15.2	1.5	12	13.8	1.4	12	13.3	1.4
10	8	14.8	1.1	8	16.8	1.8	12	15.5	1.6	12	15.0	1.7
12	8	14.9	1.1	8	17.8	2.3	12	20.5	2.2	12	20.1	2.4
13	8	13.4	1.5	8	17.6	2.7	12	23.1	2.3	12	22.7	2.4
15	6	13.6	2.0	8	20.6	3.4	12	27.5	2.6	12	27.2	2.7
16	1	16.5	-	8	21.5	4.4	12	30.3	2.6	12	29.5	3.3

TABLE 8

MEAN BODY WEIGHTS (IN GRAMS) OF PUPS FROM NON-TREATED LITTERS

Age (in days)	HC Pups		
	N	X	S.D.
2	21	6.3	.8
3	21	7.6	.7
4	21	8.3	1.2
6	21	10.6	2.0
7	21	12.7	1.5
9	21	16.0	2.0
10	21	17.9	1.8
12	21	21.6	2.6
13	21	23.5	2.0
15	21	27.5	2.4
16	21	29.3	1.7

TABLE 9

MEAN OF LAST BODY WEIGHTS (IN GRAMS) RECORDED BEFORE AUTOPSY FOR BX AND IBX PUPS AND OF CONTROL LITTERMATES' BODY WEIGHTS RECORDED ON SAME DAY

Age (in days)	BX			IBX			SC			HC		
	N	X	S.D.	N	X	S.D.	N	X	S.D.	N	X	S.D.
					Pups Treated on Day 2							
3	1	4.2	-	..	..	..	2	5.8	.5	2	5.8	.4
4	7	5.0	1.0	..	..	..	14	6.8	1.0	14	6.6	1.4
16	2	16.8	.1	..	..	..	4	32.1	1.0	4	32.8	1.0
					Pups Treated on Day 7							
9	1	6.5	-	..	..	..	2	15.4	.2	2	15.0	
10	3	9.0	1.0	..	..	..	6	18.6	1.4	6	18.0	1.2
12	1	8.1	-	..	..	..	2	23.8	1.1	2	24.4	2.0
13	1	12.5	-	..	..	..	2	28.4	.8	2	25.5	1.1
15	1	14.3	-	..	..	..	2	32.2	1.4	2	32.5	2.4
16	1	12.5	-	..	..	..	2	31.7	.3	2	28.8	1.1
					Pups Treated on Day 11							
13	2	12.4	1.2	..	..	..	4	23.9	2.2	4	22.7	3.2
15	5	13.7	2.3	..	..	..	10	26.5	1.8	10	25.8	3.5
16	1	17.3	-	8	21.5	4.4	16	30.5	2.7	16	30.5	1.7

was one-half or less than the mean body weight of the controls; and, by Day 16 the mean body weight of the IBX pups (allof which survived) was about two-thirds the mean body weight of the controls, but it was about one-fourth more than the body weight of the BX pup, treated on Day 11, which survived through Day 16.

A one-way analysis of variance comparing the Day 2 body weights of the 17 litters used in the experiment was significant ($p < 0.1$). However, when the Day 2 body weights of BX pups, IBX pups, SC pups, HC pups from treated litters, and HC pups from non-treated litters were compared by means of a one-way analysis of variance, it was found that there were no significant differences. Thus even though there were differences in Day 2 body weights among the litters, the differences were randomly distributed among the treatment groups. A one-way analysis of variance comparing the Day 2 body weights of BX pups that died before the end of the experiment with the Day 2 body weights of BX pups that survived through Day 16 again indicated no significant differences. This finding contradicts the possibility that the BX pups may have died because they weighed less even before surgery and thus were at a disadvantage when compared to the BX pups that survived.

The Day 2 body weights of the male and female pups were also compared, and the males were found to be significantly heavier than the females ($p < .05$). As all groups were balanced as nearly as possible for numbers of males and females, however, this difference (though interesting in itself) should not have biased any of the results of this study.

3. Autopsy

At the time of autopsy most of the BX pups had little or no milk in their stomachs. In contrast, almost all of the SC and HC pups had milk in their stomachs (with ratings of 3 and 4). (See page 31 for rating scale.) Seven out of eight of the IBX pups also had milk in their stomachs. Table 10 shows the autopsy results for all pups.

Inspection of the mammary glands of all 17 females indicated that all were adequately developed. Milk was expressed at the time of autopsy, from at least nine nipples on all females. These results indicate that the decreased intake of milk by the BX pups was not due to inability of the female to produce milk.

4. Histology

Based on histological evaluation, the number of pups remaining in the BX and IBX groups are shown in Table 2. Of the 15 pups that were bulbectomized on Day 2, five were disqualified from the experiment because they were missing or too decomposed to permit histological analysis. Of the ten pups for which histological preparations were made, all were judged to be completely bulbectomized. There were no IBX pups in the litters treated on Day 2.

Of the nine pups that were bulbectomized on Day 7, one was found to have a large section of tissue missing in the frontal cortex. As it could not be determined whether this occurred when the brain was in formalin or whether the brain was defective before the head was removed, it was disqualified. There were no IBX pups in the litters treated on Day 7.

Of the 18 pups which originally were supposed to be bulbectomized on Day 11, four were found to be incompletely bulbectomized. An additional four were intentionally incompletely bulbectomized making a total of eight. Histological evaluation of the brains of the eight IBX pups indicated that from two to ten adjacent sections out of approximately forty-five, showed some organized (laminated) bulb tissue. This would equal about .02 to .1 mm of bulb tissue (measured in an anteroposterior direction). In a non-treated, Day 16 pup, the bulb would be about .45 mm in length. In all of the IBX pups, the sections with organized tissue were immediately anterior to the section where frontal cortex tissue first appeared. Of the remaining 10 pups, the histological results on two of the pups were ambiguous as to whether they were complete or incomplete bulbectomies and thus they were disqualified. The remaining eight pups were judged to be completely bulbectomized. Figures 1, 2, and 3 are photomicrographs of sections from the brain of a typical BX pup, IBX pup, and (for comparison) untreated pup. Six sections from each representative specimen were chosen. They approximately correspond to the following landmarks:

a) Olfactory nerves first appear.

b) Traces of bulb tissue first appear.

c) Organized bulb tissue first appears.

d) Lens of the eye first appears.

e) Immediately before frontal cortex appears.

f) Frontal cortex first appears.

TABLE 10

AMOUNT OF MILK IN STOMACH AT AUTOPSY**

Age (in days) at Autopsy	Pups Treated on Day 2			Age (in days) at Autopsy	Pups Treated on Day 7			Age (in days) at Autopsy	Pups Treated on Day 11				Age (in days) at Autopsy	Non-treated Pups
	BX	SC	HC		BX	SC	HC		BX	IBX	SC	HC		HC
4	1			10	...[a]			14	...[a]				16	4*
	1			11	0			15	0					4*
	0			12	0				0					4*
	0				...[a]			16	0	3	4	3-4		4*
5	0				0				0	3	4	4		4*
	0			15	1				4	3-4	4	4*		4*
6	0			16	0	4	4*		0	4*	4	4*		4*
	0					4	4		0	4	4*	4*		4*
11		3				3*	4			4*	4*	3*		4*
14		0				4	4			4*	4*	4*		4*
16	1*	3-4*	4*			4*	4*			0	4*	4*		4*
	3-4*	4*	4*			4	4*				4*	4*		4*
		4	4								4*	4*		4*
		4*	4								4*	4*		4*
		4*	3*								4*	4*		4*
		4*	4*											4*
		4*	4											4*
		4*	4											4*
			4*											2*
			4*											3*
														4*

** : Rating scale for amount of milk, page 31.
* : Some solid food present
a : No data - pups partially eaten

Figure 1. Photomicrographs of sections from brain of a typical bulbectomized pup (Day 9)

A: Olfactory nerves first appear

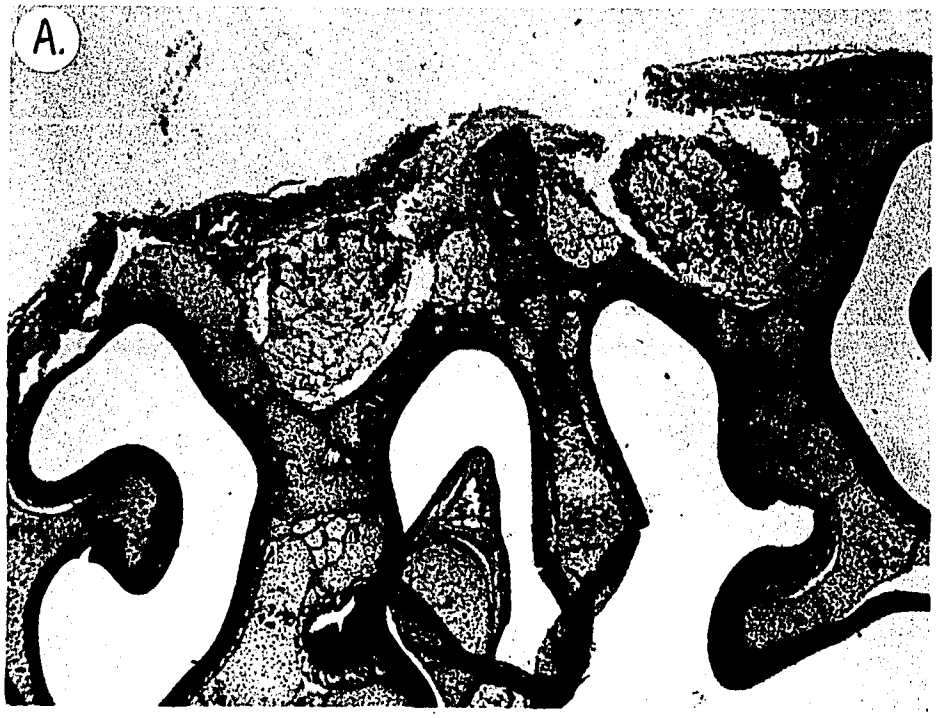
B: Traces of bulb tissue first appear

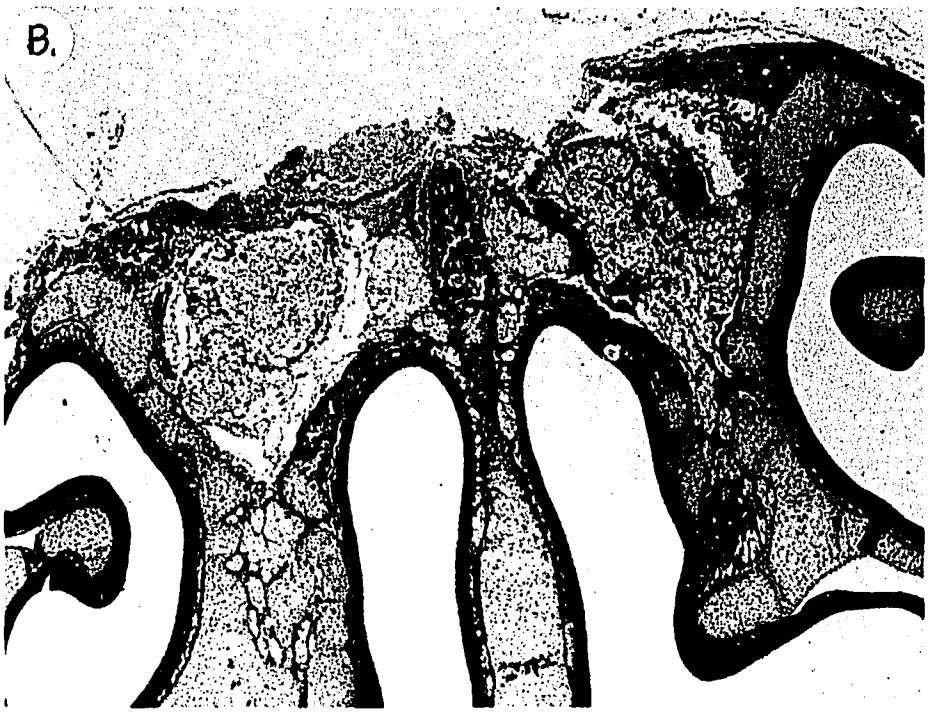
C: Organized bulb tissue first appears

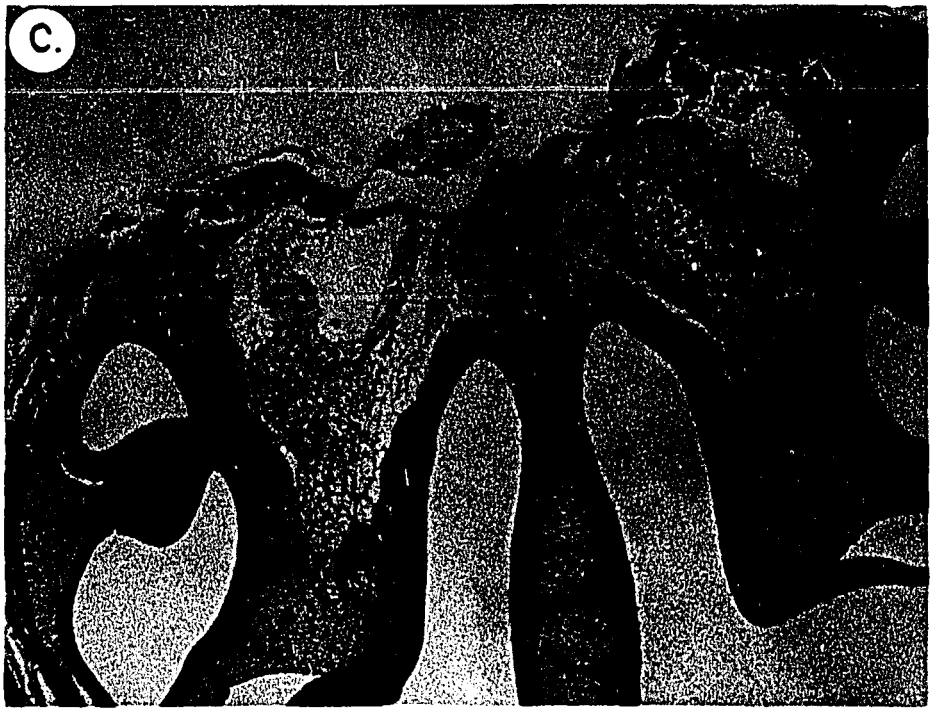
D: Lens of the eye first appears

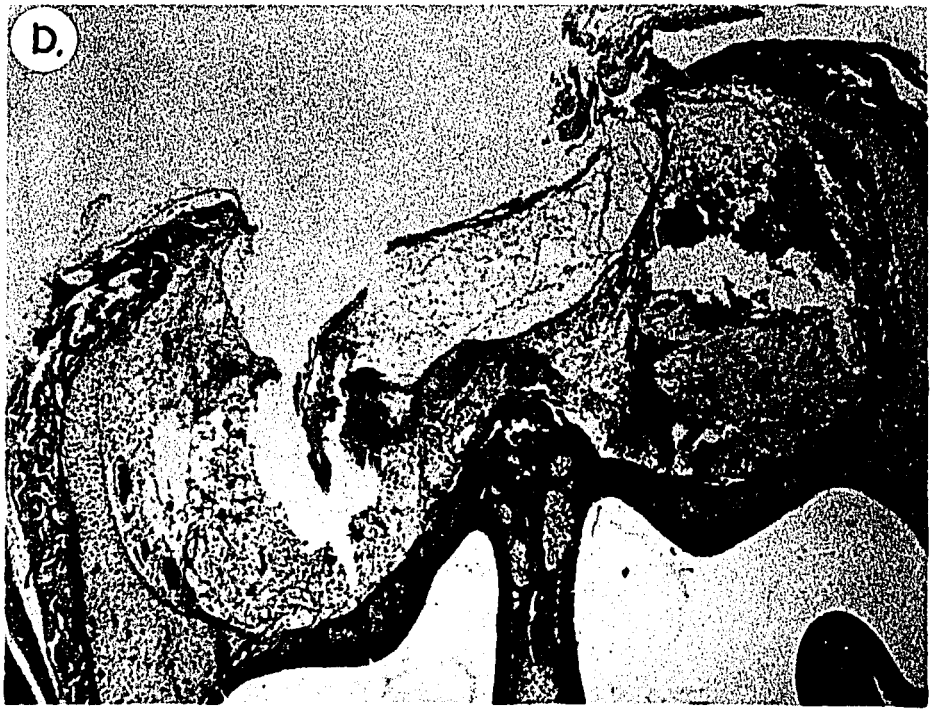
E: Immediately before frontal cortex appears

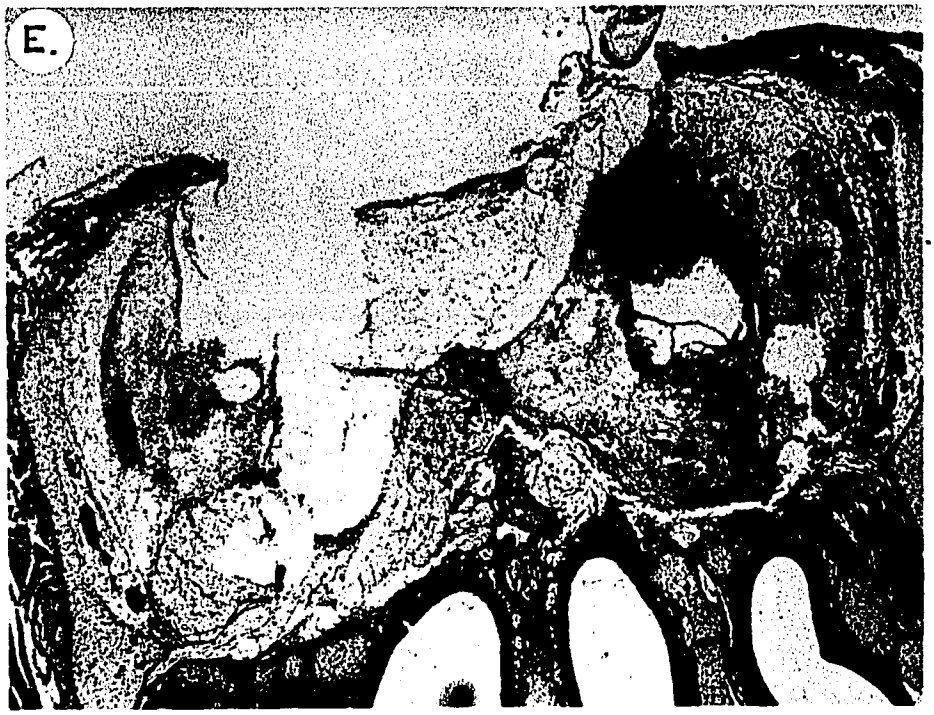
F: Frontal cortex first appears


A.


B.


C.


D.


E.

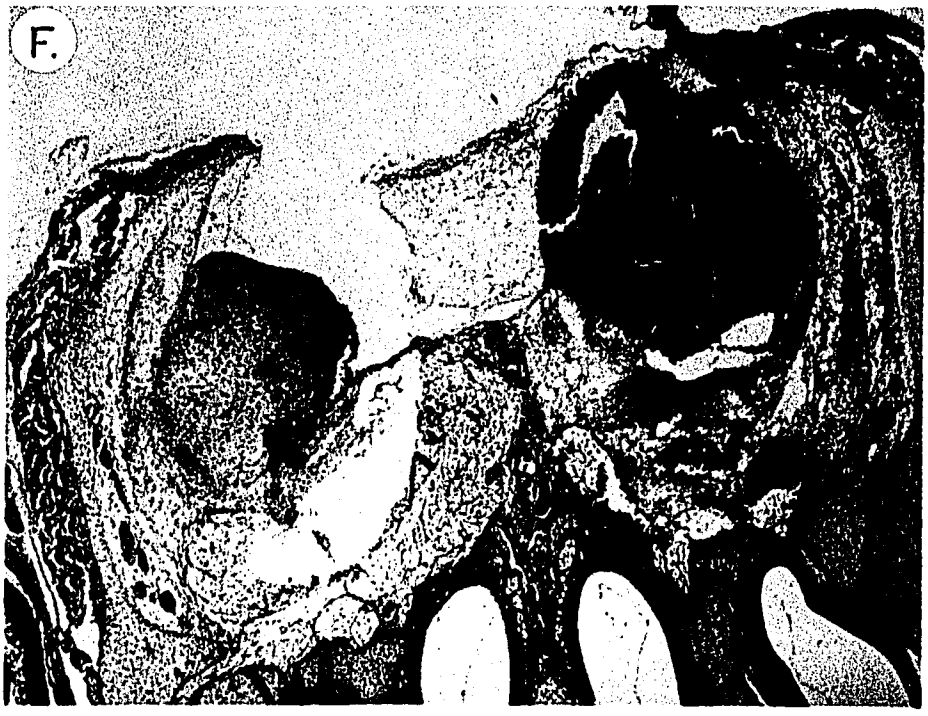

F.

Figure 2. Photomicrographs of sections from brain of a typical incompletely bulbectomized pup (Day 16)

A: Olfactory nerves first appear

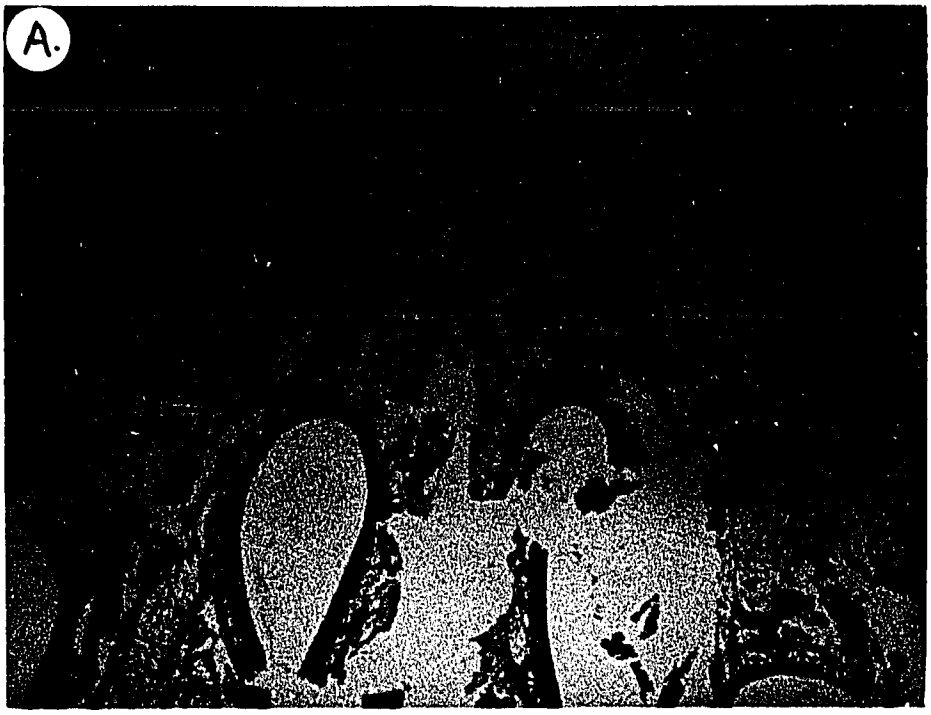
B: Traces of bulb tissue first appear

C: Organized bulb tissue first appears

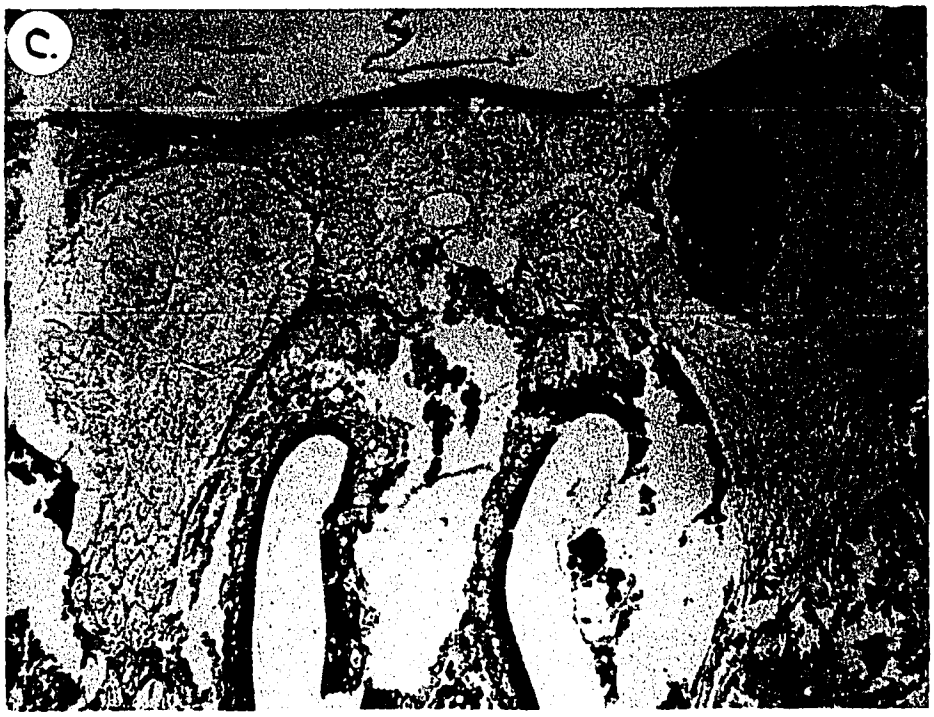
D: Lens of the eye first appears

E: Immediately before frontal cortex appears

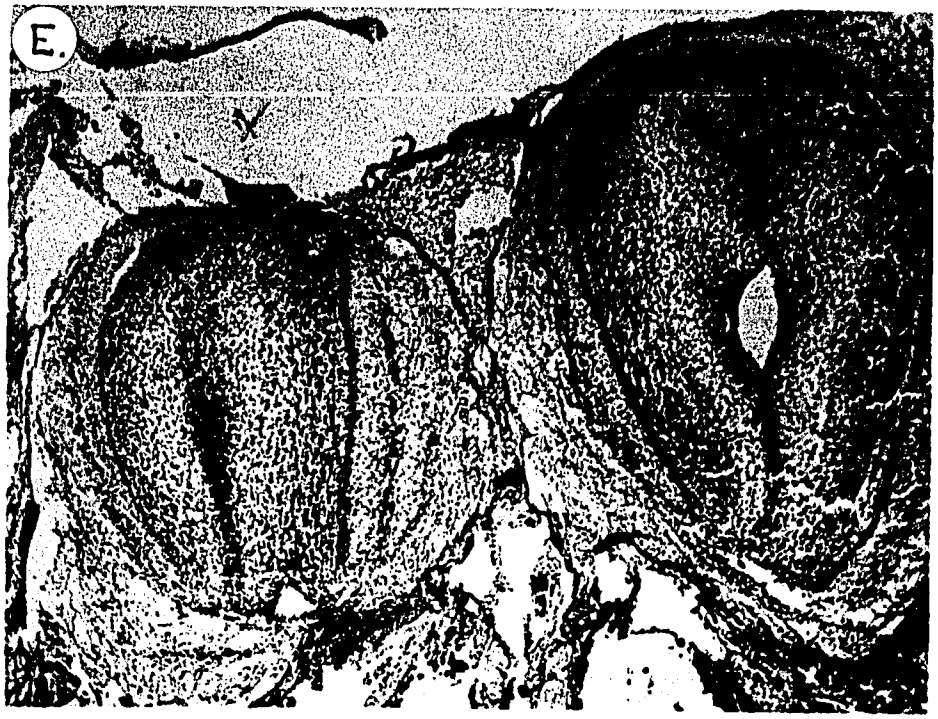
F: Frontal cortex first appears


A.


B.


C.


D.


E.


F.

Figure 3. Photomicrographs of sections from brain of a typical untreated pup (Day 8)

A: Olfactory nerves first appear

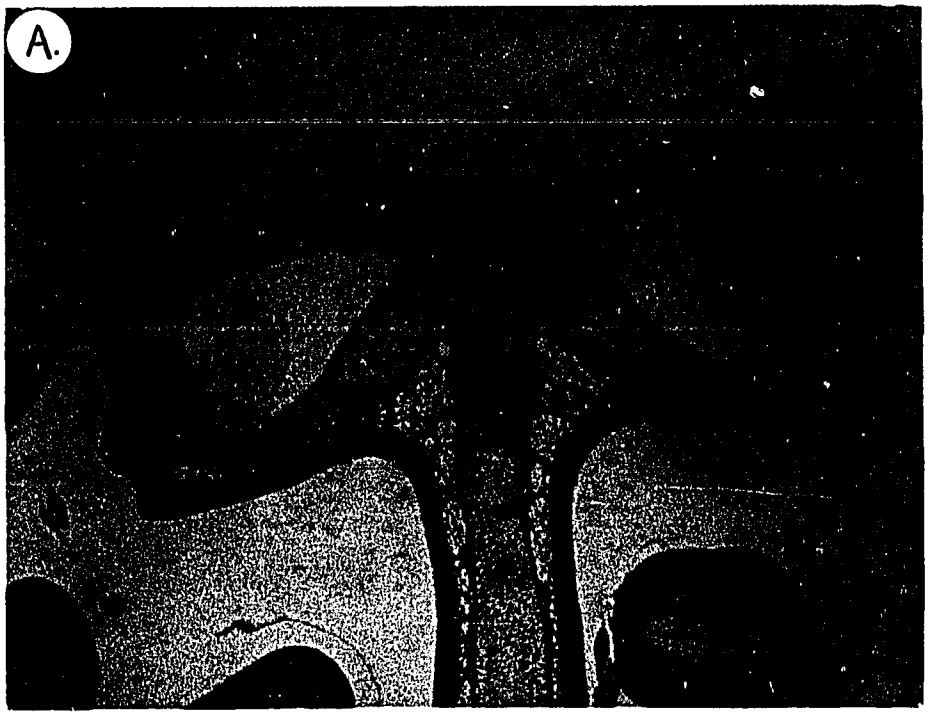
B: Traces of bulb tissue first appear

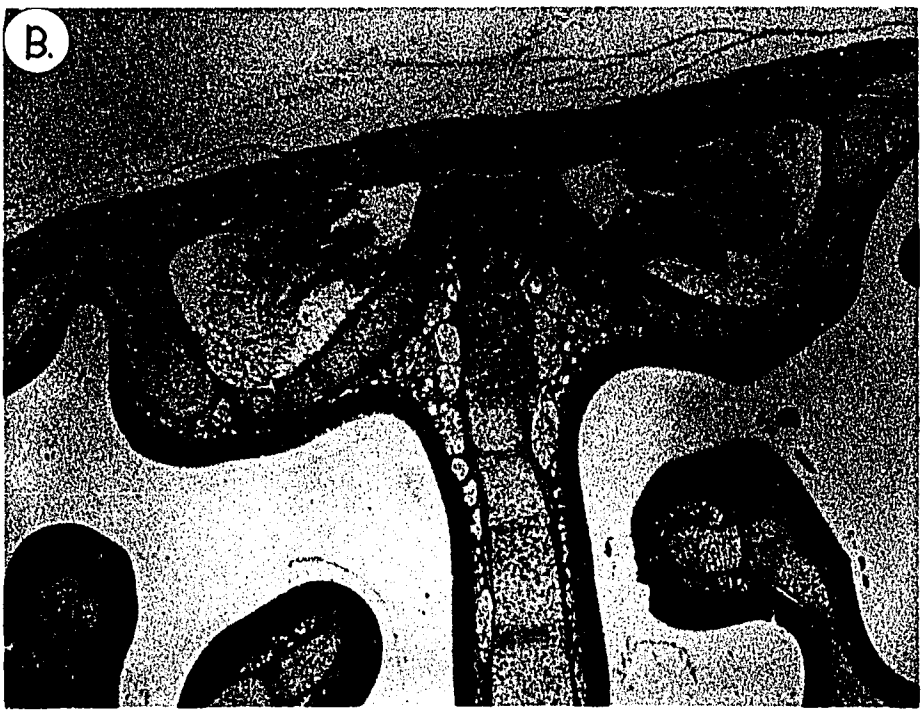
C: Organized bulb tissue first appears

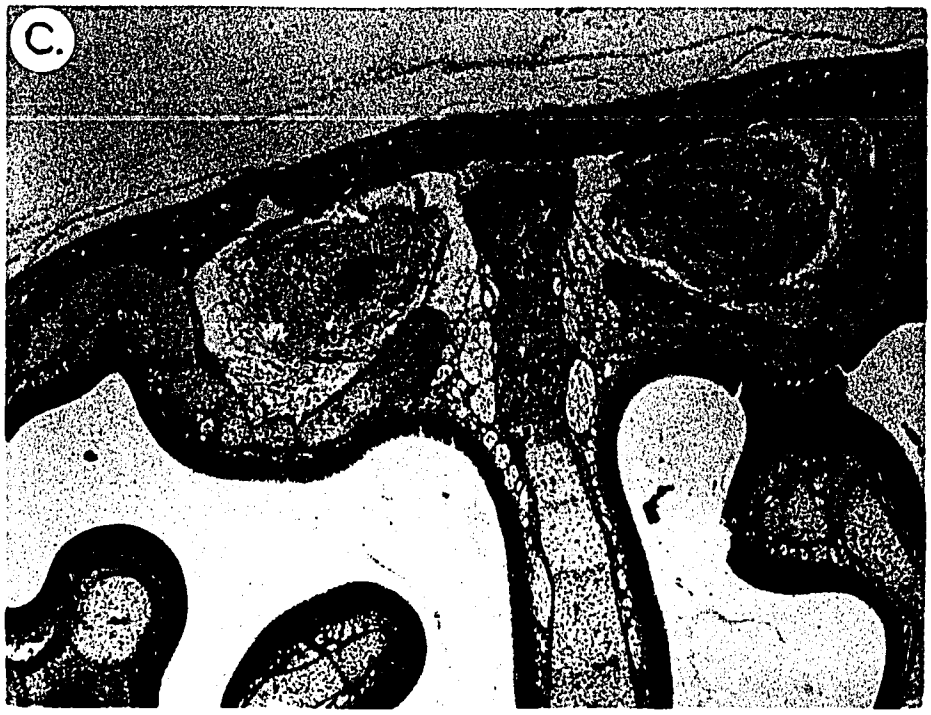
D: Lens of the eye first appears

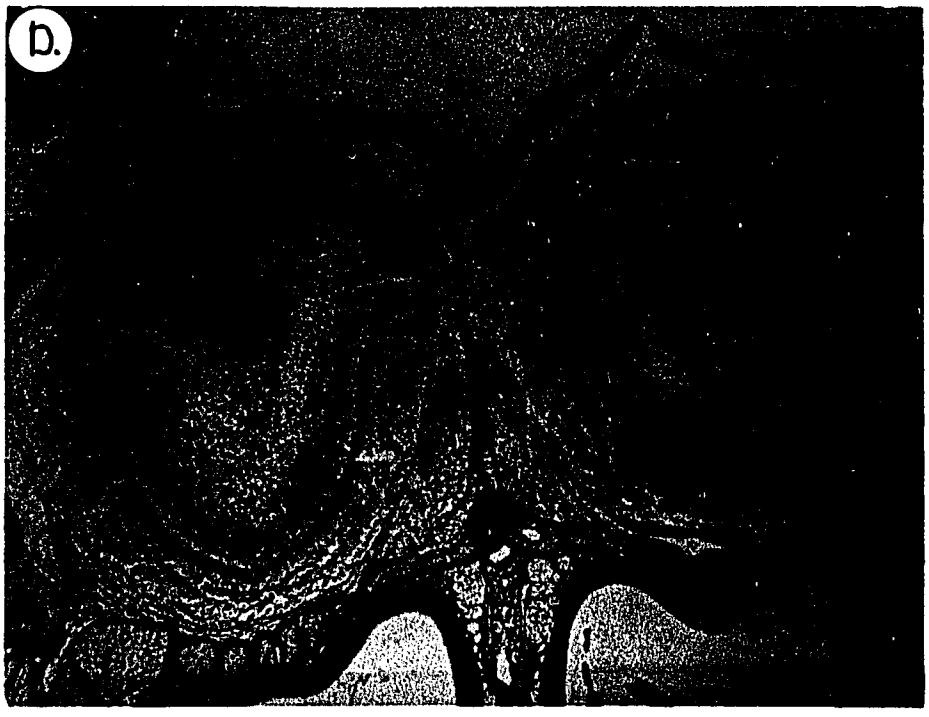
E: Immediately before frontal cortex appears

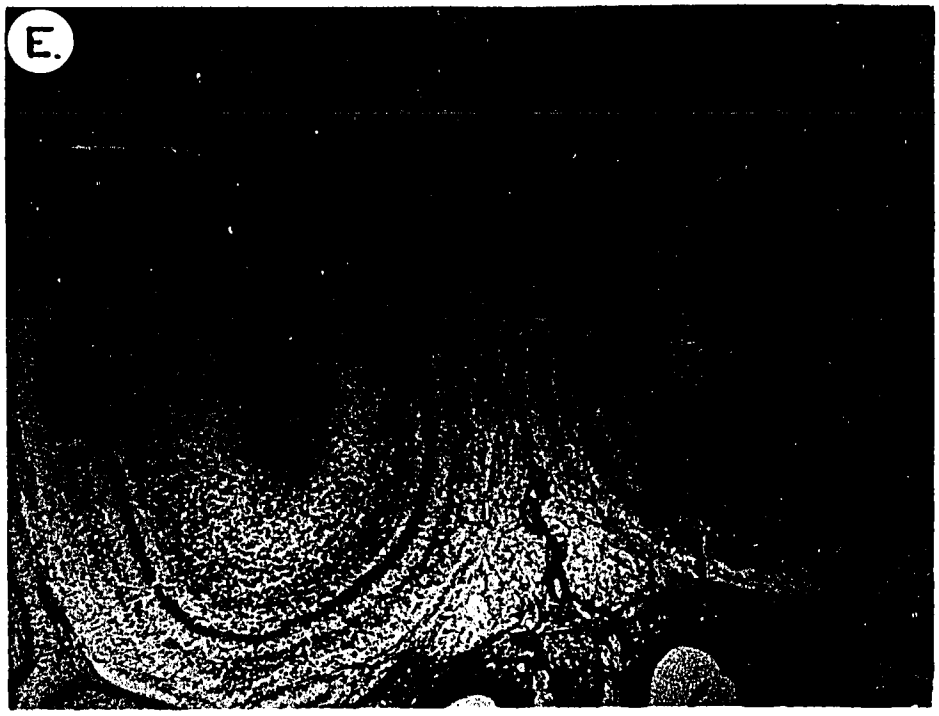
F: Frontal cortex first appears

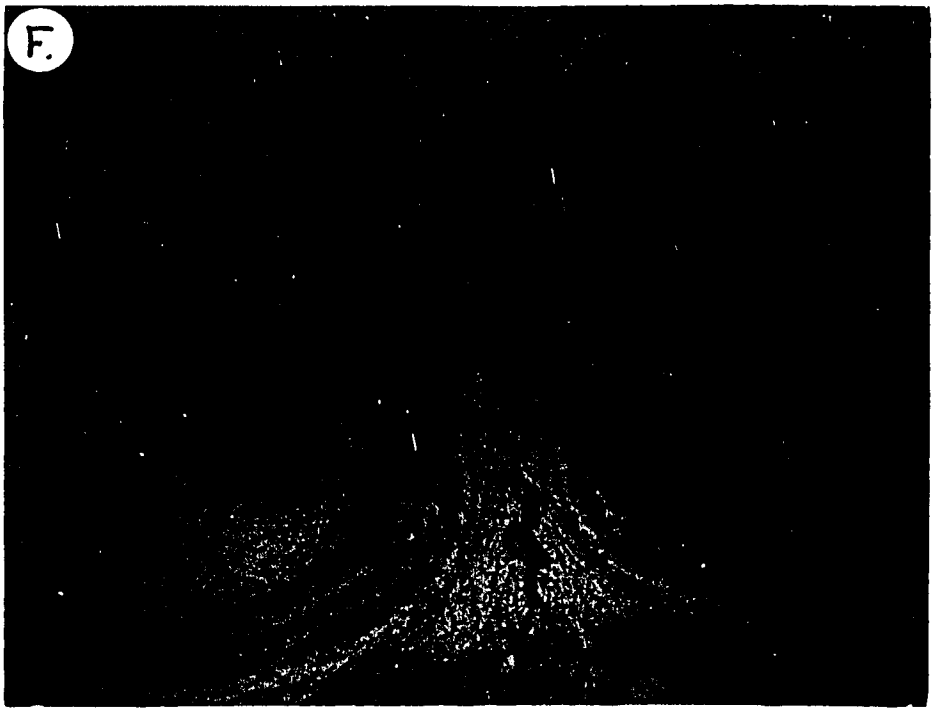

A.


B.


C.


D.


E.


F.

B. Behavioral Data

1. Cross-sectional Data from Observation Sessions in Observation Cage

Analyses of variance were done for all 19 behavioral items comparing 13 groups of pups on each of the five observation days, making a total of 1,235 separate analyses. The 19 behavioral items are listed and defined on pages 33-35. The 13 groups of pups include the 11 groups shown in Table 2 with the addition of two more groups obtained when splitting the 21 non-treated handling control pups (HC-FM) into 10 males (HC-M) and 11 females (HC-F).

Before combining the data from the morning and afternoon observation sessions, comparisons of the two were made to determine if there were any diurnal variations. These comparisons were made for each of the 19 behavioral items on each of the five observation days for each of the 13 treatment groups by using the sign test. Out of the 1,235 comparisons, eight were found in which there was a significant difference between morning and afternoon data. Of these eight, seven occurred on days when there was no significant difference among treatment groups in the particular behavioral item under consideration. Thus these differences were considered irrelevant. In the eighth comparison a difference was found in amount of time spent suckling on Day 4 for SC pups treated on Day 11 (SC-11). As these pups were not yet treated on Day 4, however, this result may have been due to chance or sampling error, because it occurred on only one day in that one particular subgroup.

Because there were no relevant significant differences between

the data from the two sessions, morning and afternoon data for all behavioral items were combined with the exception of data recorded on Day 16 for litters that were treated on Day 7 or on Day 11. In these two cases only, data from the morning session were used, because in the afternoon session only one BX pup treated on Day 7 (BX-7) and only one BX pup treated on Day 11 (BX-11) remained.

a. Pup to Female

A difference in the amount of time spent suckling was found for BX pups treated on Day 2 (BX-2). (See Figure 4. Standard deviations for all points on this graph and on all following graphs are located in Tables 1A through 5A of the Appendix.)

At four days of age they spent significantly less time suckling than did SC-2 pups, HC-2 pups, and HC pups from non-treated litters. At seven and ten days of age, although they spent less time suckling than the other controls, the difference was not statistically significant. On Day 13, however, they spent significantly less time than HC-2 pups and HC pups from non-treated litters. On Day 16 the BX-2 pups spent significantly less time suckling than the HC-2 pups. For the pups treated on Day 7, Figure 5 illustrates that although there was some variability among the treatment groups before the day of treatment, the amount of time spent suckling decreased after the day of treatment. On Days 13 and 16, BX-7 pups spent significantly less time suckling than SC-7 pups, and HC pups from non-treated litters. For pups treated on Day 11, Figure 6 indicates that the duration of suckling decreased for BX pups and was lower than all other groups on Days 13 and 16. On both of these days it was significantly lower than that of

Figure 4.

Mean Duration (Seconds) of Suckling for Pups
Treated on Day 2

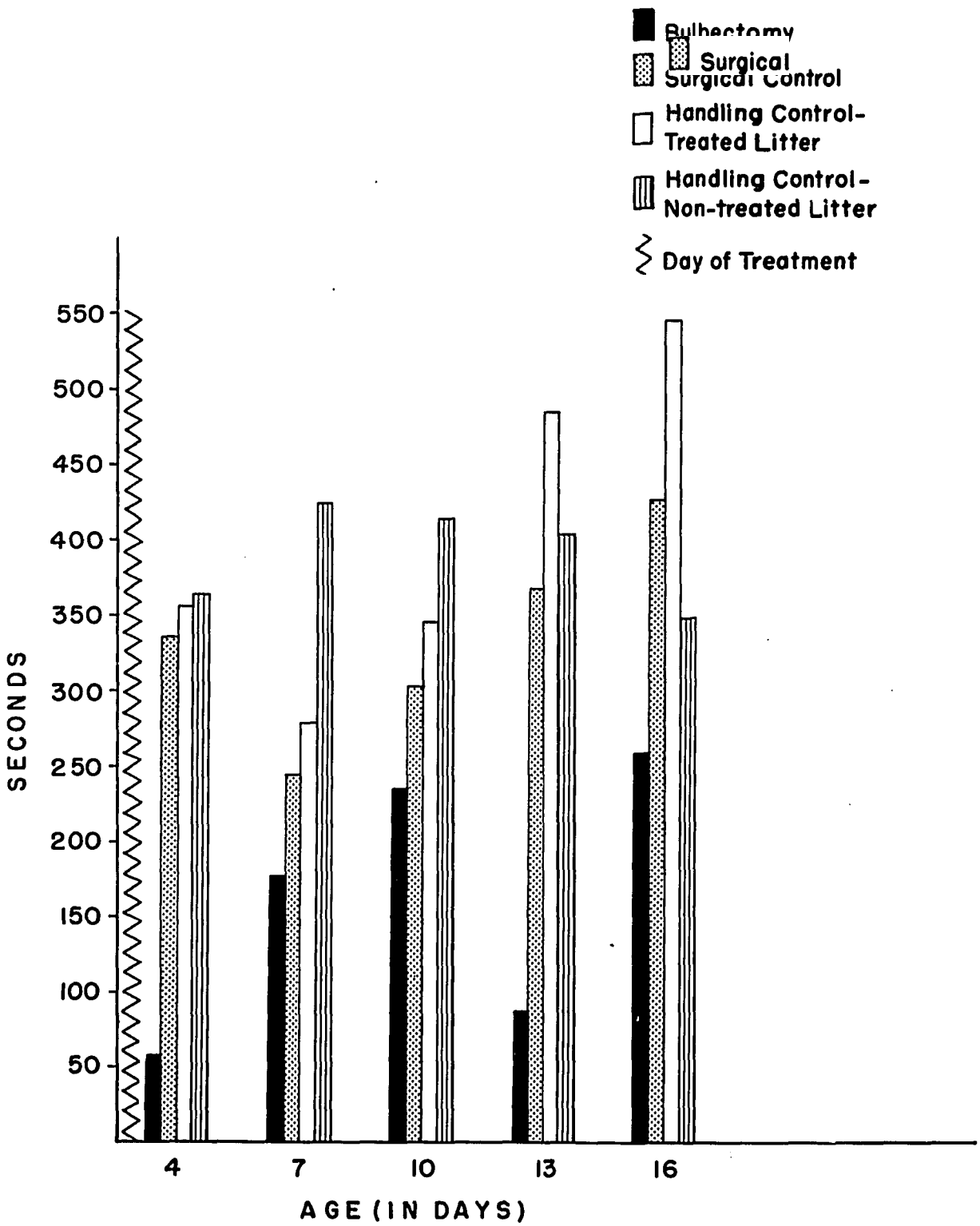

Bulbectomy
Surgical
Surgical Control
Handling Control-
Treated Litter
Handling Control-
Non-treated Litter
Day of Treatment
SECONDS
550
500
450
400
350
300
250
200
150
100
50
4
7
10
13
16
AGE (IN DAYS)

Figure 5.

Mean Duration (Seconds) of Suckling for Pups
Treated on Day 7

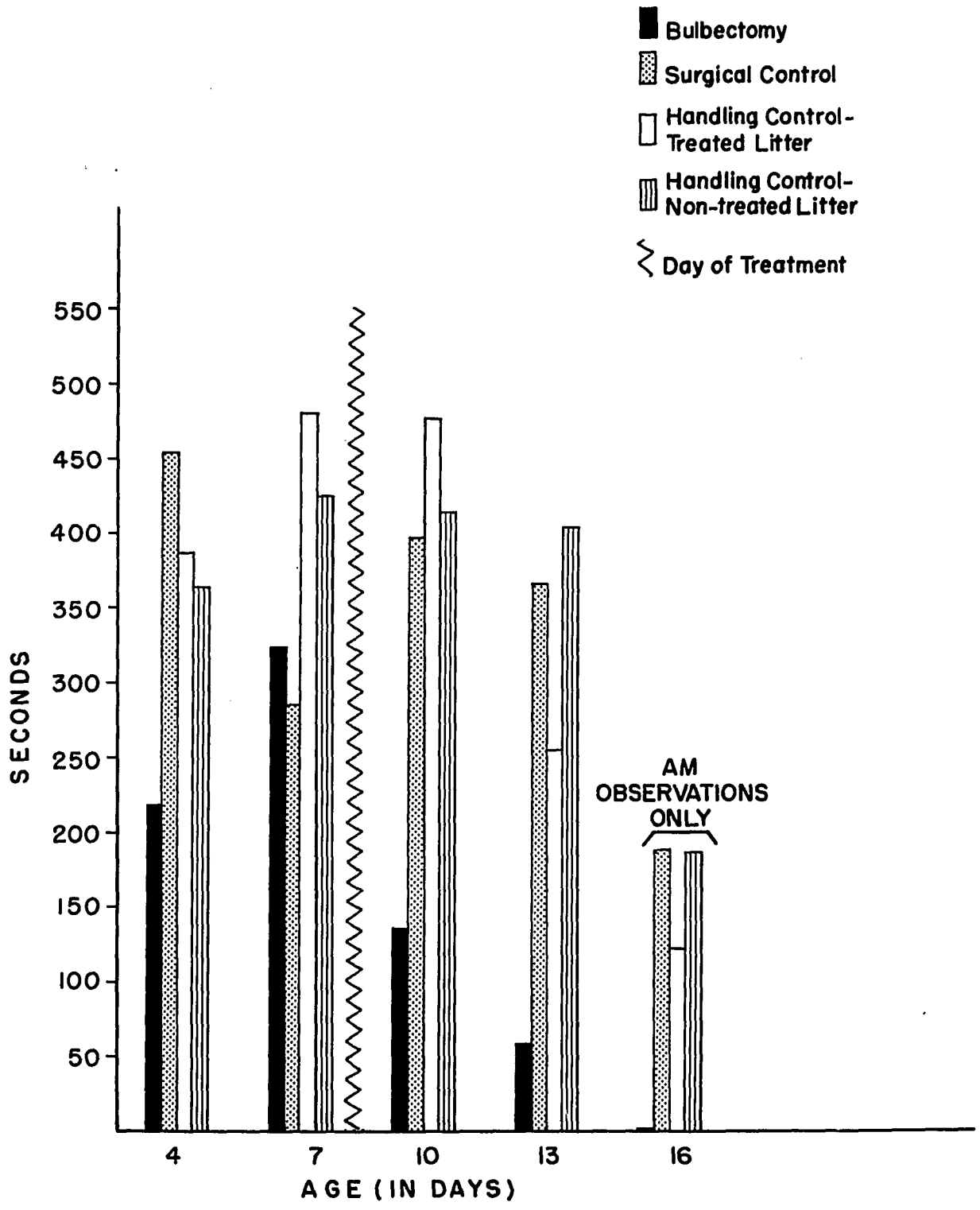
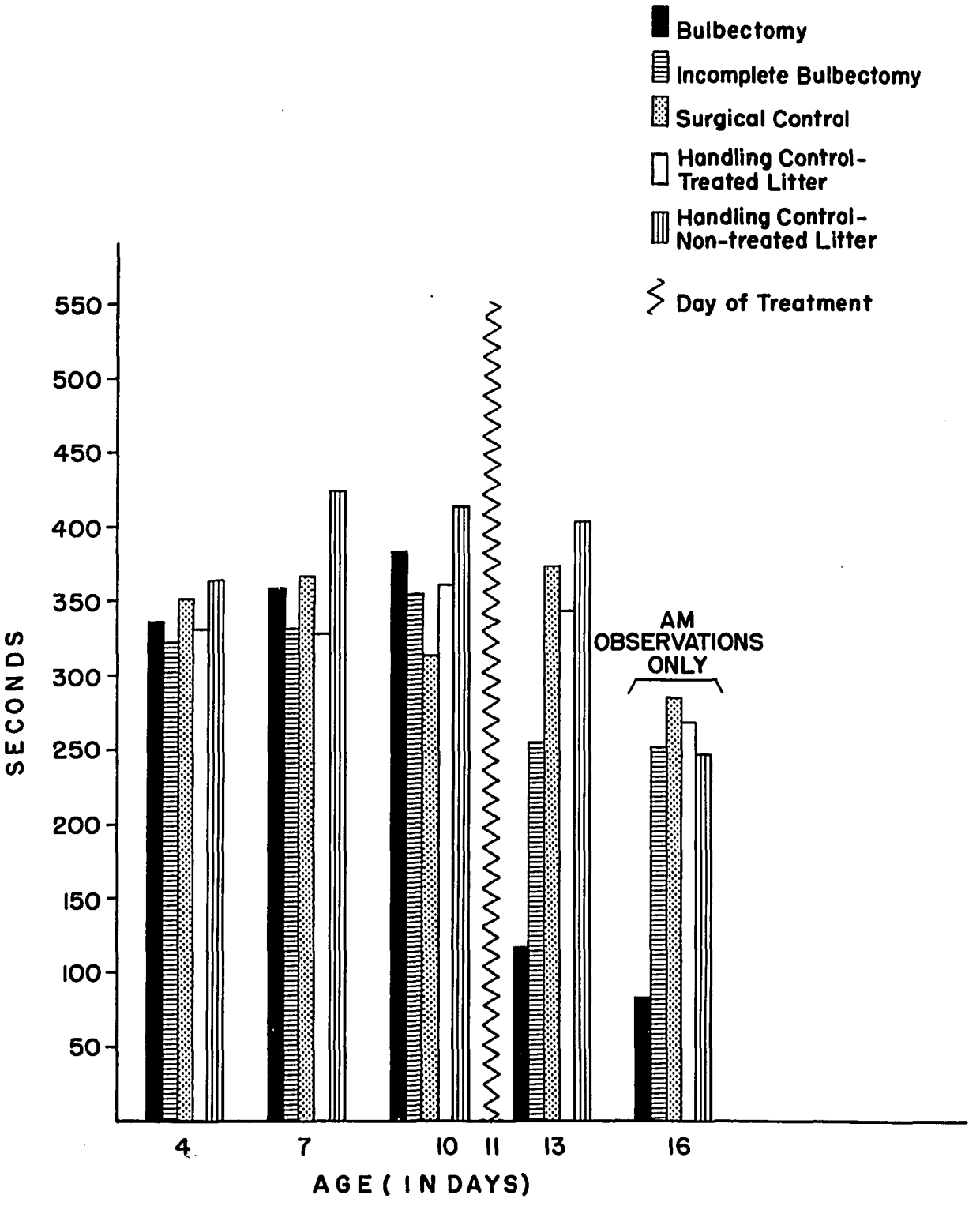

Bulbectomy
Surgical Control
Handling Control-Treated Litter
Handling Control-Non-treated Litter
Day of Treatment
SECONDS
550
500
450
400
350
300
250
200
150
100
50
AM OBSERVATIONS ONLY
4
7
10
13
16
AGE (IN DAYS)

Figure 6.

Mean Duration (Seconds) of Suckling for Pups
Treated on Day 11


Bulbectomy
Incomplete Bulbectomy
Surgical Control
Handling Control-
Treated Litter
Handling Control-
Non-treated Litter
Day of Treatment
SECONDS
550
500
450
400
350
300
250
200
150
100
50
AM
OBSERVATIONS
ONLY
4
7
10
11
13
16
AGE (IN DAYS)

HC-F pups from non-treated litters. The duration of suckling for the IBX pups also appeared to decrease somewhat on Day 13 while the duration for the other controls remained at approximately their pre-treatment level. (See Tables 11, 12, 13, and 14 for analyses of variance summaries. These tables and all following are located in the Appendix.)

Concerning the amount of time pups spent nosing the female, there were no significant differences among any of the treatment groups with the exception of the BX-7 pups on Day 13. Surprisingly, on this one day the BX-7 pups spent a significantly greater amount of time nosing the female than the BX-2 and BX-11 pups. (See Figure 7 and for analysis of variance summary, Table 15). No significant differences among treatment groups were found in number of times pups switched to lateral or posterior nipples. Concerning switching to the anterior nipple, there were no significant differences with the exception of SC-2 pups on Day 13 which did so more often than BX-2 pups, HC pups from non-treated litters, or SC-7 pups. Whatever factor or factors were responsible for this difference, they most probably are not due to the effects of bulbectomy, since in this case, the BX-2 pups and the HC pups from non-treated litters were the same. (For analysis of variance summary see Table 16).

b. Pup alone

One of the behavioral items used to measure pup activity was locomotion. It was found that BX-7 pups spent significantly more time locomoting on Days 10 and 16 than all other groups. (See Figure 8). However, this difference was not found for pups treated at the age of

Figure 7.

Mean Duration (Seconds) Pups at 13 Days of Age
Nosed Female

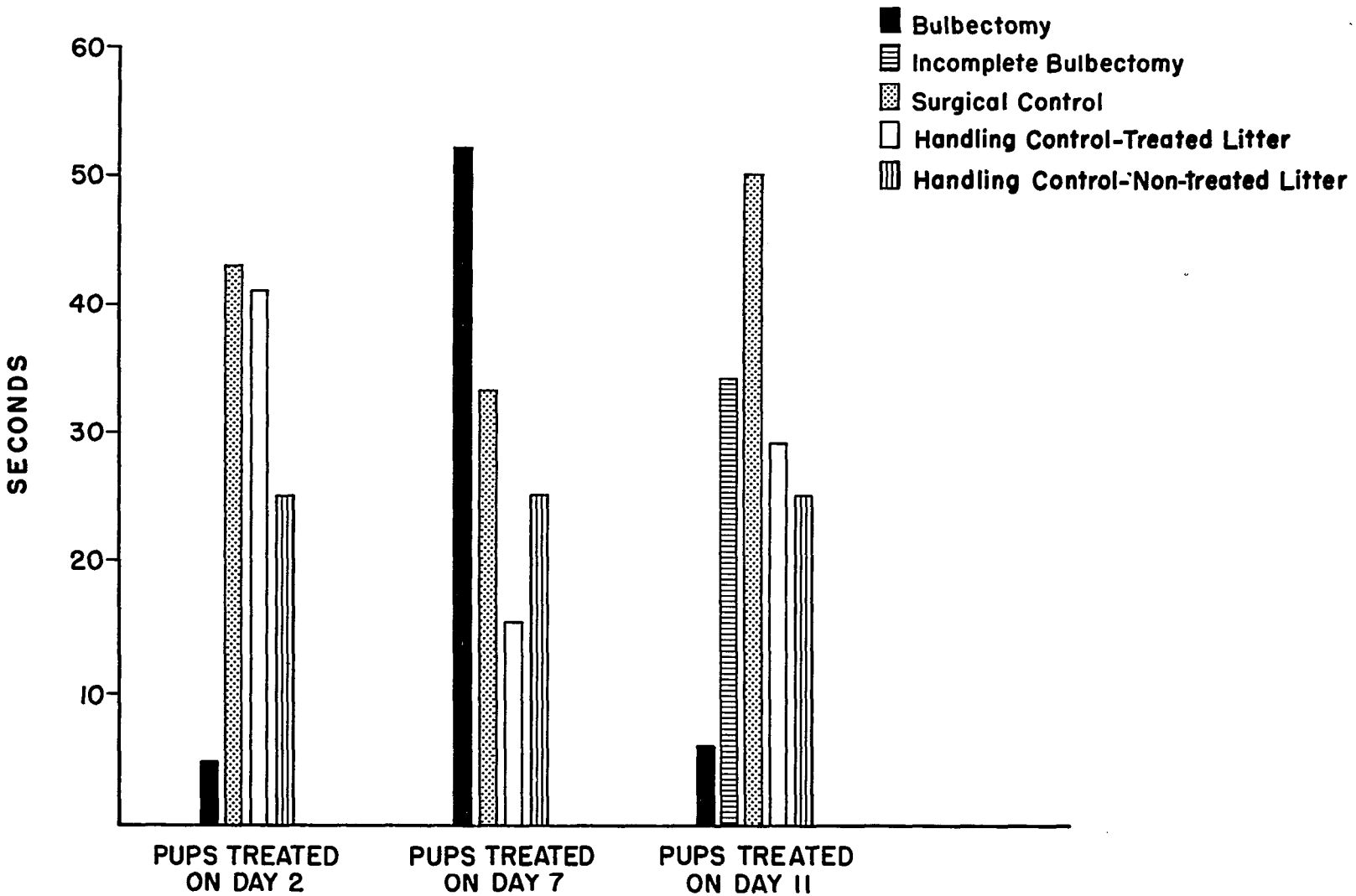
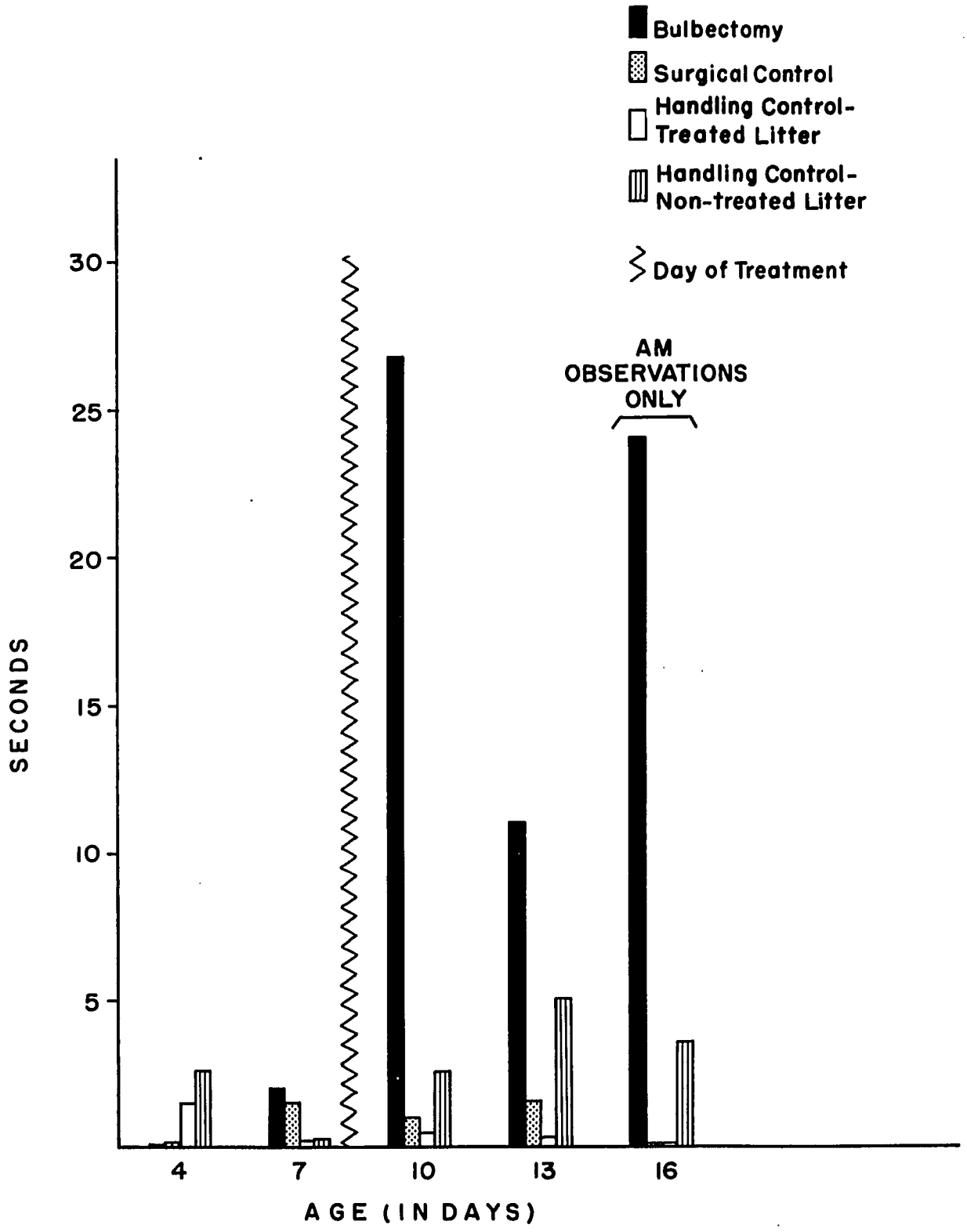

Bulbectomy
Incomplete Bulbectomy
Surgical Control
Handling Control-Treated Litter
Handling Control-Non-treated Litter
SECONDS
60
50
40
30
20
10
PUPS TREATED ON DAY 2
PUPS TREATED ON DAY 7
PUPS TREATED ON DAY 11

Figure 8.

Mean Duration (Seconds) Locomotion
For Pups Treated on Day 7


Bulbectomy
Surgical Control
Handling Control-
Treated Litter
Handling Control-
Non-treated Litter
Day of Treatment
AM
OBSERVATIONS
ONLY
SECONDS
30
25
20
15
10
5
4
7
10
13
16
AGE (IN DAYS)

Day 2 or Day 11. (See Tables 17 and 18 for analyses of variance summaries.)

In addition to locomotion, another measure of activity indicated a difference among treatment groups. On Day 10 BX-7 pups spent a significantly greater amount of time active and apart from others than BX-2 pups. (It should be noted that this behavioral item excludes locomotion.) This comparison can be made by looking at Figures 9, 10, and 11. On Day 16 (morning observation only) BX-7 pups spent significantly more time active and apart from others than BX-11 pups; however, both BX-7 and BX-11 pups did so significantly more than any other treatment group. In relation to the last result, it is interesting to note that after the morning observation on Day 16, one BX-7 pup and two BX-11 pups died. (See Tables 19 and 20 for analyses of variance summaries.)

There were no treatment differences on any of the observation days in duration of self-grooming. The same was true for duration of twitching or nosing the substrate.

c. Pup with Other Pups

Some behavioral items concerning pup-pup interaction were recorded during the observation sessions to determine whether bulbectomy would affect this aspect of pup behavior. On Days 13 and 16, IBX-11 pups spent significantly more time weaving in the clump than BX-11 pups. (Analyses of variance summaries are in Tables 21 and 22.) Otherwise, no significant differences were found for this behavioral item. No differences among treatments were found in amount of time spent active in the clump (excludes weaving) or nosing other

Figure 9.

Mean Duration (Seconds) of Activity Apart From Others
For Pups Treated on Day 2

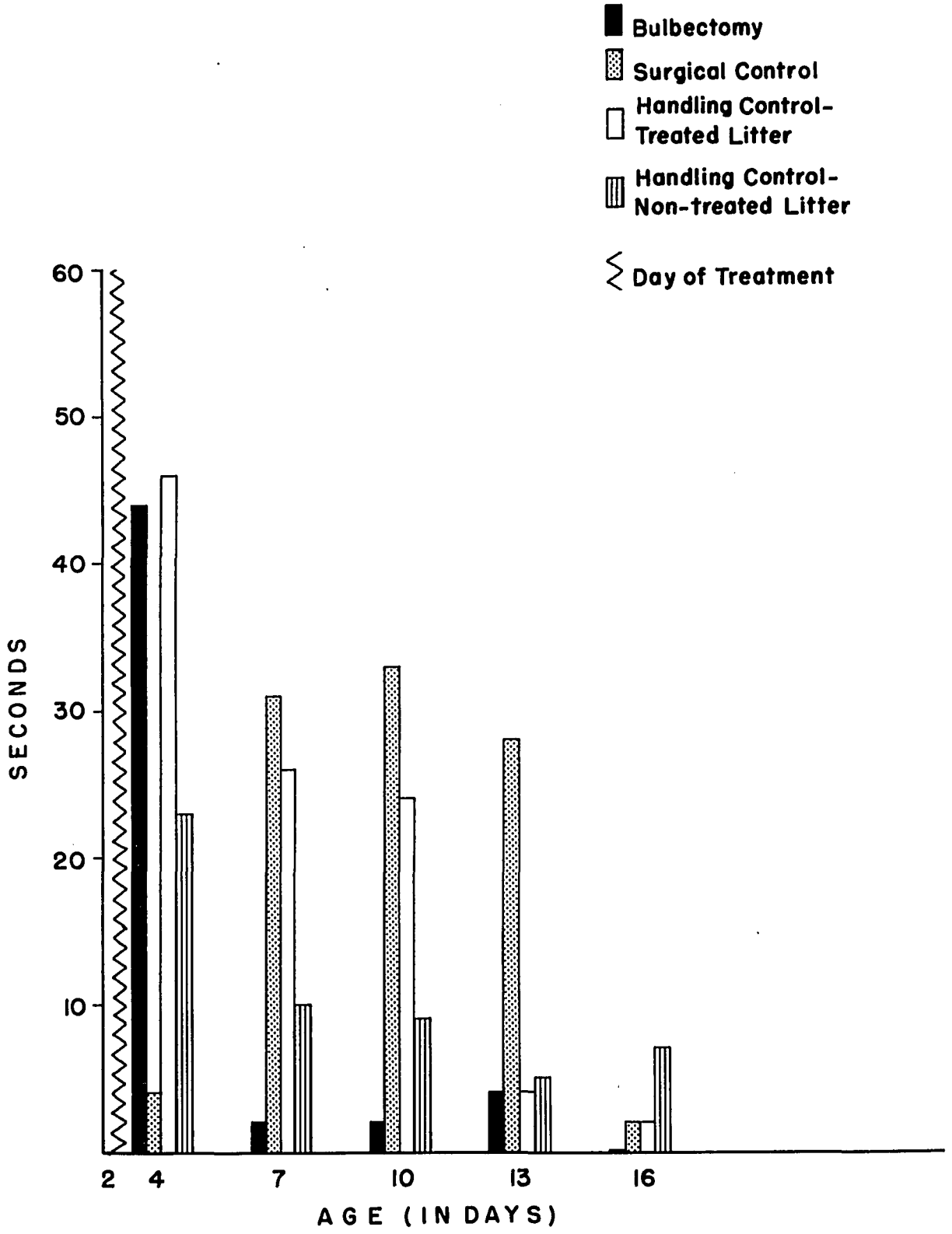

Bulbectomy
Surgical Control
Handling Control-
Treated Litter
Handling Control-
Non-treated Litter
Day of Treatment
60
50
40
30
20
10
SECONDS
2
4
7
10
13
16
AGE (IN DAYS)

Figure 10.

Mean Duration (Seconds) of Activity Apart From Others
For Pups Treated on Day 7

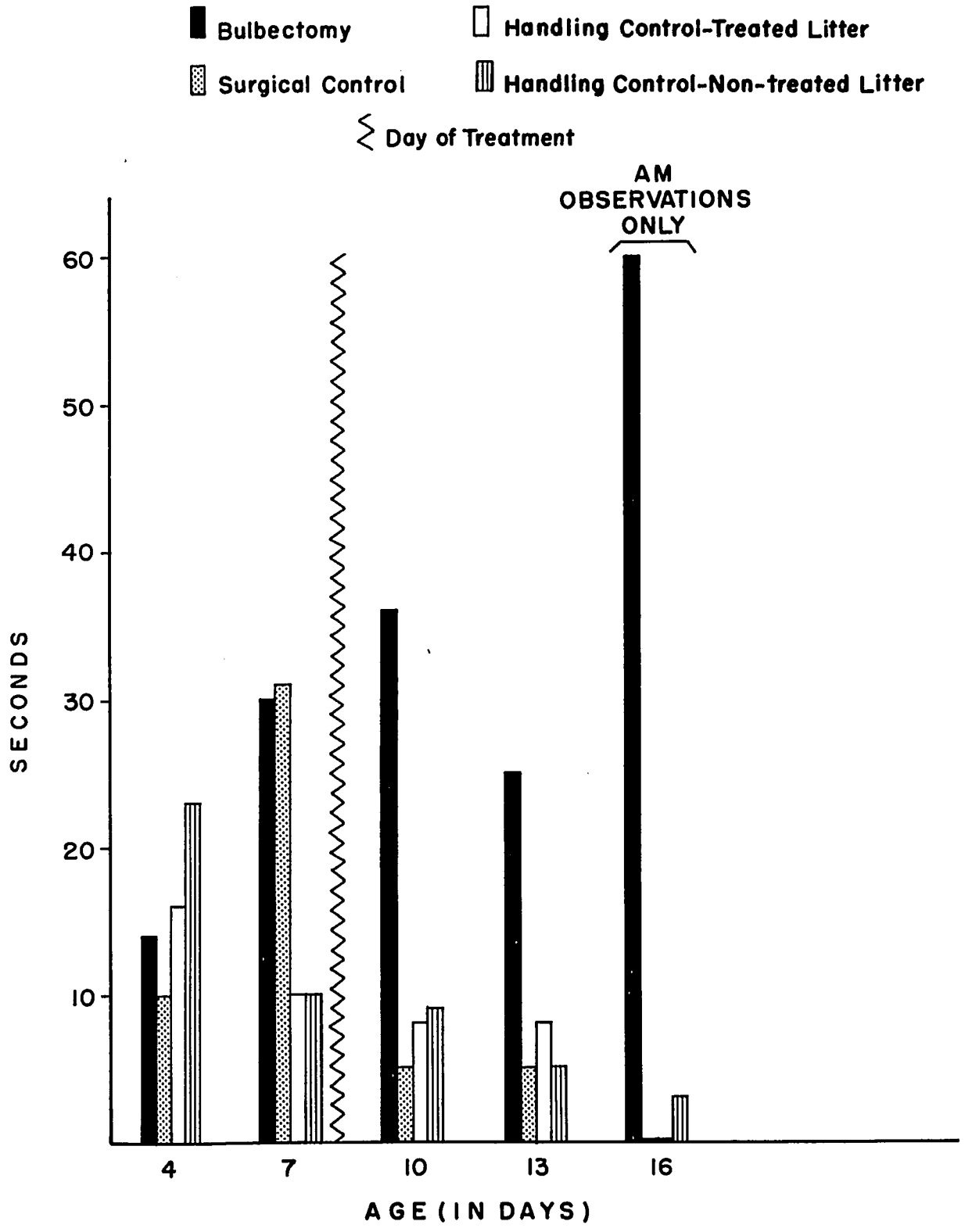
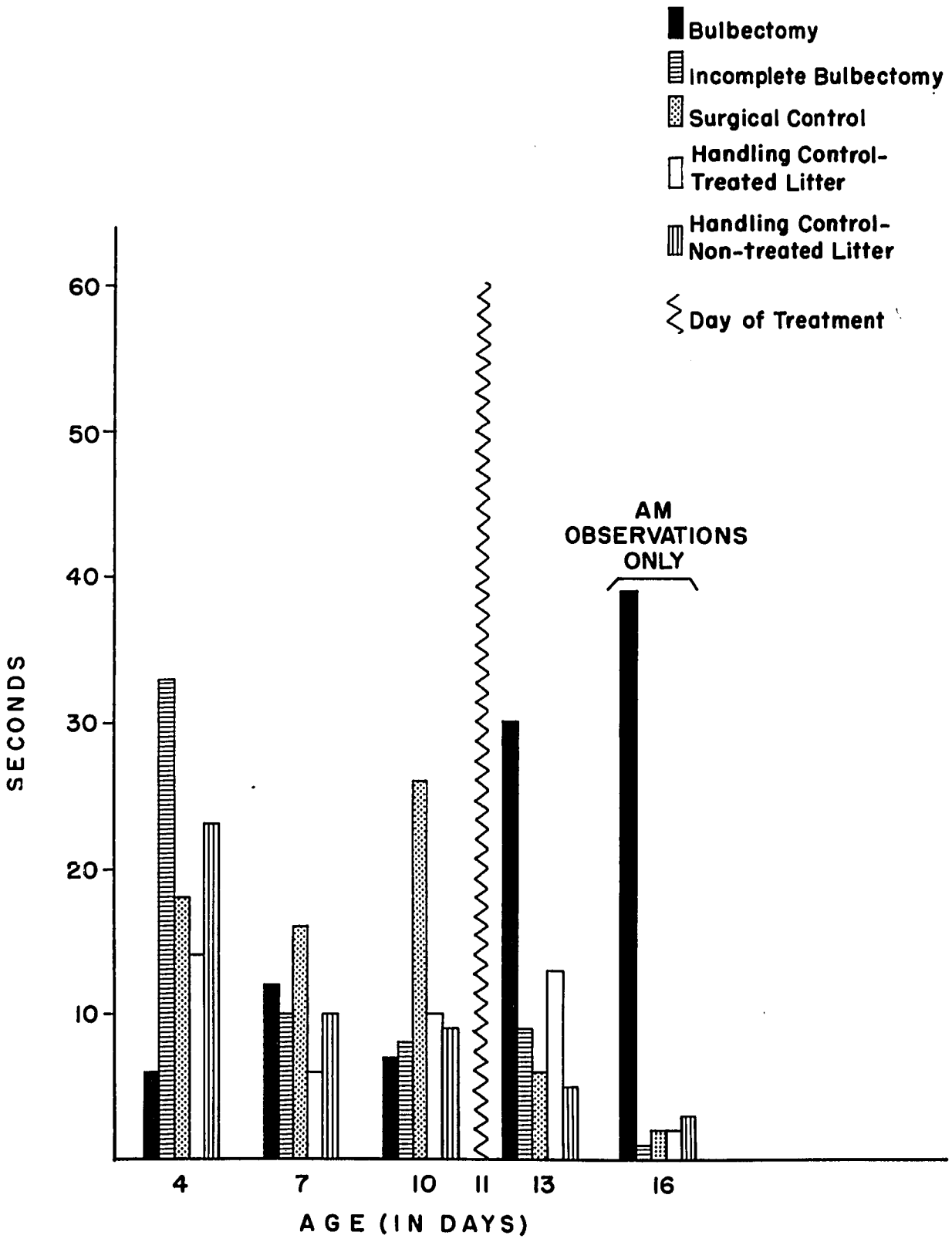

Bulbectomy
Handling Control-Treated Litter
Surgical Control
Handling Control-Non-treated Litter
Day of Treatment
AM OBSERVATIONS ONLY
SECONDS
60
50
40
30
20
10
4
7
10
13
16
AGE (IN DAYS)

Figure 11.

Mean Duration (Seconds) of Activity Apart From Others
For Pups Treated on Day 11


Bulbectomy
Incomplete Bulbectomy
Surgical Control
Handling Control-
Treated Litter
Handling Control-
Non-treated Litter
Day of Treatment
AM
OBSERVATIONS
ONLY
SECONDS
60
50
40
30
20
10
4
7
10
11
13
16
AGE (IN DAYS)

pups.

d. Female to Pup

In order to determine if any differences found in the behavior of the BX pups might be due to a difference in the behavior of the female toward the BX pups compared to the control pups, certain aspects of the female's behavior in relation to the pups were observed and recorded. No significant differences among treatment groups were found in amount of time the female spent licking the head. In fact, very little time was spent licking the head at all (usually not more than 2 to 3 sec. a day). Also, there were no significant differences among all treatment groups in amount of time the female spent licking the ano-genital area. The only significant difference in licking was found on Day 16 when the female spent more time licking the other part of the body of BX-11 pups than that of any other group. (For analysis of variance summary, see Table 23).

There were no significant differences on any of the five observation days in number of times that the female picked up and carried pups treated on Day 2. Although there was variability before treatment of Day 7 pups, there were no significant differences among these groups until the age of sixteen days. As shown in Figure 12, on Day 16, BX-7 pups were picked up and carried by the female significantly more than the three control groups. For pups treated on Day 11, there was also variability before treatment, but no significant differences appeared until Day 16. At that age, as indicated in Figure 13, the BX-11 pups were picked up and carried by the female more often than the three control groups and the IBX pups. On Day 16 the

Figure 12.

Mean Number of Times Female Picked up and Carried Pups Treated on Day 7

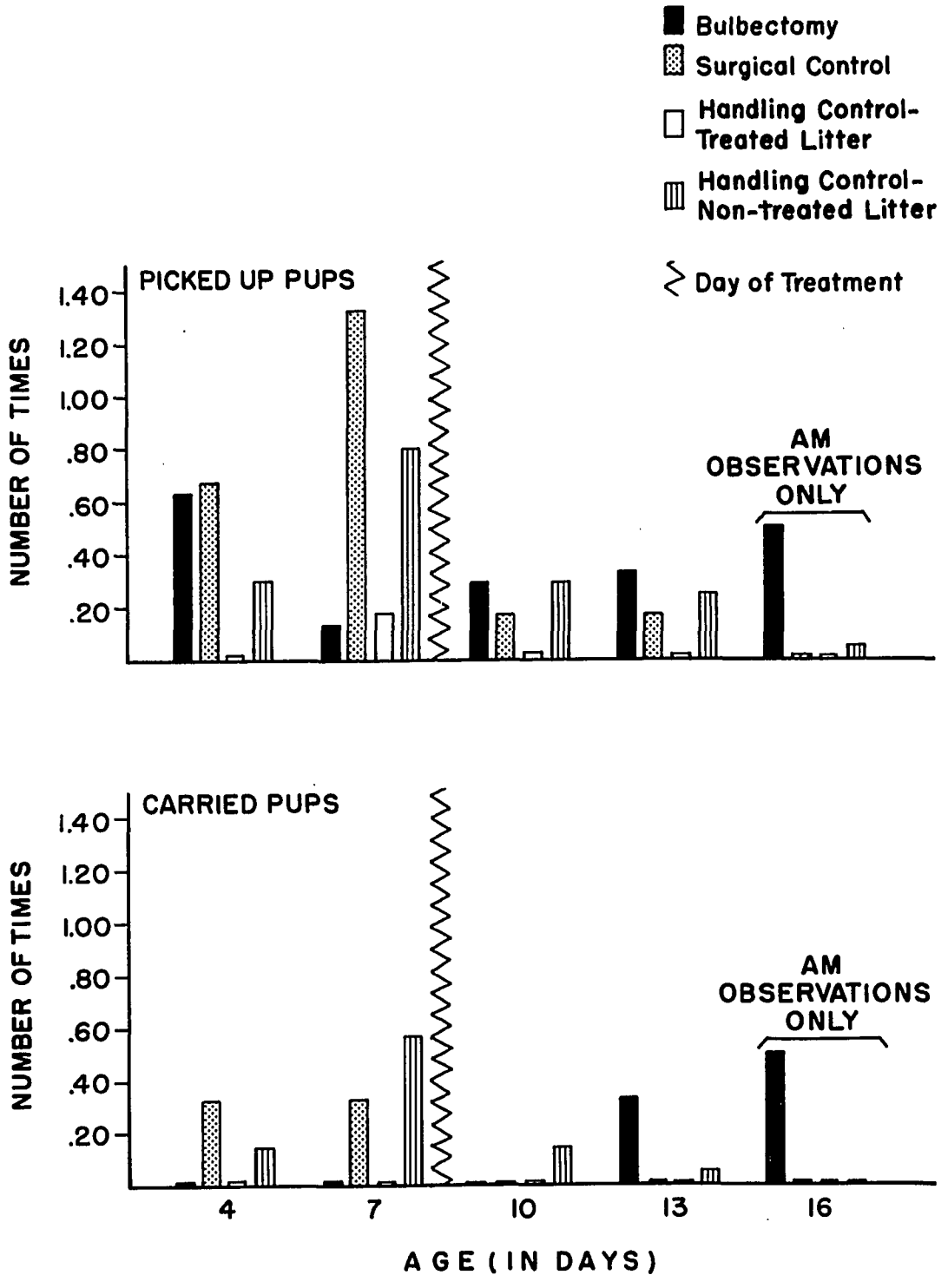
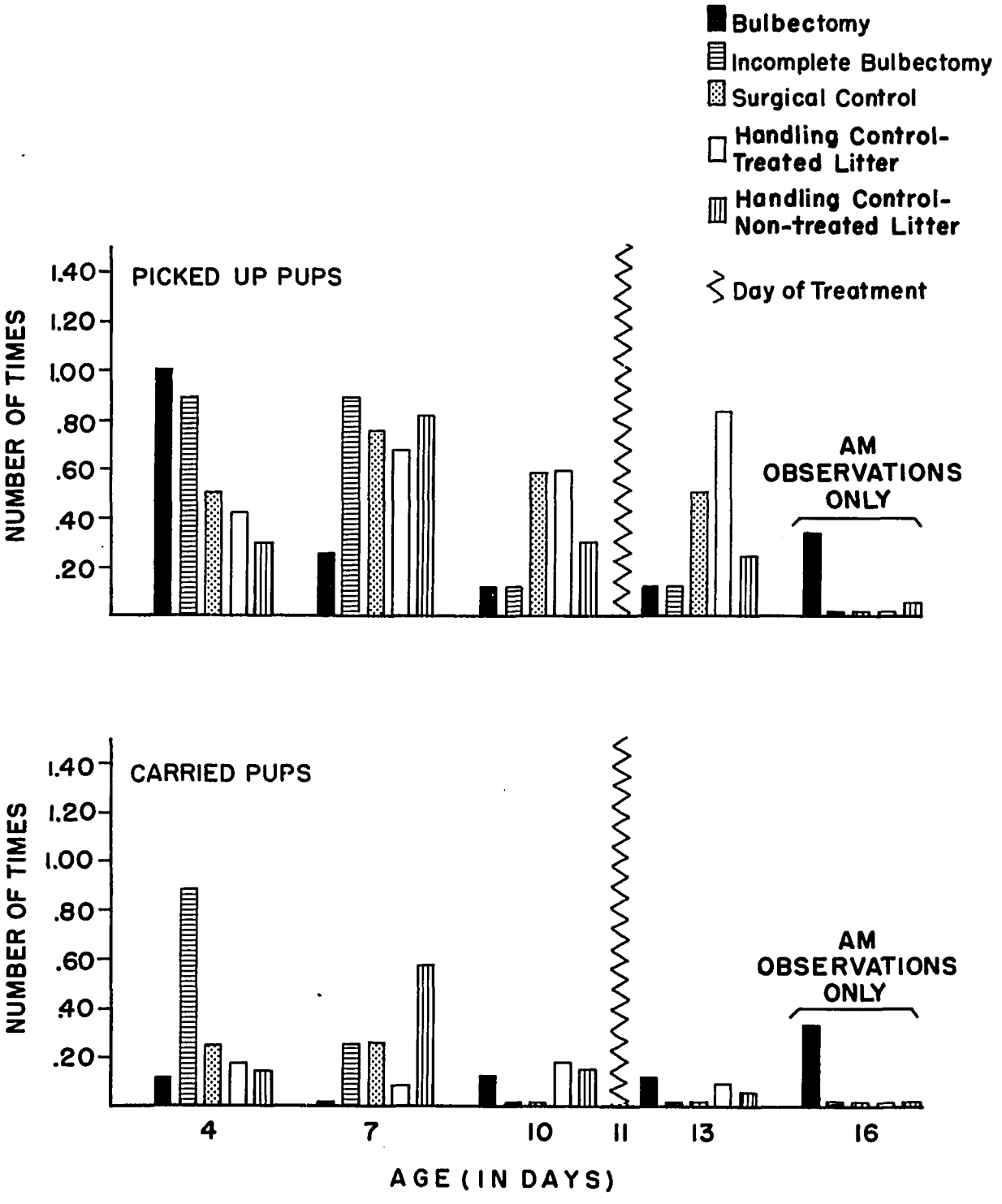

Bulbectomy
Surgical Control
Handling Control-Treated Litter
Handling Control-Non-treated Litter
Day of Treatment
PICKED UP PUPS
NUMBER OF TIMES
1.40
1.20
1.00
.80
.60
.40
.20
AM OBSERVATIONS ONLY
CARRIED PUPS
NUMBER OF TIMES
1.40
1.20
1.00
.80
.60
.40
.20
AM OBSERVATIONS ONLY
4
7
10
13
16
AGE (IN DAYS)

Figure 13.

Mean Number of Times Female Picked up and Carried Pups Treated on Day 11


Bulbectomy
Incomplete Bulbectomy
Surgical Control
Handling Control-Treated Litter
Handling Control-Non-treated Litter
Day of Treatment
PICKED UP PUPS
CARRIED PUPS
NUMBER OF TIMES
1.40
1.20
1.00
.80
.60
.40
.20
AM OBSERVATIONS ONLY
4
7
10
11
13
16
AGE (IN DAYS)

female also picked up and carried the BX-7 and BX-11 pups more than the BX-2 pups. In addition, the female spent significantly more time (duration) carrying the BX-7 and Bx-11 pups more than all other treatment groups on Day 16. (See Tables 24, 25, and 26 for analyses of variance summaries.) Again, in relation to the above-mentioned results, it should be pointed out that after the morning observation on Day 16, one BX-7 pup and two BX-11 pups died. No significant differences were found among the treatment groups in amount of time the female spent nosing the pups.

2. Longitudinal Data from Observation Sessions in Observation Cage

In addition to the cross-sectional analysis, a longtitudinal analysis was done on separate treatment groups comparing any changes in frequency or duration of each of the 19 behavioral items on Days 4, 7, 10, 13, and 16. In this analysis only pups that survived throughout the entire experiment were used. Thus two of the total 13 treatment groups (BX-7 pups and BX-11 pups) were disqualified from this analysis, because by the afternoon of Day 16 only one pup was left in each of these groups. Undoubtedly, the BX pups which survived throughout the course of the experiment were different from those that died before Day 16 and comprised a separate subgroup of BX subjects. A total of 209 longitudinal analyses of variance were done.

The behavioral items which showed some sort of pattern in regard to age differences in most of the treatment groups were self-grooming, twitching, and active in the clump. The amount of time spent self-grooming for HC-2 pups, HC-11 pups, HC pups from non-treated litters, and male HC pups from non-treated litters was significantly longer on Day 16 than on Days 4, 7, 10 and 13. For

SC-11 pups, duration of self-grooming was significantly longer on Day 16 than on Days 4, 7, and 13. Tables 27B through 32B show the pattern of age differences for this behavioral item in the above-mentioned groups. (See Tables 27 through 32 for analyses of variance summaries). This general pattern was not found in BX-2 pups, IBX-11 pups, SC-2 pups, SC-7 pups, or HC-7 pups.

Twitching also showed a pattern of age differences with more twitching usually occurring on Days 7, 10, and 13 than on Days 4 and 16. SC-11 pups, HC-7 pups, HC-11 pups, HC pups from non-treated litters, and female HC pups from non-treated litters spent a significantly longer amount of time twitching on Days 7, 10, and 13 than on Days 4 and 16. The male HC pups from non-treated litters spent significantly more time twitching on Days 7 and 10 than on Days 4 and 16. The SC-2 pups and SC-7 pups had significantly longer twitching durations on Days 10 and 13 than on Day 4, and SC-7 pups also had a significantly longer twitching duration on Day 13 than on Days 16 or 7. The IBX-11 pups spent a significantly greater amount of time twitching on Day 10 than on Days 4, 13, and 16. Tables 33B through 41B illustrate the pattern of age differences for twitching in these groups. (For analyses of variance summaries of twitching data see Tables 33 through 41.) No longitudinal differences were found for BX-2 pups and HC-2 pups.

In general pups tended to spend more time active in the clump on Days 4 and 7 than on later days. For BX-2 pups the amount of time spent active in the clump was significantly longer on Days 4 and 7 than on Days 10, 13 and 16. On Days 4 and 7 the IBX-11 pups had a significantly longer duration of activity in the clump than on Day 16.

SC-7 pups were active significantly longer on Days 4, 7, 10, and 13 than on Day 16 and significantly longer on Day 4 than on Day 16, On Day 7, HC-7 pups had a significantly longer duration of activity in the clump than on Days 4, 10, 13, and 16. For HC-11 pups a significantly longer amount of time was spent active in the clump on Days 4, 7, and 10 than on Day 16 and significantly longer on Days 4 and 7 than on Day 13. Male HC pups from non-treated litters and HC pups from non-treated litters were significantly more active in the clump on Day 7 than on Day 16. SC-2 pups, HC-2 pups, and female HC pups from non-treated litters did not show these differences. The pattern of age differences in amount of time spent active in the clump for these groups is indicated in Tables 42B through 47B. When evaluating the above-mentioned results, it is important to remember that pups treated on Day 7 were like HC pups from non-treated litters on Day 4 and 7 and that pups treated on Day 11 were like HC pups from non-treated litters on Days 4, 7, and 10. (See Tables 42 through 47 for analyses of variance summaries.) A trend in age differences was not evident in other behavioral items.

3. Auxiliary Data

a. Cage drawings

The cage drawings showed changes in nest location which were used as an indication of possible disturbance of the female as a result of experimental procedure. The drawings also showed the number of times pups were found out of the nest and apart from others. Using a Kruskal-Wallis one-way analysis of variance, no significant differences were found when comparing the females of litters in the four

main groups on percentage of changes in nest location. Friedman two-way analyses of variance did not indicate any significant difference for number of times pups were found out of the nest apart from others in respect to treatment and litters. A Mann-Whitney U test failed to indicate significant differences between the sexes.

Significant differences were found in all cases, however, when comparing the observation cage and the home cage in regard to number of times pups were found out of the nest apart from others, the number of times always being greater in the observation cage. For the pups treated on Day 2, the Mann-Whitney U test (one-tailed) was significant at the .01 level ($U = 3$, $n_1 = 5$, $n_2 = 8$). For the pups treated on Day 7, the same test was significant at the .02 level ($U = 6$, $n_1 = 5$, $n_2 = 8$). The difference in home cage and observation cage for the pups treated on Day 11 was significant at the .05 level (Mann-Whitney U, one-tailed, $U = 8$, $n_1 = 5$, $n_2 = 8$). For the three non-treated HC litters, the difference was significant at the .02 level (Mann-Whitney U, one-tailed, $U = 6$, $n_1 = 5$, $n_2 = 8$). One-tailed tests were used because the direction of the difference could be predicted. (Reasons for this are mentioned in the Discussion.) Although the total number of times pups were found out of the nest apart from others was very small in comparison to the number of times pups were found in the nest, whenever they were out of the nest, it occurred a significantly greater number of times in the observation cage rather than in the home cage.

b. Pup Placement Tests

Another measure of activity of the pups was number of

intervals that they moved (changed location) during the pup placement tests. An interval consisted of the time which elapsed between placing two pups in the cage (usually about 20 sec.). The total number of intervals equaled six. Thus the first pup had six intervals within which it could change its location and the sixth pup placed in the cage had one. Spearman rank-order correlation coefficients between age in days and total number of intervals moved out of each of the six possibilities generally indicated a positive correlation between number of intervals moved and age in days. (See Table 48). However, inspection of the scattergrams of these data indicated no treatment or sex differences.

An additional measure of pup-pup interaction was the number of times pups made contact with another pup for at least one interval in the pup placement test. Friedman two-way analyses of variance did not reveal any treatment, age, or litter differences for any of the main groups (pups treated on Days 2, 7, or 11) and any age or litter differences among the three HC non-treated litters. No sex differences were found in the three HC non-treated litters using the Wald-Wolfowitz runs test. Comparing the HC-2 pups, HC-7 pups, HC-11 pups and HC pups from non-treated litters in number of times pups made contact with another pup, a Friedman two-way analysis of variance indicated significance at the .02 level ($\chi_r^2 = 10.17$, df = 3). Wilcoxon matched-pairs signed ranks test showed that HC-2 pups made contact with other pups a significantly greater number of times than did HC-11 pups or HC pups from non-treated litters. (For HC-2 and HC-11 pups: $T = 0$, $N = 9$, $p < .05$ and for HC-2 and HC pups from non-treated litters:

T = 0, N = 9, $p < .05$.)

The number and identification of pups that ended in the nest in the pup placement test were tabulated as a measure of orientation toward the nest. Only data from the pup placement tests which occurred in the home cage were used, because when pups are first placed in the observation cage there is no defined nest. Using Friedman two-way analyses of variance for all comparisons, no statistically significant differences were revealed in respect to treatments, litters, and ages.

c. Retrieving Tests

The following measures from the retrieving test were analyzed:

1) Latency to the first time the female picked up each pup.
2) Number of times female picked up each pup.
3) Number of intervals female was climbing or rising, chasing her tail, digging, or self-grooming.

Kruskal-Wallis one-way analyses of variance were used to compare BX, SC, and HC pups from litters treated on Day 2 in latency to the first time female picked up pups. At the ages of Days 3 and 4, no significant differences were found. By Day 6, all litters except one contained only SC and HC pups. Thus only the one litter, Litter 37, which contained some BX pups was analyzed from Days 6 through 15. A Friedman two-way analysis of variance comparing BX, SC, and HC pups in Litter 37 was significant at the .05 level ($\chi r^2 = 12.40$, df = 5). Wilcoxon matched-pairs signed-ranks tests for differences between pairs of pups indicated that the latency to the first pick up for one SC pup (T = 0, n = 7, $p < .05$) and two BX pups (T = 0, n = 7, $p < .05$ was significantly longer than that for another SC pup.

However, when ranking the latencies to the first pick up for the six pups in the litter, it was found that the latencies for the two SC pups were on opposite ends of the continuum, that is the latency for one was the longest while that for the other was the shortest. The latencies of the two BX pups and the two HC pups were in between, with those for the two BX pups being longer and those for the two SC pups being shorter.

For litters treated on Day 7, Kruskal-Wallis analyses of variance comparing BX, SC, and HC pups did not indicate any differences in latency to the first pick up on all days except on Day 3 when there was a significant difference at the .001 level ($H = 29.03$, $df = 2$). However, since on Day 3 all of the pups were like non-treated HC pups because treatment did not occur until Day 7, this difference was considered to be irrelevant especially since it did not reappear on any of the following days.

Comparing BX, IBX, and HC pups in litters treated on Day 11, no treatment differences in latency to the first pick up were found in any litters before or after treatment except in Litter 12 before treatment. However, since this difference occurred before treatment when all pups were like non-treated HC pups, it was considered irrelevant and probably due to chance or sampling error. A Friedman two-way analysis of variance on Litter 12 after treatment failed to indicate any differences in latency to the first pick up among treatments. Most litters did show differences among days with the latency to the first pick up generally being shorter on Days 6, 7, 9 and 10 than on Days 3, 4, 12, 13 and 15 as indicated by Wilcoxon matched-pairs

signed-ranks tests. The same pattern of age differences for this measure was found in the three non-treated HC litters. No differences among pups of these three litters were found using Friedman analyses of variance.

In regard to the number of times, the female picked up a pup, Friedman analyses of variance on each of the handling litters did not show any differences among pups but differences among days. The results of Wilcoxon matched-pairs signed-ranks tests, to determine exactly which days were significantly different from others, did not show a definite pattern of age differences although in two of the litters pups generally were picked up more times in the observation cage than in the home cage. (See Tables 49, 50, and 51).

For litters treated on Day 2, Kruskal-Wallis one-way analyses of variance comparing treatments for all litters on Day 3 and on Day 4, regarding number of times the female picked up a pup, failed to show any significant differences. Friedman analyses of variance on the one litter which included BX pups from Days 6 through 15 did not reveal any significant difference among treatments but a significant difference among days ($\chi r^2 = 22.74$, $df = 5$, $p < .001$). Further analysis indicate that for the most part, the number of times the female picked up the pups was larger if the test was conducted in the observation cage rather than in the home cage. (See Table 52).

Friedman analyses of variance on each of the three litters treated on Day 7 did not demonstrate any differences among pups and days before treatment in number of times picked up. Kruskal-Wallis analyses of variance comparing the three treatments after Day 7 were

all not significant.

For litters treated on Day 11, Friedman analyses of variance to test for differences among pups of all six litters in number of times picked up were not significant either before or after treatment. However, when comparing days, all except one of the analyses were significant revealing that, in general, the female picked up pups a greater number of times when the retrieving test occurred in the observation cage compared to when it was held in the home cage. (See Tables 53 through 57).

Some behavioral items which the females exhibited during the retrieving tests were observed and recorded in order to obtain an indication of relative disturbance of each female (compared to the other females) and for the purpose of comparing the female's behavior in the observation cage and the home cage. Even though there were differences among the females in regard to number of intervals in which climbing and rising occurred (Friedman two-way analysis of variance, $p < .001$), they were randomly distributed among the four main groups as indicated by a Kruskal-Wallis one-way analysis of variance. A Friedman two-way analysis of variance comparing days for number of intervals climbing and rising was not significant indicating that these behavioral items did not occur more often in the home cage than in the observation cage.

There also were differences among the females in number of intervals in which they chased their tails (Friedman two-way analysis of variance, $p < .02$); however, a Kruskal-Wallis one-way analysis of variance comparing females in the four main groups was not

significant, again indicating that the differences were randomly distributed among the four main groups. A Friedman two-way analysis of variance comparing days for number of intervals in which females chased their tails was not significant, indicating that this behavior did not occur more frequently in the observation cage than in the home cage.

A Friedman two-way analysis of variance comparing all females for number of intervals in which digging occurred was not significant; however, the same type of analysis indicated a difference in days in number of intervals in which digging occurred ($\chi r^2 = 99.76$, $df = 8$, $p < .001$). Wilcoxon matched-pairs signed-rank tests revealed that the number of intervals in which digging occurred was greater in the home cage than in the observation cage (See Table 58).

For number of intervals in which self-grooming occurred, a Friedman two-way analysis of variance indicated a significant difference among the females ($p < .01$). However, a Kruskal-Wallis one-way analysis of variance did not demonstrate any differences in number of intervals in which this behavioral item occurred among the females in the four main groups, again showing that the differences were randomly distributed among the females in the four main groups. A Friedman two-way analysis of variance comparing days for number of intervals in which self-grooming occurred was significant ($\chi r^2 = 28.65$, $df = 8$, $p < .001$). Wilcoxon matched-pairs signed-ranks tests revealed that there were more intervals in which self-grooming occurred when the retrieving tests were held in the home cage than in the observation cage. (See Table 59).

IV. DISCUSSION

In general, this dissertation was concerned with the role of the olfactory system in the development of behavior. By investigating the effect of olfactory bulbectomy on the development of nursing and other related behaviors in the rat pup, a part of this general area of research was explored. By ablating the olfactory bulbs, the sensory system of olfaction became non-functional but, because of the many connections of the bulbs, other effects besides the loss of smell also probably occurred. The ramifications of bilateral olfactory bulbectomy, however, are beyond the scope of this investigation and can only be speculated upon.

The developmental approach is a way of viewing behavior, emphasizing behavioral changes in an organism beginning from a definite point in time such as at birth. Thus the development of behavior can be seen as a multi-dimensional process, since it involves many factors and levels of organization including the genetic make-up of the organism, the internal and external environments, and the interaction of all these factors and levels at every stage in ontogeny. When one considers the environment alone in a constant state of flux or change from the prenatal period and throughout life, the amount of interactions becomes staggering. It is impossible to deal with all of these factors in any one investigation. It would require numerous experiments and years of time to elucidate all of the factors which

affect the development of behavior. In fact, because of the limitations of present technical knowledge, such experimentation is still not feasible. Nevertheless, in the planning of an experiment, the factors of which one is aware, should be taken into consideration.

In this investigation, the genetic make-up of the organisms was similar, because only one strain of animals was used; and an attempt was made to keep the physical environment as constant as possible. For this reason, the temperature and lighting were closely monitored, all animals were housed in the same room in identical cages, and all were observed in the same chamber. The experimental manipulations were performed in the same way at approximately the same time of day by the same individual for the purpose of reducing variability.

Obviously, the physical environment was definitely altered when the pups were transferred from the home cage to the observation cage, since one had a sawdust-covered substrate and the other a smooth, transparent substrate. To obtain some comparative measures that would assess the effect of this rather abrupt change, the pup-placement tests, retrieving tests, and cage drawings were performed in both cages.

The social environment for the young rat pup consists of the female and the other pups. For this reason the female's behavior toward the pup was observed and the pup's interaction with other pups was also studied. Because varied amounts of previous maternal experience among the females might have contributed to variation of conditions among litters, only primiparous females were used. This

was considered acceptable because Moltz (1965) has pointed out that primiparous females are capable of taking very adequate care of their litters. The litters were culled to the same number of pups and balanced for numbers of males and females in a attempt to keep the social aspects of the environment as nearly alike as possible.

In this investigation, data were gathered at three different levels, namely, the anatomical, physiological and the behavioral. The anatomical and physiological data were restricted by the demands of the behavioral data. The behavioral data collected also had to be limited, but they were obtained by employing a judicious selection of behavioral items and tests necessary for investigating the problem. Because of the data-collection system used, the actual amount of data obtained was overwhelming, but it yielded information about some interesting patterns and relationships. In this discussion, the anatomical and physiological data will be considered first, followed by the behavioral data.

A. Anatomical and Physiological Data

The low survival rate of the BX pups was expected since in previous investigations (Rouger et al., 1967; Kling, 1964) similar results had been obtained. The low survival rate of the BX-11 pups, however, was somewhat of a surprise because Rouger et al. (1967) had reported about a 60% survival rate for pups bulbectomized at this age. This discrepancy might be due to the fact that in this experiment the pups were periodically transferred to the observation cage and back to the home cage. These transfers might have been dis-

ruptive as indicated in studies by Tobach and Schneirla (1962) and Tobach, Turkewitz, Vroman and Schneirla (1968). Another possibility is that in the Rouger et al. (1967) study some of the BX pups might have actually been IBX pups, since the extent of bulbectomy was never confirmed histologically but determined by visual inspection only. Interestingly, all the IBX pups in the present study survived. This 100% survival rate, however, was not surprising because pilot studies on survival indicated that when a small amount of bulb tissue was present adjacent to the frontal cortex, the animals survived, although they were runts compared to littermates.

These results are puzzling because one would think that the loss of olfaction would be complete even if only the antero-ventral portion of the bulb, where the olfactory nerve fibers enter, were removed. How could a small amount of tissue of the posterior part of the bulb make such a difference in survival? There are two possibilities for the function of this portion of the bulb. One is that it has some connections, with the olfactory receptor area, that are still intact. The area which remained in the IBX pups roughly corresponded to the accessory olfactory bulb as defined by Rehmer (1970). Raisman (1972) has recently proposed that there is a dual olfactory system on the basis of the separate central nervous system (CNS) connections of the olfactory bulb and the accessory olfactory bulb. He further proposed that the former is for "general stimulation" and the latter for cues related to behaviors such as reproduction and feeding (since the accessory bulb is connected to the ventro-medial portion of the hypothalamus and the corticomedial amygdala). This proposal

is in agreement with the view that sensory stimulation consists of two processes, cue and arousal (Hebb, 1949; Aronson, 1963). It is possible that this "second olfactory system," which consists of the vomeronasal organ and accessory bulb with its CNS connections, was mostly intact in the IBX pups and this is why they survived. Even though the vomeronasal nerve enters the antero-medial portion of the accessory bulb, it is possible that some of the fibers were not severed, and it is very possible that the terminal nerve, which runs along the ventro-medial surface of the bulb, was still intact. However, to determine the feasibility of this hypothesis would require more detailed histology using both cell and fiber stains and another experiment in which careful attention was paid to removing only the olfactory bulb proper and not the accessory bulb. Raisman (personal communication) has found that when the accessory bulb or vomeronasal organ is removed in mice the "Bruce Effect" (Bruce and Parrot, 1960) does not occur. These results support his dual olfactory system hypothesis.

The second possibility is that this portion of the bulb may have to do with some "non-olfactory" function that is necessary for survival. Non-olfactory functions of the bulb such as inhibition of certain behaviors are suggested by the studies in which removal of bulbs causes an increase in emotional behavior and studies in which behaviors such as mouse-killing and cannibalism of young do not occur if animals are made only peripherally anosmic with zinc sulfate but do occur if animals are bulbectomized (Hull, 1972, and Fleming, personal communication). The answers to these questions, however, are beyond the scope of this investigation.

It was found that when the bulbs were completely or partially removed, the frontal cortex was somewhat displaced into the olfactory bulb cavity forming a herniation. The determination of this was possible because of the in situ histological method used with which one could see the relationship of the bulb and frontal cortex to other structures in the skull. In the two BX-2 pups that survived, this herniation almost completely filled the olfactory bulb cavity. The same was true of the BX-7 and BX-11 pups that survived. The herniation was most probably due to displacement into the empty cavity. It is possible, however, that it could also be related to cell production in the subependymal layer of the lateral ventricle. This process has been reported by Altman (1969). He has also demonstrated that the subependymal layer of the lateral ventricle shows noticeable changes in size in the rat pup from four to 10 days of age and from 10 to 15 days of age and that the major target structure of cell production in this layer of the lateral ventricle is the olfactory bulb.

It might be argued that the survival results of this experiment were not specifically due to removal of olfactory bulb tissue but that removal of an approximately equal amount of brain tissue would have produced the same mortality rate. In an experiment by Tobach, Singh, Lederhendler, De Santis, and Beckhorn (in preparation), volume controls were obtained by removing an approximately equal amount of frontal cortex tissue which was directly posterior to the bulb. These animals were found to be very similar to surgical controls in survival.

One might also propose that the loss of any other mode of sensory stimulation might produce the same results. In answer to this, it can be again pointed out that the rat pup does not have a fully functional auditory or visual system until about 12 and 15 days of age, respectively. At best, before these ages its audition and vision are minimally functional and thus, in a way, the rat pup could be considered as being under visual and auditory deprivation. In studies where ocular enucleation has been performed on rat pups between six and ten days of age, there seemed to be no problem in survival (Orbach and Kling, 1966).

The body weight data corresponded very nicely with the survival data in that there appears to be a positive correlation between weight gain and survival. There also appears to be a positive correlation between amount of milk in the stomach at autopsy and probability of survival as suggested by body weight at time of autopsy. These results agree with those of a previous pilot study.

The data obtained from inspecting the female's mammary glands confirmed that the lack of milk in the stomachs of some pups, mainly the bulbectomized, was not due to the inability of the female to produce it. It was also observed that the anterior mammary glands were usually more developed than the posterior ones. These data agree with those of Rosenblatt (1970).

B. Behavioral Data

1. Cross-sectional and Auxiliary

Since the hypothesis which stimulated the design of this

experiment was that bilateral olfactory bulbectomy in young rat pups leads to a decrease in nursing behavior which then results in a high mortality rate, let us first discuss suckling. Bulbectomy did lead to a general decrease in suckling as is apparent in Figures 4, 5, and 6 in the Results. In the following, several hypotheses which could account for this decrease in suckling will be considered. They will be discussed in relation to other findings from the analysis of the behavioral data and from other investigations.

It is very probable that the BX pups, receiving no olfactory cues, were not able to orient towards the nest and the female, therefore spending less time in the nest area near the female. Thus when a nursing session occurred, they missed all or part of it. The fact that BX-7 and BX-11 pups were found active apart from others more than other treatment groups tends to support this proposition. It is also supported by an observation, not quantitatively recorded, which revealed that BX pups were found out of the nest alone when inactive more than other treatment groups. These results agree with those from previous studies (Rouger et al., 1967 and Tobach et al., in preparation) in which it was noted that whenever a pup was found out of the nest and apart from others, it was usually a bulbectomized pup.

The fact that after surgery the BX-7 pups exhibited a dramatic increase in amount of time spent locomoting could also account for spending less time in the nest area near the female. However, because this increase was not shown by BX-2 and BX-11 pups, it is difficult to interpret. Levitsky and Barnes (1972) demonstrated that open-field locomotion was significantly increased in

rat pups by early malnutrition. Schapiro and Salas (1970) presented evidence that rats exhibit a behavioral response to the odor of their mother which consists of an inhibition of motor activity. Glickman (1958) has postulated that when deprived of a sensory system, animals become more active. These findings correspond with the locomotion data of the BX-7 pups but not with that of the BX-2 and BX-11 pups. Perhaps the bulb acts as a moderating structure inhibiting certain behavior such as motor activity at certain ages. As mentioned in the Introduction, Kumadaki et al. (1967) have suggested that the olfactory bulb has a depressant function on hypothalamic activity associated with emotional states. Hyperactivity is often considered an indication of an emotional state. It is also possible that there are crucial periods in the development and expression of motor activities such as locomotion. Watson (1903) pointed out that myelinization in the cerebellum first appears at approximately eight days of age in the white rat. Perhaps the loss of an inhibiting structure (such as the olfactory bulbs) at a particular period in the development and expression of locomotion may have resulted in the dramatic increase in locomotion of the BX-7 pups. It is interesting to note that on Day 13 when this locomotion effect was not as obvious, the BX-7 pups spent more time nosing the female than did the BX-2 and BX-11 pups.

A side effect of spending less time in contact with the female or other pups, which would contribute toward the debilitated state of the BX pups, is loss of body heat. Since young rats are essentially poikilothermic with underdeveloped capacities for either producing heat or minimizing its loss (Adolph, 1957), not being in contact with

others could have seriously affected the physical well-being of the BX pups.

Another factor contributing to a decrease in suckling could be motivational since the olfactory and accessary olfactory bulbs are connected to parts of the hypothalamus which have been associated with appetite and satiation. This is also conjecture and, again, is beyond the scope of this study. The exploration of this possibility would require detailed histological analysis of these brain structures in BX and control pups.

It could also be argued that an aspect of gustation might be impaired with olfactory bulbectomy and that this would contribute to a decrease in suckling, especially since a small branch of the trigeminal nerve enters the cranial cavity with the ethmoid artery at the olfactory depression. Wenzel (1971) has postulated that for any macrosomatic animal the feeding response has a trigeminal component and that the total response is a combination of these two inputs, tactocutaneous and olfactory. Zeigler (1972) has found that in birds trigeminal deafferentation disrupts the sensory control of mandibulation due to deprivation of tactile and proprioceptive information usually involved.

It is reasonable to think that perhaps competition for nipples among the pups could also be a factor contributing to the decreased suckling in the BX pups. Perhaps the BX pups were not able to attach to a nipple or, if attached, were pushed off by control littermates. In order to test this hypothesis, a small pilot study was conducted in which a few litters were culled to two pups. One was bulbectomized and the other was a handling control. The handling control was added

for the purpose of stimulating the female to produce milk. With only two pups in a litter, there should have been no competition problem; however, the BX pups in all cases died within several days after surgery. The HC pups survived indicating that the female was producing some milk.

Related to the above hypothesis is the data obtained on switching nipples in which there was no instance of certain treatment groups regularly switching to posterior or anterior nipples, the anterior being "preferred" since the anterior mammaries are more developed than the posterior. Even though on Day 13, SC-2 pups switched to an anterior nipple more often than BX-2 pups, they also did this more often than the SC-7 pups and the HC pups from non-treated litters. Thus the difference probably does not have to do with bulbectomy per se, because these two control groups are like the BX-2 pups in this respect.

The next logical question to ask, in trying to ascertain the reason why BX pups were different from other groups in amount of time spent suckling and active apart from others, is whether or not the female treated them differently from the other pups. In order to answer this question, several behavioral items of female-pup interaction were recorded during the observation session. In addition, retrieving tests were conducted in both the observation cage and the home cage so that there would be some measure to assess the effect of being in the observational apparatus on this important aspect of maternal behavior.

The fact that for the most part there were no treatment

differences in amount of time the female licked pups and in the latency to the first pick up and the number of times she retrieved pups indicates that differential treatment by the female was not a major factor in the behavioral differences of the BX pups. These general findings are in agreement with Rouger et al. (1967). They did not detect any differences in the response of the female to the different groups in the litter in terms of retrieving, nosing, licking, and huddling in the nursing position. A possible explanation for the fact that the female licked the other part of body of BX-11 pups more than other groups on Day 16 is that by this time the pups in the other groups are almost twice as heavy, except for the IBX-11 pups (although they are still heavier than the BX pups). In frequency of picking up and carrying pups the same reason could be used for the significant differences found on Day 16. The BX-7 and BX-11 pups may have been picked up and carried more often and carried for a longer duration because they were lighter than the others at this age. However, this does not explain why BX-2 pups were not picked up and carried more than others on Day 16.

The corresponding measures derived from retrieving tests in the observation cage and home cage also indicated no treatment differences. However, there seemed to be a difference in latency to the first time a pup was picked up by the female which depended upon the age of the litter. In general the latency to the first pick up was shorter on Days 6, 7, 9, and 10 than on Days 3, 4, 12, 13, and 15. These data agree with those of Beach and Jaynes (1956) who found that latencies to retrieving decreased by the time the litters were five

to seven days of age and with those of Rosenblatt and Lehrman (1963) who found that retrieving improves during the first four days and declines between the twelfth and sixteenth day. For the most part, no differences in latency to the first pick up were found between data obtained from retrieving tests held in the home cage and in the observation cage indicating that this aspect of retrieving behavior was not greatly disrupted by a sudden change in environment.

In regard to the number of times the female picked up pups, there were generally no treatment differences, but there did seem to be an effect related to changing the environment with more picking up occurring in the observation cage than in the home cage. This is not surprising because when the female was first placed in the observation cage there was no established nest corner because the substrate was a clean, acrylic tray. The establishment of the nest corner was usually done while picking up and carrying the pups. Often a few pups were put in one corner while others were placed in another corner. Then the female would go back to the first corner and transfer those pups to the newly-established nest area. When the test occurred in the home cage, probably not as much picking up occurred because the nest was defined. Usually the female picked up each pup once and deposited it in the nest. A developmental trend is not as evident in this measure although, for the most part, the female tended to pick up pups less often on Day 3 and 15. Perhaps this was because on Day 3 the pups were seldom out of the nest and by Day 15 picking up is more difficult because of their size.

Other behavioral items of the female, namely climbing and

rising, chasing tail, digging, and self-grooming, were recorded during the retrieving test to get an indication of amount of female disturbance. The first two items did not occur more or less often in the home cage or observation cage. Digging did occur more often in the home cage which is not surprising, because there was no sawdust in the observation cage. Self-grooming also took place more frequently in the home cage than in the observation cage. One reason for this difference might be that the female had more time to exhibit this activity in the home cage since she picked up pups fewer times there. Another factor might be the fact that there was sawdust on the substrate. This could result in more self-grooming.

Percentage of nest location changes were also used as a measure of female disturbance. It was found, however, that females with both high and low percentages of changes were randomly distributed among the four main treatment groups. This was fortunate and indicates that the litters were indeed randomly assigned to the four main treatment groups.

For the most part one could claim that the BX pup did not elicit changes in the behavior of the female toward itself or toward the litter in general. The last part of this statement is supported by the fact that the HC pups from non-treated litters were usually not different from the HC pups from the treated litters.

Concerning pup-pup interaction, as measured in this investigation, it did not appear to be affected, for the most part, by olfactory bulbectomy, because there were no differences in amount of time spent nosing other pups or active in the clump. The

difference between the BX-11 and IBX-11 pups after treatment in time spent weaving in the clump is difficult to interpret. However, even before treatment the IBX-11 pups seemed to have longer durations of weaving in the clump than the other groups. Perhaps this effect is due to sampling error.

Another measure of pup-pup interaction was obtained from the pup-placement tests. This was the number of times a pup made contact with another pup. Although no differences were found comparing ages, sexes, and data from the observation cage and the home cage, an unusual treatment difference was found. The HC-2 pups made more contact with others than the HC-11 pups or HC pups from non-treated litters. The interpretation of this finding is obscure. Perhaps it has something to do with the fact that after about five days of age, most of the HC-2 pups were in litters consisting of only four or five pups and thus were more active in making contact with them. However, one would then also expect the SC-2 pups to exhibit the same kind of behavior. Other measures derived from the pup-placement tests such as number of intervals pups moved (changed location) and number of times pups ended in the nest did not reveal any differences among treatments and ages, and between sexes and (for the former measure) home cage and observation cage.

2. Longitudinal Data

It is very unfortunate that the BX-7 and BX-11 pups could not be longitudinally analyzed due to lack of sufficient number. Because of this, a great deal of information was lost. Although cross-sectional

differences were found for behavioral items discussed in the preceding section, the fact that longitudinal differences were not found for the same items indicates that patterns of age differences, within each of the 11 treatment groups longitudinally analyzed, were not involved in the treatment differences found on any particular day. An exception to this is the greater frequency of switching to an anterior nipple exhibited by the SC-2 pups on Day 13 in comparison to the BX-2 pups and HC pups from non-treated litters. This result could be related to the fact that SC-2 pups switched to the anterior nipple a significantly greater number of times on Day 13 than on another day; whereas no longtitudinal differences were found for the BX-2 pups, and the HC pups from non-treated litters switched to the anterior nipple at a significantly lower frequency on Day 13 than on another day.

Concerning the more systematic longtitudinal differences that were revealed, the pattern of age differences found for self-grooming was expected and agrees with the result of Bolles and Woods (1964) who also found that by 16 days of age this behavior is evident. An interesting point, however, is that with one exception (SC-11 pups) this difference (more self-grooming occurring on Day 16 than on other days) was found only in groups that did not have surgery. The BX-2, IBX-11, SC-2, SC-7, and HC-7 pups did not exhibit this developmental trend. One could hypothesize that undergoing a surgical procedure, even a sham operation only, in some way interfered with the development of self-grooming in these groups. Of course, further research would be necessary to determine the critical factors in the development of this particular behavior.

The Bx-2 and HC-2 pups did not show the typical pattern of age differences for twitching (occurring more often on Days 7, 10, and 13 than on Days 4 and 16). If it were the BX-2 pups alone who did not show the pattern, one could postulate that it may have been due to being olfactorily bulbectomized in very early postnatal life. The fact that the HC-2 pups also did not exhibit this pattern makes the interpretation of this finding difficult without additional relevant data.

The longitudinal results of analysis on activity in the clump were not surprising, because the pups spent much more time in the clump on Days 4 and 7 than on later days. In this behavioral item, the BX-2 and IBX-11 pups were like the other groups indicating that both of these surgical treatments do not seem to affect the pattern of age differences for this activity.

C. Concluding Remarks

The data from this investigation seem to indicate that the problem of a decrease in amount of time spent suckling by the BX pups is not mainly due to differential treatment of the BX pups by the female (or by littermates) but rather due to some changes in the behavior of the pups themselves. Perhaps due to their lack of ability to pick up olfactory cues, the BX pups are not able to orient towards the female and nest area as well as the other pups and thus often are not near the female when a nursing session begins. The results showing that BX pups spent more time apart from others whether active or inactive and that some of the BX pups spent a great deal of time locomoting about the cage support this proposal. Because they are not always in

the nest area when a nursing session occurs, the BX pups may miss part or all of the session resulting in a decreased amount of time spent suckling. This result leads to inadequate nutrition which, in turn, leads to impaired growth or early death. Also, the lack of contact with the female or other pups results in a loss of body heat which could contribute toward the debilitated state of the BX pups.

It is possible that survival rate improves if olfactory bulbectomy is performed at a later age, because not only do the animals have more days of nursing experience in a normal situation, but by Day 12 or 15 they may be able to compensate somewhat for the loss of olfaction with the use of another sensory system such as audition, which becomes fully functional on about Day 12, and vision, which becomes fully functional at approximately 15 days of age.

APPENDIX

Page

Description of the olfactory system 104

1. Receptor area 104
2. Bulb 105
3. Accessory bulb 105
4. Vomeronasal organ 106
5. Olfactory nerve complex 107
6. Central projection areas 108

Table

1A	Suckling	110
2A	Nosing female	111
3A	Locomotion	112
4A	Activity apart from others	113
5A	Female picking up pup	114
11	Amount of time (seconds) spent suckling Day 4	115
12	Amount of time (seconds) spent suckling Day 13	116
13	Amount of time (seconds) spent suckling Day 16	117
14	Amount of time (seconds) spent suckling Day 16 AM	118
15	Amount of time (seconds) spent nosing female Day 13	119
16	Frequency of switching to anterior nipple Day 13	120
17	Amount of time (seconds) spent locomoting, Day 10	121

Table		Page
18	Amount of time (seconds) spent locomoting Day 16 AM	122
19	Amount of time (seconds) spent apart from others Day 10	123
20	Amount of time (seconds) spent apart from others Day 16 AM	124
21	Amount of time (seconds) spent weaving in the clump Day 13	125
22	Amount of time (seconds) weaving in the the clump Day 16 AM	126
23	Amount of time (seconds) female spent licking other part of pup's body Day 16 AM	127
24	Frequency of female lifting pup Day 16 AM	128
25	Frequency of female carrying pup Day 16 AM	129
26	Amount of time (seconds) female spent carrying pup Day 16	130
27	"Self-grooming" HC-2 pups	131
28	"Self-grooming" HC-11 pups	132
29	"Self-grooming" HC pups from non-treated litters	133
30	"Self-grooming" male HC pups from non-treated litters	134
31	"Self-grooming" SC-11 pups	135
32	"Self-grooming" female HC pups from non-treated litters	136
33	"Pup-twitching" SC-11 pups	137
34	"Pup-twitching" HC-7 pups	138
35	"Pup-twitching" HC-11 pups	139
36	"Pup-twitching" HC pups from non-treated litters	140

Table		Page
37	"Pup-twitching" female HC pups from non-treated litters	141
38	"Pup-twitching" male HC pups from non-treated litters	142
39	"Pup-twitching" SC-2 pups	143
40	"Active in the clump" SC-7 pups	144
41	"Pup-twitching" IBX-11 pups	145
42	"Active in the clump" BX-2 pups	146
43	"Active in the clump" IBX-11 pups	147
44	"Pup twitching" SC-7 pups	148
45	"Active in the clump" HC-7 pups	149
46	"Active in the clump" HC-11 pups	150
47	"Active in the clump" male HC pups from non-treated litters	151
48	Spearman rank-order correlation coefficients between number of intervals moved and age	152
49	Wilcoxon matched-pairs signed-ranks tests comparing days for number of times female picked up pups. Litter 11, non-treated handling control	153
50	Wilcoxon matched-pairs signed-ranks tests Litter 17, non-treated handling control	154
51	Wilcoxon matched-pairs signed-ranks tests Litter 28, non-treated handling control	155
52	Wilcoxon matched-pairs signed-ranks tests Litter 37, treated on Day 2	156
53	Wilcoxon matched-pairs signed-ranks tests Litter 12 before treatment on Day 11	157
54	Wilcoxon matched-pairs signed-ranks tests Litter 16 before treatment on Day 11	158

Table		Page
55	Wilcoxon matched-pairs signed-ranks tests Litter 29 before treatment on Day 11	159
56	Wilcoxon matched-pairs signed-ranks tests Litter 25 before treatment on Day 11	160
57	Wilcoxon matched-pairs signed-ranks tests Litter 36 before treatment on Day 11	161
58	Wilcoxon matched-pairs signed-ranks tests comparing days for number of intervals in which females were digging	162
59	Wilcoxon matched-pairs signed-ranks tests comparing days for number of intervals in which females were self-grooming	163

DESCRIPTION OF THE OLFACTORY SYSTEM

The following description deals with the mammalian system and emphasizes the peripheral and bulbar aspects. The description includes the olfactory receptor area, the olfactory bulb, the accessory olfactory bulb, the vomeronasal organ, and a summary of the central olfactory projection areas.

1. Receptor Area

This area is on the inner surface of the nasal cavities which lines the upper part of the roof of each nasal cavity and consists of a thick pseudostratified epithelium and a thick lamina propria. The epithelium contains a yellow pigment which accounts for the yellowish color of the mucous membrane. (The function of this pigment is not known but Sinclair (1971) has postulated that it may be involved with specific olfactory sensitivity since albinos which lack the pigment are less able to cope with obnoxious stimuli.) The epithelium also contains the olfactory receptor cells which are somewhat unique in that they are also primary nerve cells. The dendrites of these nerve cells protrude small hairlike endings into the nasal mucosa. These hair-dendrites are the receptors proper. Contact of these hair-dendrites by odorous molecules in solution is the adequate stimulus for smell. Activation of the hair cells by odors produces a relatively slow and long lasting generator potential (Moulton and Beidler, 1967 and Ottoson, 1963). The unmyelinated axons from each olfactory receptor cell pass from the bundles

of olfactory nerve fibers. Collectively, these make up the olfactory nerve (the first cranial nerve), which enters the bulb by way of the cribiform plate of the ethmoid bone (Ham, 1965).

2. Bulb

The olfactory bulb is large in lower mammals such as rodents, ungulates, and carnivores. It is relatively small in higher primates particularly in man. In lower mammals the bulb is located directly anterior to the frontal pole of the forebrain. The olfactory nerve fibers enter the bulb mainly at the antero-ventral part of the bulb and spread out over the entire surface of the bulb.

In sections the olfactory bulb is seen to consist of the following layers proceeding from the outer surface to the olfactory ventricle: layer of olfactory nerve fibers, layer of glomeruli, external plexiform layer, internal plexiform layer, granular layer, and periventricular layer (Allison, 1953, and Valverde, 1965).

3. Accessory Bulb

The accessory olfactory bulb is a small hemispherical body which is present in most orders of mammals including the rat (Kappers, Huber, and Crosby, 1936; Raisman, 1971). It is located in the dorso-posterior region of the main bulb directly in front of the anterior olfactory nucleus. It receives fibers from the vomeronasal organ of Jacobson. The size of the accessory bulb in different species varies in direct proportion to the vomeronasal organ. Kappers et al. (1936) have suggested that the accessory bulb represents an adaptation to

life on land because in forms below amphibians, it is reduced or disappears during development.

In sections the accessory bulb shows lamination similar to that in the main bulb. However, instead of having an outer layer of olfactory nerve fibers, it has an outer layer of vomeronasal nerve fibers, since the vomeronasal nerve enters the antero-medial area of the accessory bulb. Also, in the external plexiform layer, instead of mitral cells, there are small and medium-sized triangular neurons, each of which has several dendrites reaching into the glomerular layer (Allison, 1953).

4. Vomeronasal Organ

The accessory bulb receives projections from the vomeronasal organ. In mammals the organ generally has the form of a long, thin tube, partly lined by sensory epithelium, lying in the floor of the nasal cavity alongside the nasal septum and protected by bone or cartilage. The tube is blind posteriorly, and its narrow duct opens anteriorly into the nasal cavity (as in the rat, rabbit, and guinea pig), or, more commonly, into the naso-palatine canal (Fleming, 1953). The epithelium lining the organ resembles olfactory epithelium except it does not have the terminal hairs characteristic of the olfactory receptor cells. Comparatively little is known about the physiological significance of the vomeronasal organ, but it is generally thought to have some sort of chemoreceptive function. The opening is located where entry of moisture-borne substances picked up by the snout or taken into

the mouth is possible (Negus, 1958).

5. Olfactory Nerve Complex

Before elaborating on the central olfactory projection areas, let us briefly discuss the three nerves which enter the telencephalon from the region of the nose. They are the olfactory nerve, the vomeronasal nerve, and the terminal nerve. The olfactory nerve,as mentioned before,is made up of bundles of axons of sensory cells and enters the olfactory bulb through the cribiform plate. The vomeronasal nerve connects the vomeronasal organ with the accessory olfactory bulb which, in turn, is connected with the medio-cortical complex of the amygdala (Winans and Scalia, 1970). These connections and the similarlity in structure of the accessory bulb and the main olfactory bulb suggest that the vomeronasal nerve is a special differentiation of the olfactory system. The terminal nerve enters the ventromedial portion of the telencephalon by small roots. Traced peripheralward, it runs along the olfactory bulb on its ventro-medial side. When it reaches the system,the terminal nerve joins the vomeronasal nerve and accompanies this nerve to the vomeronasal organ. The terminal nerve also supplies the septal area near the vomeronasal organ and probably distributes to the septal mucosa and to blood vessels of the region (Kappers et al., 1936). Both the vomeronasal and terminal nerves are constant features of mammalian embryos, though the vomeronasal division is only embryonic in some mammals (Sinclair, 1971).

Another nerve, a small branch of the trigeminal, enters the cranial cavity at the olfactory depression with the ethmoid artery. There is evidence to support the hypothesis that olfactory responses are partially mediated by the trigeminal system (Stone, 1969).

6. Central Projection Areas

The following is a widely accepted description of the central projections of the olfactory bulb. The lateral olfactory tract carries sensory afferents to the cortical and medial amygdaloid nuclei, the piriform cortex, and the uncus. The intermediate olfactory tract passes to the anterior perforated substance and from there goes to the medial and lateral parts of the hypothalamus from which centrifugal fibers proceed back to the bulb. The medial olfactory tract goes to the septum and from there to the epithalamus (Allison, 1953).

However, an account of the central projection areas of the olfactory bulb from a study done by Powell, Cowan, and Raisman (1965) on the rat differs from this widely accepted description in limiting projection to the lateral olfactory tract. They propose that the olfactory bulb projects only through the lateral olfactory tract to (1) the dorsal and external parts of the anterior olfactory nucleus, (2) the antero-lateral part of the olfactory tubercule, (3) the entire piriform cortex, (4) the nucleus of the lateral olfactory tract, and (5) the cortical and medial amygdaloid nuclei. They go on to say that the antero-lateral part of the olfactory tubercle and the piriform cortex are connected to the medial forebrain bundle and that the cortical and medial parts of the amygdala are connected to the

medial preoptic area and medial hypothalamus. They also claim that the anterior limb of the anterior commissure receives no fibers from the olfactory bulb and projects only to the contralateral anterior olfactory nucleus and olfactory bulb.

TABLE 1A

SUCKLING

NUMBER OF PUPS, MEAN DURATION, AND STANDARD DEVIATION

Treatment	Pups Treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			Non-treated Pups		
					Day 4							
	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
BX	9	57.33	113.77	8	219.12	108.47	8	334.75	148.43	..	..	..
IBX	..	..	..	..	..	..	8	320.75	221.00	..	..	..
SC	10	337.30	150.13	6	454.00	145.15	12	351.42	155.81	..	..	..
HC	10	357.00	207.38	6	387.83	146.99	12	330.67	210.52	21	363.00	186.03
					Day 7							
BX	2	175.50	248.19	8	321.50	119.12	8	354,12	132.39	..	..	..
IBX	..	..	..	..	..	..	8	331.00	170.96	..	..	..
SC	10	242.50	158.55	6	284.67	129.16	12	467.42	194.14	..	..	..
HC	10	278.90	220.36	6	480.17	175.94	12	328.92	160.22	21	423.67	168.26
					Day 10							
BX	2	23.50	75.66	7	136.00	130.64	8	383.38	97.20	..	..	..
IBX	..	..	..	..	..	..	8	353.88	135.72	..	..	..
SC	10	301.80	206.06	6	397.33	202.94	12	312.67	183.14	..	..	..
HC	10	344.80	167.90	6	477.17	125.26	12	361.17	170.17	21	411.90	200.77
					Day 13							
BX	2	85.50	120.92	3	57.67	99.88	8	116.88	101.18	..	..	..
IBX	..	..	..	..	..	..	8	255.12	242.90	..	..	..
SC	9	367.44	183.21	6	365.50	159.72	12	372.83	179.63	..	..	..
HC	10	483.50	129.08	6	263.83	201.11	12	342.92	144.74	21	403.14	155.85
					Day 16							
BX	2	259.50	115.26	2	0	-	3	81.67	141.45	..	..	..
IBX	..	..	..	..	..	..	8	251.88	97.21	..	..	..
SC	7	426.86	103.63	6	348.83	155.90	12	285.08	131.45	..	..	..
HC	10	544.70	218.06	6	238.83	140.77	12	268.83	129.52	21	348.24	142.01

TABLE 2 A

NOSING FEMALE

NUMBER OF PUPS, MEAN DURATION, AND STANDARD DEVIATION

Treatment	Pups Treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			Non-treated Pups		
	Day 13											
	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
BX	2	5.00	7.07	3	51.67	45.00	8	5.62	7.37	-	--	--
IBX	-	--	--	-	--	--	8	34.37	27.92	-	--	--
SC	9	42.67	32.56	6	33.00	29.09	12	49.67	36.64	-	--	--
HC	10	41.20	28.91	6	15.33	23.11	12	28.75	17.46	21	24.81	17.38

TABLE 3A

LOCOMOTION

NUMBER OF PUPS, MEAN DURATION, AND STANDARD DEVIATION

Treatment	Pups Treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			Non-treated Pups		
					Day 4							
	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
BX	9	.78	1.72	8	.12	.35	8	.25	.46	..	..	..
IBX	..	..	..	..	..	..	8	3.25	3.10	..	..	..
SC	10	.80	1.62	6	.17	.41	12	.58	1.00	..	..	..
HC	10	.40	.84	6	1.50	2.81	12	4.92	8.30	21	2.57	4.34
					Day 7							
BX	2	.50	.71	8	1.88	3.18	8	.12	.35	..	..	..
IBX	..	..	..	..	..	..	8	.75	1.75	..	..	..
SC	10	.90	1.91	6	1.50	2.81	12	1.42	2.02			
HC	10	2.70	4.72	6	.17	.41	12	1.33	2.81	21	.28	.96
					Day 10							
BX	2	3.50	2.12	7	26.86	25.39	8	.38	.74	..	..	..
IBX	..	..	..	..	..	..	8	2.50	4.00	..	..	..
SC	10	1.50	2.17	6	1.00	1.26	12	6.17	10.21	..	..	..
HC	10	2.30	3.16	6	.50	.55	12	1.50	1.93	21	2.52	5.50
					Day 13							
BX	2	1.50	2.12	3	11.00	5.00	8	4.25	9.24	..	..	..
IBX	..	..	..	..	..	..	8	.87	1.12	..	..	..
SC	9	.44	1.01	6	1.50	1.76	12	2.58	6.65	..	..	..
HC	10	1.40	3.75	6	.33	.52	12	10.50	21.49	21	5.00	15.77
					Day 16							
BX	2	0	-	2	24.00	14.14	3	7.67	8.02	..	..	..
IBX	..	..	..	..	..	..	8	7.25	8.46	..	..	..
SC	7	1.00	1.73	6	0	-	12	2.75	4.63	..	..	..
HC	10	1.30	2.67	6	0	-	12	3.17	6.31	21	10.40	17.40

TABLE 4A

ACTIVITY APART FROM OTHERS

NUMBER OF PUPS, MEAN DURATION, AND STANDARD DEVIATION

Treatment	Pups treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			Non-treated Pups		
					Day 4							
	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
BX	9	44.00	49.14	8	13.75	14.45	8	6.25	11.09	..	..	..
IBX	..	..	..	..	..	..	8	33.12	35.23	..	..	..
SC	10	3.60	4.12	6	10.00	16.78	12	17.67	29.66	..	..	..
HC	10	46.20	67.77	6	16.33	26.37	12	14.33	24.57	21	23.38	41.21
					Day 7							
BX	2	1.50	2.12	8	29.62	37.46	8	12.25	15.73	..	...	..
IBX	..	..	..	..	..	..	8	9.75	13.81	..	..	..
SC	10	31.10	40.24	6	31.33	34.43	12	16.42	25.86	..	..	..
HC	10	26.10	38.54	6	10.33	16.81	12	5.67	9.51	21	10.38	24.25
					Day 10							
BX	2	1.50	2.12	7	35.85	49.18	8	7.12	10.32	..	..	..
IBX	..	..	..	..	..	..	8	8.00	8.45	..	..	..
SC	10	32.70	28.66	6	5.17	7.17	12	25.75	32.27	..	..	..
HC	10	23.90	30.91	6	8.17	16.81	12	10.08	11.77	21	8.90	14.01
					Day 13							
BX	2	4.50	6.36	3	25.00	20.88	8	30.25	46.75	..	..	..
IBX	..	..	..	..	..	..	8	8.62	16.93	..	..	..
SC	9	28.22	73.32	6	5.33	7.23	12	6.00	9.23	..	..	..
HC	10	3.90	5.65	6	8.33	13.00	12	12.67	25.28	21	5.48	11.15
					Day 16							
BX	2	0	-	2	59.50	31.82	3	43.33	47.44	..	..	..
IBX	..	..	..	..	..	..	8	3.38	7.25	..	..	..
SC	7	2.57	4.54	6	0	-	12	3.67	4.10	..	..	..
HC	10	1.70	3.33	6	0.33	.52	12	2.75	5.65	21	7.19	9.54

TABLE 5A

FEMALE PICKING UP PUP

NUMBER OF PUPS, MEAN FREQUENCY, AND STANDARD DEVIATION

Treatment	Pups Treated on Day 2			Pups Treated on Day 7			Pups Treated on Day 11			Non-treated Pups		
	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.
Day 4												
BX	9	.67	.71	8	.62	1.41	8	1.00	1.07			
IBX	--	--	--	--	--	--	8	.87	1.12	--	--	--
SC	10	.70	1.25	6	.66	.82	12	.50	.90	--	--	--
HC	10	1.10	1.67	6	0	--	12	.42	.67	21	.29	.56
Day 7												
BX	2	.50	.71	8	.12	.35	8	.25	.71			
IBX	--	--	--	--	--	--	8	.87	.83	--	--	--
SC	10	.40	.70	6	1.33	1.03	12	.75	.87	--	--	--
HC	10	.40	.52	6	.17	.41	12	.67	.98	21	.81	1.36
DAY 10												
BX	2	0	--	7	.28	.49	8	.12	.35			
IBX	--	--	--	--	--	--	8	.12	.35	--	--	--
SC	10	.90	1.10	6	.17	.41	12	.58	.90	--	--	--
HC	10	.28	1.10	6	0	--	12	.58	.90	21	.28	.56
DAY 13												
BX	2	0		3	.33	.58	8	.12	.35			
IBX	--	--		--	--	--	8	.12	.35	--	--	--
SC	9	.33	.71	6	.17	.41	12	.50	.90	--	--	--
HC	10	.10	.32	6	0		12	.83	2.12	21	.24	.70
DAY 16												
BX	2	0	--	2	.50	.71	3	.33	.58			
IBX	--	--	--	--	--	--	8	.25	.46	--	--	--
SC	7	0	--	--	0	--	12	0	--	--	--	--
HC	10	.10	.32	6	0	--	12	.08	.29	21	.24	.54

TABLE 11A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT SUCKLING

DAY 4

Source	d.f.	M.S.	F
Between subjects	12	81062.750	2.664**
Within subjects	118	30427.727	
Total	130		

TABLE 11B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-2	BX-7	IX-11	HC-F	H-11	BX-11	SC-2	SG-11	H-2	HC-FM	H-7	HC-M	SC-7
	Means	57.33	219.12	320.75	321.00	330.67	334.75	337.30	351.42	357.00	363.00	387.83	401.18	454.00
BX-2	57.33		2.80**	4.56**	4.57**	4.73**	4.80**	4.85**	5.09**	5.19**	5.29**	5.72**	5.95**	6.87**
BX-7	219.12			1.76	1.76	1.93	2.00	2.05	2.29	2.39	2.49	2.92	3.15	4.07
IX-11	320.75				0.00	0.17	0.24	0.29	0.53	0.63	0.73	1.16	1.39	2.31
HC-F	321.00					0.17	0.24	0.28	0.53	0.62	0.73	1.16	1.39	2.30
H-11	330.67						0.07	0.11	0.36	0.46	0.56	0.99	1.22	2.14
BX-11	334.75							0.04	0.29	0.39	0.49	0.92	1.15	2.07
SC-2	337.30								0.24	0.34	0.45	0.88	1.11	2.02
SC-11	351.42									0.10	0.20	0.63	0.86	1.78
H-2	357.00										0.10	0.54	0.77	1.68
HC-FM	363.00											0.43	0.66	1.58
H-7	387.83												0.23	1.15
HC-M	401.18													0.91
SC-7	454.00													

** $p<0.01$

TABLE 12 A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT SUCKLING

DAY 13

Source	d.f.	M.S.	F
Between subjects	12	108412.250	4.085**
Within subjects	105	26541.227	
Total	117		

TABLE 12B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-7	BX-2	BX-11	H-7	IX-11	H-11	HC-M	SC-7	SC-2	SC-11	HC-FM	HC-F	H-2
	Means	57.67	85.50	116.87	253.83	255.12	342.92	362.82	365.50	367.44	372.83	403.14	447.50	483.50
BX-7	57.67		0.43	0.92	3.04	3.06	4.43**	4.74**	4.78**	4.81**	4.89**	5.36**	6.05**	6.61**
BX-2	85.50			0.49	2.61	2.63	4.00	4.30	4.35	4.38	4.46	4.93**	5.62**	6.18**
BX-11	116.87				2.13	2.15	3.51	3.82	3.86	3.89	3.97	4.44	5.13**	5.69**
H-7	253.83					0.02	1.38	1.69	1.73	1.76	1.85	2.32	3.01	3.56
IX-11	255.12						1.36	1.67	1.71	1.74	1.83	2.30	2.99	3.54
H-11	342.92							0.31	0.35	0.38	0.46	0.93	1.62	2.18
HC-M	362.82								0.04	0.07	0.16	0.63	1.31	1.87
SC-7	365.50									0.03	0.11	0.58	1.27	1.83
SC-2	367.44										0.08	0.55	1.24	1.80
SC-11	372.83											0.47	1.16	1.72
HC-FM	403.14												0.69	1.25
HC-F	447.50													0.56
H-2	483.50													

** $p<0.01$

TABLE 13A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT SUCKLING

DAY 16

Source	d.f.	M.S.	F
Between subjects	12	95029.875	4.619**
Within subjects	97	20575.566	
Total	109		

TABLE 13B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-7	BX-11	H-7	IX-11	BX-2	H-11	SC-11	HC-M	HC-FM	SC-7	HC-F	SC-2	H-2
	Means	0.00	81.67	238.83	251.87	259.50	268.83	285.08	320.45	348.24	348.83	378.80	426.86	544.70
BX-7	0.00		1.31	3.84**	4.05**	4.18**	4.33**	4.59**	5.16**	5.60**	5.61**	6.10**	6.87**	8.77**
BX-11	81.67			2.53	2.74	2.86	3.01	3.27	3.84	4.29	4.30	4.78**	5.56**	7.45**
H-7	238.83				0.21	0.33	0.48	0.74	1.31	1.76	1.77	2.25	3.03	4.92**
IX-11	251.87					0.12	0.27	0.53	1.10	1.55	1.56	2.04	2.82	4.71**
BX-2	259.50						0.15	0.41	0.98	1.43	1.44	1.92	2.69	4.59**
H-11	268.83							0.26	0.83	1.28	1.29	1.77	2.54	4.44**
SG-11	285.08								0.57	1.02	1.03	1.51	2.28	4.18
HC-M	320.45									0.45	0.46	0.94	1.71	3.61
HC-FM	348.24										0.01	0.49	1.27	3.16
SC-7	348.33											0.48	1.26	3.15
HC-F	378.80												0.77	2.67
SC-2	426.86													1.90

** $p < 0.01$

TABLE 14A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT SUCKLING

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	38575.426	4.573**
Within subjects	97	8434.820	
Total	109		

TABLE 14B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-7	BX-2	BX-11	IX-11	H-11	H-7	SC-11	HC-F	HC-FM	SC-7	HC-M	SC-2	H-2
	Means	0.0	0.0	31.00	117.37	118.42	121.50	124.08	164.70	185.76	187.67	204.91	243.00	288.40
BX-7	0.0		0.0	0.78	2.95	2.98	3.05	3.12	4.14	4.67**	4.72**	5.15**	6.11**	7.25**
BX-2	0.0			0.78	2.95	2.98	3.05	3.12	4.14	4.67**	4.72**	5.15**	6.11**	7.25**
BX-11	31.00				2.17	2.20	2.27	2.34	3.36	3.89	3.94	4.37	5.33**	6.47**
IX-11	117.37					0.03	0.10	0.17	1.19	1.72	1.77	2.20	3.16	4.30
H-11	118.42						0.07	0.14	1.16	1.69	1.74	2.17	3.10	4.27
H-7	121.50							0.06	1.09	1.62	1.66	2.10	3.05	4.19
SC-11	124.08								1.02	1.55	1.60	2.03	2.99	4.13
HC-F	164.70									0.53	0.58	1.01	1.97	3.11
HC-FM	185.76										0.05	0.48	1.44	2.58
SC-7	187.67											0.43	1.39	2.53
HC-M	204.91												0.96	2.10
SC-2	243.00													1.14
H-2	288.40													

** $p < 0.01$

TABLE 15A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT NOSING FEMALE

DAY 13

Source	d.f.	M.S.	F
Between subjects	12	1503.491	2.530**
Within subjects	105	594.157	
Total	117		

TABLE 15B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-2	BX-11	H-7	HC-F	HC-FM	H-11	HC-M	HC-7	IX-11	H-2	SC-2	SC-11	BX-7
	Means	5.00	5.63	15.33	19.00	24.81	28.75	30.09	33.00	34.38	41.20	42.67	49.67	51.67
BX-2	5.00		0.06	1.07	1.45	2.06	2.46	2.60	2.90	3.05	3.76	3.91	4.63	4.84**
BX-11	5.63			1.01	1.39	1.99	2.40	2.54	2.84	2.98	3.69	3.84	4.57	4.78**
H-7	15.33				0.38	0.98	1.39	1.53	1.83	1.98	2.68	2.84	3.56	3.77
HC-F	19.00					0.60	1.01	1.15	1.45	1.60	2.30	2.46	3.18	3.39
HC-FM	24.81						0.41	0.55	0.85	0.99	1.70	1.85	2.58	2.79
H-11	28.75							0.14	0.44	0.58	1.29	1.44	2.17	2.38
HC-M	30.09								0.30	0.44	1.15	1.30	2.03	2.24
SC-7	33.00									0.14	0.85	1.00	1.73	1.94
IX-11	34.38										0.71	0.86	1.59	1.79
H-2	41.20											0.15	0.88	1.09
SC-2	42.67												0.73	0.93
SC-11	49.67													0.21
BX-7	51.67													

** p ≤ 0.01

TABLE 16A

ANALYSIS OF VARIANCE ON FREQUENCY OF SWITCHING TO ANTERIOR NIPPLE

DAY 13

Source	d.f.	M.S.	F
Between subjects	12	0.605	3.108**
Within subjects	105	0.195	
Total	117		

TABLE 16B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-11	BX-2	BX-7	SC-7	HC-F	HC-M	HC-FM	IX-11	H-7	H-2	SC-11	H-11	SC-2
	Means	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.13	0.33	0.40	0.42	0.58	0.67
BX-11	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.72	1.91	2.29	2.39	3.34	3.82**
BX-2	0.0			0.0	0.0	0.0	0.0	0.0	0.72	1.91	2.29	2.39	3.34	3.82**
BX-7	0.0				0.0	0.0	0.0	0.0	0.72	1.91	2.29	2.39	3.34	3.82**
SC-7	0.0					0.0	0.0	0.0	0.72	1.91	2.29	2.39	3.34	3.82**
HC-F	0.0						0.0	0.0	0.72	1.91	2.29	2.39	3.34	3.82**
HC-M	0.0							0.0	0.72	1.91	2.29	2.39	3.34	3.82**
HC-FM	0.0								0.72	1.91	2.29	2.39	3.34	3.82**
IX-11	0.13									1.19	1.58	1.67	2.63	3.10
H-7	0.33										0.38	0.48	1.43	1.91
H-2	0.40											0.10	1.05	1.53
SC-11	0.42												0.96	1.43
H-11	0.58													0.48
SC-2	0.67													

** $p<0.01$

TABLE 17A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT LOCOMOTING

DAY 10

Source	d.f.	M.F.	F
Between subjects	12	354.773	6.016**
Within subjects	110	58.972	
Total	122		

TABLE 17B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-11	H-7	SC-7	HC-M	SC-2	H-11	H-2	IX-11	HC-FM	BX-2	HC-F	SG-11	BX-7
	Means	0.38	0.50	1.00	1.18	1.50	1.50	2.30	2.50	2.52	3.50	4.00	6.17	26.86
BX-11	0.38		0.04	0.22	0.28	0.39	0.39	0.67	0.74	0.75	1.08	1.26	2.01	9.19**
H-7	0.50			0.17	0.24	0.35	0.35	0.62	0.69	0.70	1.04	1.21	1.97	9.12**
SC-7	1.00				0.06	0.17	0.17	0.45	0.52	0.53	0.87	1.04	1.79	8.97**
HC-M	1.18					0.11	0.11	0.39	0.46	0.47	0.80	0.98	1.73	8.91**
SC-2	1.50						0.0	0.28	0.35	0.36	0.69	0.87	1.62	8.80**
H-11	1.50							0.28	0.35	0.36	0.69	0.87	1.62	8.80**
H-2	2.30								0.07	0.08	0.42	0.59	1.34	8.52**
IX-11	2.50									0.01	0.35	0.52	1.27	8.45**
HC-FM	2.52										0.34	0.51	1.26	8.44**
BX-2	3.50											0.17	0.93	8.10**
HC-F	4.00												0.75	7.93**
SC-11	6.17													7.18**
BX-7	26.86													

** $p<0.01$

TABLE 18A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT LOCOMOTING

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	99.877	2.061*
Within subjects	97	48.452	
Total	109		

TABLE 18B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		SC-7	BX-2	SC-2	H-7	H-2	SC-11	H-11	HC-F	HC-FM	HC-M	IX-11	BX-11	BX-7
	Means	0.0	0.0	0.0	0.0	0.50	1.58	2.75	3.40	3.52	3.64	4.00	6.00	24.00
SC-7	0.0		0.0	0.0	0.0	0.17	0.53	0.91	1.13	1.17	1.21	1.33	1.99	7.96*
BX-2				0.0	0.0	0.17	0.53	0.91	1.13	1.17	1.21	1.33	1.99	7.96*
SC-2					0.0	0.17	0.53	0.91	1.13	1.17	1.21	1.33	1.99	7.96*
H-7						0.17	0.53	0.91	1.13	1.17	1.21	1.33	1.99	7.96*
H-2	0.50						0.36	0.75	0.96	1.00	1.04	1.16	1.82	7.79*
SC-11	1.58							0.39	0.60	0.64	0.68	0.80	1.46	7.43*
H-11	2.75								0.22	0.26	0.29	0.41	1.08	7.05*
HC-F	3.40									0.04	0.08	0.20	0.86	6.83*
HC-FM	3.52										0.04	0.16	0.82	6.79*
HC-M	3.64											0.12	0.68	6.75*
IX-11	4.00												0.66	6.63*
BX-11	6.00													5.97*
BX-7	24.00													

* $p<0.05$

TABLE 19A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT ACTIVE APART FROM OTHERS

DAY 10

Source	d.f.	M.S.	F
Between subjects	12	1045.961	2.130*
Within subjects	110	491.102	
Total	122		

TABLE 19B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-2	SC-7	HC-F	BX-11	IX-11	H-7	HC-FM	H-11	HC-M	H-2	SC-11	SC-2	BX-7
	Means	1.50	5.17	5.40	7.12	8.00	8.17	8.90	10.08	12.09	23.90	25.75	32.70	35.86
BX-2	1.50		0.44	0.47	0.68	0.78	0.80	0.89	1.03	1.27	2.69	2.92	3.75	4.13*
SC-7	5.17			0.03	0.24	0.34	0.36	0.45	0.59	0.83	2.25	2.47	3.31	3.69
HC-7	5.40				0.21	0.31	0.33	0.42	0.56	0.80	2.22	2.45	3.28	3.66
BX-11	7.12					0.11	0.13	0.21	0.36	0.60	2.02	2.24	3.07	3.45
IX-11	8.00						0.02	0.11	0.25	0.49	1.91	2.13	2.97	3.35
H-7	8.17							0.09	0.23	0.47	1.89	2.11	2.95	3.33
HC-FM	8.90								0.14	0.38	1.80	2.03	2.86	3.24
H-11	10.08									0.24	1.66	1.88	2.72	3.10
HC-M	12.09										1.42	1.64	2.48	2.86
H-2	23.90											0.22	1.06	1.44
SC-11	25.75												0.84	1.22
SC-2	32.70													0.38
BX-7	35.86													

* $p<0.05$

TABLE 20A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT ACTIVE APART FROM OTHERS

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	871.747	9.109**
Within subjects	97	95.697	
Total	109		

TABLE 20B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments	Means	SC-2	SC-7	BX-2	H-7	IX-11	H-2	HC-F	H-11	SC-11	HC-FM	HC-M	BX-11	BX-7
	Means	0.0	0.0	0.0	0.33	0.63	0.70	1.40	1.92	2.50	2.76	4.00	38.67	59.50
SC-2	0.0		0.0	0.0	0.08	0.15	0.17	0.33	0.45	0.59	0.65	0.94	9.12**	14.04**
SC-7	0.0			0.0	0.08	0.15	0.17	0.33	0.45	0.59	0.65	0.94	9.12**	14.04**
BX-2	0.0				0.08	0.15	0.17	0.33	0.45	0.59	0.65	0.94	9.12**	14.04**
H-7	0.33					0.07	0.09	0.25	0.37	0.51	0.57	0.87	9.05**	13.96**
IX-11	0.63						0.02	0.18	0.30	0.44	0.50	0.80	8.98**	13.89**
H-2	0.70							0.17	0.29	0.42	0.49	0.78	8.96**	13.87**
HC-F	1.40								0.12	0.26	0.32	0.61	8.79**	13.71**
H-11	1.92									0.14	0.20	0.49	8.67**	13.59**
SC-11	2.50										0.06	0.35	8.53**	13.45**
HC-FM	2.76											0.29	8.47**	13.39**
HC-M	4.00												8.18**	13.10**
BX-11	38.67													4.92**
BX-7	59.50													

** $p<0.01$

TABLE 21A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) SPENT WEAVING IN THE CLUMP

DAY 13

Source	d.f.	M.S.	F
Between subjects	12	410.302	3.126**
Within subjects	105	131.259	
Total	117		

TABLE 21B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-11	H-7	SC-2	H-2	SC-7	H-11	HC-F	HG-FM	SG-11	HC-M	BX-2	BX-7	IX-11
	Means	3.87	5.00	8.33	9.60	10.00	13.83	15.30	16.67	17.58	17.91	18.00	25.33	30.50
BX-11	3.87		0.25	0.98	1.26	1.35	2.20	2.52	2.82	3.03	3.10	3.12	4.74	5.88**
H-7	5.00			0.74	1.02	1.10	1.95	2.27	2.58	2.78	2.85	2.87	4.49	5.63**
SC-2	8.33				0.28	0.37	1.21	1.54	1.84	2.04	2.11	2.13	3.75	4.89**
H-2	9.60					0.09	0.93	1.26	1.56	1.76	1.83	1.85	3.47	4.61**
SC-7	10.00						0.85	1.17	1.47	1.67	1.75	1.77	3.38	4.52**
H-11	13.83							0.32	0.63	0.83	0.90	0.92	2.54	3.68
HC-F	15.30								0.30	0.50	0.58	0.60	2.21	3.35
HC-FM	16.67									0.20	0.27	0.29	1.91	3.05
SC-11	17.58										0.07	0.09	1.71	2.85
HC-M	17.91											0.02	1.64	2.78
BX-2	18.00												1.62	2.76
BX-7	25.33													1.14
IX-11	30.50													

** $p < 0.01$

TABLE 22A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) WEAVING IN THE CLUMP

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	116.275	2.145*
Within subjects	97	54.199	
Total	109		

TABLE 22B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

DAY 16 (AM OBSERVATIONS ONLY)

Treatments		BX-11	BX-7	H-7	SC-7	SC-2	H-2	H-11	HC-F	HC-FM	HC-M	SC-11	BX-2	IX-11
	Means	2.00	2.50	2.83	3.00	3.29	3.30	4.17	4.60	5.29	5.91	6.67	14.50	16.50
BX-11	2.00		0.16	0.26	0.31	0.40	0.41	0.68	0.82	1.03	1.23	1.46	3.92	4.55*
BX-7	2.50			0.10	0.16	0.25	0.52	0.52	0.66	0.87	1.07	1.31	3.76	4.39
H-7	2.83				0.05	0.14	0.15	0.42	0.55	0.77x	0.96	1.20	3.66	4.29
SC-7	3.00					0.09	0.09	0.37	0.50	0.72	0.91	1.15	3.61	4.23
SC-2	3.29						0.00	0.28	0.41	0.63	0.82	1.06	3.52	4.14
H-2	3.30							0.27	0.41	0.62	0.82	1.06	3.51	4.14
H-11	4.17								0.14	0.35	0.55	0.78	3.24	3.87
HC-F	4.60									0.22	0.41	0.65	3.10	3.73
HC-FM	5.29										0.20	0.43	2.89	3.52
SC-11	6.67											0.24	2.69	3.32
BX-2	14.50												2.46	3.08
IX-11	16.50													0.63

* $p < 0.05$

TABLE 23A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME(SECONDS) FEMALE SPENT LICKING OTHER PART OF PUP'S BODY

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	23.448	2.283*
Within subjects	97	10.273	
Total	109		

TABLE 23B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-7	BX-2	IX-11	HC-F	HC-M	HC-FM	H-11	SC-11	SC-2	SC-7	H-2	H-7	BX-11
	Means	0.0	0.0	0.0	0.0	0.0	0.0	0.08	0.17	0.71	1.17	1.20	5.67	6.33
BX-7	0.0		0.0	0.0	0.0	0.0	0.0	0.06	0.12	0.51	0.84	0.86	4.08	4.56*
BX-2	0.0			0.0	0.0	0.0	0.0	0.06	0.12	0.51	0.84	0.86	4.08	4.56*
IX-11	0.0				0.0	0.0	0.0	0.06	0.12	0.51	0.84	0.86	4.08	4.56*
HC-F	0.0					0.0	0.0	0.06	0.12	0.51	0.84	0.86	4.08	4.56*
HC-M	0.0						0.0	0.06	0.12	0.51	0.84	0.86	4.08	4.56*
HC-FM	0.0							0.06	0.12	0.51	0.84	0.86	4.08	4.56*
H-11	0.08								0.06	0.45	0.78	0.80	4.02	4.50*
SC-11	0.17									0.39	0.72	0.74	3.96	4.44*
SC-2	0.71										0.33	0.35	3.57	4.05*
SC-7	1.17											0.02	3.24	3.72*
H-2	1.20												3.22	3.70*
H-7	5.67													0.48
BX-11	6.33													

* $p<0.05$

TABLE 24A

ANALYSIS OF VARIANCE ON FREQUENCY OF FEMALE LIFTING PUP

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	0.069	2.206*
Within subjects	97	0.031	
Total	109		

TABLE 24B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		SC-2	SC-7	SC-11	H-2	H-7	H-11	HC-F	BX-2	IX-11	HC-FM	HC-M	BX-11	BX-7
	Means	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.09	0.33	0.50
SC-2	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
SC-7	0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
SC-11	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
H-2	0.0					0.0	0.0	0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
H-7	0.0						0.0	0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
H-11	0.0							0.0	0.0	0.0	0.62	1.19	4.35*	6.53*
HC-F	0.0								0.0	0.0	0.62	1.19	4.35*	6.53*
BX-2	0.0									0.0	0.62	1.19	4.35*	6.53*
IX-11	0.0										0.62	1.19	4.35*	6.53*
HC-FM	0.05											0.57	3.73*	5.91*
HC-M	0.09												3.17*	5.34*
BX-11	0.33													2.18*
BX-7	0.50													

* $p < 0.05$

TABLE 25A

ANALYSIS OF VARIANCE ON FREQUENCY OF FEMALE CARRYING PUP

DAY 16 (AM OBSERVATIONS ONLY)

Source	d.f.	M.S.	F
Between subjects	12	0.066	5.522**
Within subjects	97	0.012	
Total	109		

TABLE 25B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-2	IX-11	SC-2	SC-7	SC-11	H-2	H-7	H-11	HC-F	HC-M	HC-FM	BX-11	BX-7
	Means	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33	0.50
BX-2	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
IX-11	0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
SC-2	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
SC-7	0.0					0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
SC-11	0.0						0.0	0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
H-2	0.0							0.0	0.0	0.0	0.0	0.0	7.02**	10.52**
H-7	0.0								0.0	0.0	0.0	0.0	7.02**	10.52**
H-11	0.0									0.0	0.0	0.0	7.02**	10.52**
HC-F	0.0										0.0	0.0	7.02**	10.52**
HC-M	0.0											0.0	7.02**	10.52**
HC-FM	0.0												7.02**	10.52**
BX-11	0.33													3.51**
BX-7	0.50													

** $p<0.01$

TABLE 26A

ANALYSIS OF VARIANCE ON AMOUNT OF TIME (SECONDS) FEMALE SPENT CARRYING PUPS

DAY 16

Source	d.f.	M.S.	F
Between subjects	12	0.188	6.825**
Within subjects	97	0.027	
Total	109		

TABLE 26B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS (NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatments		BX-2	IX-11	SC-2	SC-7	SC-11	H-2	H-7	H-11	HC-F	HC-M	HC-FM	BX-11	BX-7
	Means	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33	1.00
BX-2	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
IX-11	0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
SC-2	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
SC-7	0.0					0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
SC-11	0.0						0.0	0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
H-2	0.0							0.0	0.0	0.0	0.0	0.0	4.64**	13.92**
H-7	0.0								0.0	0.0	0.0	0.0	4.64**	13.92**
H-11	0.0									0.0	0.0	0.0	4.64**	13.92**
HC-F	0.0										0.0	0.0	4.64**	13.92**
HC-M	0.0											0.0	4.64**	13.92**
HC-FM	0.0												4.64**	13.92**
BX-11	0.33													9.28**
BX-7	1.00													

** $p<0.01$

TABLE 27A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

HC-2 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	40		
Between Treatments	4	771.150	3.470*
Residual	36	222.239	
Between Animals	9		
Total	49		

TABLE 27B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		7	10	4	13	16
	Means	0.30	0.70	2.20	2.80	21.00
7	0.30		0.08	0.40	0.53	4.39*
10	0.70			0.32	0.45	4.31*
4	2.20				0.13	3.99*
13	2.80					3.86*
16	21.00					

* $p < 0.05$

TABLE 28A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

HC-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	48		
Between Treatments	4	1010.183	5.114**
Residual	44	197.520	
Between Animals	11		
Total	59		

TABLE 28B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		7	4	10	13	16
	Means	0.17	0.50	0.67	9.08	21.33
7	0.17		0.08	0.12	2.20	5.22**
4	0.50			0.04	2.12	5.14**
10	0.67				2.07	5.09**
13	9.08					3.02**
16	21.33					

** $p < 0.01$

TABLE 29A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	84		
Between Treatment	4	6436.293	15.359**
Residual	80	419.055	
Between Animals	20		
Total	104		

TABLE 29B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATICTICS

Treatment (Days)		4	7	13	10	16
	Means	0.38	1.05	2.62	6.95	41.48
4	0.38		0.15	0.50	1.47	9.20**
7	1.05			0.35	1.32	9.05**
13	2.62				0.97	8.70**
10	6.95					7.72**
16	41.48					

** $p<0.01$

TABLE 30A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

MALE HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	44		
Between Treatment	4	5934.008	12.955**
Residual	40	458.039	
Between Animals	10		
Total	54		

TABLE 30B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS
(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	10	13	7	16
	Means	0.36	0.73	2.00	2.00	53.18
4	0.36		0.06	0.25	0.25	8.19**
10	0.73			0.20	0.20	8.13**
13	2.00				0.0	7.93**
7	2.00					7.93**
16	53.18					

** $p<0.01$

TABLE 31A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

SC-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	48		
Between Treatments	4	304.933	2.929*
Residual	44	104.097	
Between Animals	11		
Total	59		

TABLE 31B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	10	7	13	16
	Means	0.08	0.42	1.42	8.25	11.00
4	0.08		0.11	0.45	2.77	3.71*
10	0.42			0.34	2.66	3.59
7	1.42				2.32	3.25
13	8.25					0.93
16	11.00					

* $p<0.05$

TABLE 32A

ANALYSIS OF VARIANCE OF "SELF-GROOMING"

FEMALE HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	40		
Between Treatment	4	1486.019	4.748**
Residual	36	312.998	
Between Animals	9		
Total	49		

TABLE 32B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		7	4	13	10	16
	Means	0.00	0.40	3.30	13.80	28.60
7	0.00		0.07	0.59	2.47	5.11**
4	0.40			0.52	2.40	5.04**
13	3.30				1.88	4.52**
10	13.80					2.65
16	28.60					

** $p < 0.01$

TABLE 33A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

SC-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	48		
Between Treatment	4	3284.513	14.265*
Residual	44	230.245	
Between Animals	11		
Total	59		

TABLE 33B

TESTS OF DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	7	13	10
	Means	6.00	17.08	29.67	33.50	49.50
4	6.00		2.53	5.40**	6.28**	9.93**
16	17.08			2.87**	3.75**	7.40**
7	29.67				0.88	4.53**
13	33.50					3.65**
10	49.50					

** $p<0.01$

TABLE 34A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

HC-7 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	24		
Between Treatment	4	1597.297	12.859**
Residual	20	124.221	
Between Animals	5		
Total	29		

TABLE 35B

TESTS OF DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	4	7	10	13
	Means	5.83	6.33	24.67	36.33	40.67
16	5.83		0.11	4.14**	6.70**	7.66**
4	6.33			4.03**	6.59**	7.55**
7	24.67				2.56	3.52
10	36.33					0.95
13	40.67					

** $p < 0.01$

TABLE 35A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

HC-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	48		
Between Treatment	4	3454.139	15.826**
Residual	44	218.251	
Between Animals	11		
Total	59		

TABLE 35B

TESTS OF DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	7	13	10
	Means	6.92	14.50	31.33	34.50	49.75
4	6.92		1.78	5.73**	6.47**	10.04**
16	14.50			3.95**	4.69**	8.27**
7	31.33				0.74	4.32**
13	34.50					3.58**
10	49.75					

** $p < 0.01$

TABLE 36A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	84		
Between Treatment	4	7948.797	24.014**
Residual	80	331.013	
Between Animals	20		
Total	104		

TABLE 36B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	13	7	10
	Means	15.38	15.52	38.57	47.24	59.24
4	15.38		0.04	5.84**	8.02**	11.05**
16	15.52			5.81**	7.99**	11.01**
13	38.57				2.18	5.21**
7	47.24					3.02
10	59.24					

** $p < 0.01$

TABLE 37A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

FEMALE HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	40		
Between Treatment	4	3209.946	31.069**
Residual	36	103.317	
Between Animals	9		
Total	49		

TABLE 37B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Day)		16	4	13	7	10
	Means	12.30	15.00	43.10	45.80	49.30
16	12.30		0.84	9.58**	10.42**	11.51**
4	15.00			9.74**	9.58**	10.67**
13	43.10				0.84	1.93
7	45.80					1.09
10	49.30					

** $p < 0.01$

TABLE 38A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

MALE HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	44		
Between Treatment	4	5263.992	10.191**
Residual	40	516.522	
Between Animals	10		
Total	54		

TABLE 38B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	13	7	10
	Means	15.73	18.45	34.45	48.55	68.27
4	15.73		0.40	2.73	4.79**	7.67**
16	18.45			2.33	4.39**	7.27**
13	34.45				2.06	4.94**
7	48.55					2.88**
10	68.27					

** $p < 0.01$

TABLE 39A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

SC-2 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	28		
Between Treatment	4	1249.612	3.808*
Residual	24	328.182	
Between Animals	6		
Total	34		

TABLE 39B

TESTS OF DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	7	13	10
	Means	11.57	17.71	31.29	38.57	42.71
4	11.57		0.90	2.88	3.94*	4.55*
16	17.71			1.98	3.05	3.65
7	31.29				1.06	1.67
13	38.57					0.61
10	42.71					

* $p < 0.05$

TABLE 40A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

SC-7 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	24		
Between Treatment	4	21512.984	7.955**
Residual	20	2704.490	
Between Animals	5		
Total	29		

TABLE 40B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	13	7	10	4
	Means	86.83	161.83	187.83	189.17	252.67
16	86.83		3.53**	4.76**	4.82**	7.81**
13	161.83			1.22	1.29	4.28**
7	187.83				0.06	3.05
10	189.17					2.99
4	252.67					

**$p < 0.01$

TABLE 41A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

IBX-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	32		
Between Treatment	4	4271.500	6.016**
Residual	28	709.975	
Between Animals	7		
Total	39		

TABLE 41B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	4	13	7	10
	Means	15.12	18.62	34.62	47.37	71.75
16	15.12		0.37	2.07	3.42	6.01**
4	18.62			1.70	3.05	5.64**
13	34.62				1.35	3.94**
7	47.37					2.59
10	71.75					

** $p<0.01$

TABLE 42A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

BX-2 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	8		
Between Treatment	4	19852.578	13.472*
Residual	4	1453.547	
Between Animals	1		
Total	9		

TABLE 42B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		13	16	10	4	7
	Means	80.00	94.50	125.00	275.00	281.00
13	80.00		0.54	1.67	7.23*	7.46*
16	94.50			1.13	6.70*	6.92*
10	125.00				5.56*	5.79*
4	275.00					0.22
7	281.00					

* $p<0.05$

TABLE 43A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

IBX-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	32		
Between Treatment	4	14502.500	4.186**
Residual	28	3464.821	
Between Animals	7		
Total	39		

TABLE 43B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	10	13	7	4
	Means	116.00	137.37	148.37	204.37	212.62
16	116.00		1.03	1.56	4.25**	4.64**
10	137.37			0.53	3.22	3.62
13	148.37				2.69	3.09
7	204.37					0.40
4	212.62					

** $p < 0.01$

TABLE 44A

ANALYSIS OF VARIANCE FOR "PUP TWITCHING"

SC-7 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	24		
Between Treatment	4	1497.915	7.370**
Residual	20	203.257	
Between Animals	5		
Total	29		

TABLE 44B

TESTS OF DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		4	16	7	10	13
	Means	8.50	15.67	18.00	33.33	47.83
4	8.50		1.23	1.63	4.27**	6.76**
16	15.67			0.40	3.04	5.53**
7	18.00				2.63	5.13**
10	33.33					2.49
13	47.83					

** $p<0.01$

TABLE 45A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

HC-7 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	24		
Between Treatment	4	16095.629	3.763*
Residual	20	4277.039	
Between Animals	5		
Total	29		

TABLE 45B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	13	10	4	7
	Means	117.83	122.33	138.33	145.33	244.00
16	117.83		0.17	0.77	1.03	4.73*
13	122.33			0.60	0.86	4.56*
10	138.33				0.26	3.96*
4	145.33					3.70*
7	244.00					

* $p<0.05$

TABLE 46A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

HC-11 PUPS (DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	48		
Between Treatment	4	39709.719	8.071**
Residual	44	4919.820	
Between Animals	11		
Total	59		

TABLE 46B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS

(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	13	10	4	7
	Means	98.25	126.42	173.42	218.42	231.92
16	98.25		1.39	3.71**	5.93**	6.60**
13	126.42			2.32	4.54	5.21
10	173.42				2.22	2.89
4	218.42					0.67
7	231.92					

** $p < 0.01$

TABLE 47A

ANALYSIS OF VARIANCE FOR "ACTIVE IN THE CLUMP"

MALE HC PUPS FROM NON-TREATED LITTERS
(DURATION IN SECONDS)

Source	d.f.	M.S.	F
Within Animals	44		
Between Treatment	4	9037.887	2.944*
Residual	40	3070.011	
Between Animals	10		
Total	54		

TABLE 47B

TESTS ON DIFFERENCES BETWEEN ALL PAIRS OF MEANS
(NEUMAN-KEULS METHOD) TABLE OF Q STATISTICS

Treatment (Days)		16	13	4	10	7
	Means	131.73	149.64	151.45	186.18	201.27
16	131.73		1.07	1.18	3.26	4.16*
13	149.64			0.11	2.19	3.09
4	151.45				2.08	2.98
10	186.18					0.90
7	201.27					

* $p < 0.05$

TABLE 48

SPEARMAN RANK-ORDER CORRELATION COEFFICIENTS

BETWEEN NUMBER OF INTERVALS MOVED AND AGE (IN DAYS)

Pups Treated on Day 2		Pups Treated on Day 7	
Possible Number of Intervals Out of Which Pup Could Move	r_s	Possible Number of Intervals Out of Which Pup Could Move	r_s
1	.55	1	.66*
2	.60*	2	.65*
3	.53	3	.71*
4	.59	4	.60*
5	.62*	5	.73*
6	...[a]	6	.21

Pups Treated on Day 11		Non-treated Pups	
Possible Number of Intervals Out of Which Pup Could Move	r_s	Possible Number of Intervals Out of Which Pup Could Move	r_s
1	.53	1	.94**
2	.83**	2	.81**
3	.83**	3	.83**
4	.65*	4	.78**
5	.76*	5	.58
6	.68*	6	.66*

* $p < .05$
** $p < .01$
a Insufficient data

TABLE 49

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 11, NON-TREATED HANDLING CONTROL

	OC	HC	OC	HC	OC	HC	OC	HC	OC
Day	3	4	6	7	9	10	12	13	15
3									
4	T=0*								
6	N.S.	T=0*							
7	T=0*	T=0*	T=0*						
9	N.S.	T=1.5*	N 6	N.S.					
10	T=0*	N<6	T=0*	N<6	T=0*				
12	T=0*	N<6	T=0*	N<6	T=1*	N.S.			
13	T=0*	N<6	T=0*	N.S.	T=0*	N<6	N.S.		
15	T=0*	N<6	T=0*	N<6	T=0*	N<6	N<6	N<6	

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant
N 6 Test not possible

TABLE 50

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 17, NON-TREATED HANDLING CONTROL

	OC	HC	OC	HC	OC	HC	OC	HC	OC
Day	3	4	6	7	9	10	12	13	15
3		N<6	N<6	N<6	T=0*	N<6	T=0*	T=0*	T=0*
4			N<6	N<6	N<6	N.S.	N<6	N<6	N<6
6				N<6	T=0*	N<6	T=0*	T=0*	T=0*
7					N<6	N<6	N<6	N<6	N<6
9						N<6	N<6	N<6	N<6
10							N<6	N<6	T=0*
12								N<6	T=1*
13									N<6
15									

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home case
N.S. Not significant

TABLE 51

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 28, NON-TREATED HANDLING CONTROL

	OC	HC	OC	HC	OC	HC	OC	HC	OC
Day	3	4	6	7	9	10	12	13	15
3									
4	T=0*								
6	N.S.	T=0*							
7	T=0*	N < 6	T=1*						
9	N.S.	T=0*	N.S.	T=0*					
10	T=0*	N < 6	N.S.	N < 6	N 6				
12	T=0*	T=0*	N.S.	T=0*	N.S.	T=0*			
13	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N < 6		
15									

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 52

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 37 TREATED ON DAY 2

	OC	HC	OC	HC	OC	HC	OC
Day	6	7	9	10	12	13	15
6		T=0*	N<6	T=0*	N < 6	N < 6	T=0*
7			N<6	N < 6	T=0*	N < 6	N < 6
9				T=0*	N < 6	N < 6	N < 6
10					T=0*	N < 6	N < 6
12						T=0*	T=1.0*
13							N < 6
15							

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 53

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 12 BEFORE TREATMENT ON DAY 11

	HC	OC	HC	OC	HC	OC
Day	10	9	7	6	4	3
10						
9	T=0*					
7	N < 6	T=1*				
6	T=0*	N.S.	T=0*			
4	N < 6	T=0*	N < 6	T=0*		
3	T=0*	N.S.	T=0*	N.S.	T=0*	

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TEST 54

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 16 BEFORE TREATMENT ON DAY 11

	HC	OC	HC	OC	HC	OC
Day	10	9	7	6	4	3
10						
9	T=0*					
7	N < 6	T=0*				
6	N < 6	N < 6	N < 6			
4	N < 6	T=0*	N < 6	T=0*		
3	T=0*	T=0*	T=0*	T=0*	T=0*	

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 55

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 29 BEFORE TREATMENT ON DAY 11

	HC	OC	HC	OC	HC	OC
Day	10	9	7	6	4	3
10		N.S.	N<6	T=0*	N<6	T=0*
9			T=1.5*	N.S.	T=0*	N.S.
7				T=0*	N < 6	T=0*
6					T=0*	N < 6
4						T=0*
3						

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 56

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 35 BEFORE TREATMENT ON DAY 11

	HC	OC	HC	OC	HC	OC
Day	10	9	7	6	4	3
10		T=0*	N < 6	T=0*	N.S.	N < 6
9			T=0*	N.S.	T=0*	N.S.
7				N < 6	N < 6	N < 6
6					N.S.	N < 6
4						
3						

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 57

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF TIMES FEMALE PICKED UP PUPS. LITTER 36 BEFORE TREATMENT ON DAY 11

	HC	OC	HC	OC	HC	OC
Day	10	9	7	6	4	3
10		T=0*	N<6	T=0*	N<6	N<6
9			N.S.	N.S.	T=1.5*	N.S.
7				T=1.5*	N<6	N<6
6					T=0*	T=1.5*
4						N<6
3						

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

TABLE 58

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF INTERVALS IN WHICH FEMALES WERE DIGGING

	OC	HC	OC	HC	OC	HC	OC	HC	O
Days	3	4	6	7	9	10	12	13	1
3		T=0*	N < 6	T=0*	N < 6	T=0*	N < 6	T=0*	N <
4			T=0*	N.S.	T=0*	T=19*	T=0*	N.S.	T=
6				T=0*	N < 6	T=0*	N < 6	T=0*	N <
7					T=0*	N.S.	T=0*	N.S.	T=
9						T=0*	N < 6	T=0*	N <
10							T=0*	N.S.	T=
12								T=0*	N <
13									T=
15									

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occured in home cage
N.S. Not significant

TABLE 59

RESULTS OF WILCOXON MATCHED-PAIRS SIGNED-RANKS TESTS COMPARING DAYS FOR NUMBER OF INTERVALS IN WHICH FEMALES WERE SELF-GROOMING

	OC	HC	OC	HC	OC	HC	OC	HC	OC
Days	3	4	6	7	9	10	12	13	15
3		T=11*	N.S.	T=9*	N.S.	T=9*	T=14.5*	T=13*	N.S.
4			N.S.	N.S.	N.S.	N.S.	N.S.	T=34*	N.S.
6				N.S.	N.S.	T=25*	N.S.	T=10.5*	N.S.
7					N.S.	N.S.	N.S.	T=6.5*	N.S.
9						T=19*	N.S.	T=15*	N.S.
10							N.S.	N.S.	T=20.5*
12								T=7.5*	N.S.
13									T=7.5*
15									

* $p < .05$
OC Indicates test occurred in observation cage
HC Indicates test occurred in home cage
N.S. Not significant

BIBLIOGRAPHY

Adolph, E. F. Ontogeny of physiological regulations in the rat. Quart. Rev. Biol., 1957. 32, 89-137.

Allison, A.C. The morphology of the olfactory system in the vertebrates. Biolog. Rev., 1953. 28, 195-244.

Allison, A.C. The structure of the olfactory bulb and its relationship to the olfactory pathways in the rabbit and rat. J. Comp. Neurol., 1953, 98, 309-353.

Altman, J. Autoradiographic and histological studies of postnatal neurogenesis. J. Comp. Neur., 1969. 137, 433-458.

Angulo y Gonzales, A.W. The prenatal development of behavior in the albino rat. J. Comp. Neurol., 1932. 55, 395-442.

Aron, C., Roos, J., & Asch, G. Effect of removal of the olfactory bulbs on mating behavior and ovulation in the rat. Neuroendocrinology, 1970. 6, 109-117.

Aronson, L.R. The Central nervous system of sharks and bony fishes with special reference to sensory and integrative mechanisms. In Gilbert, P.W. (Ed.) Sharks and survival. Boston: D.C. Heath, 1963.

Aronson, L.R. & Kaplan, H. Function of the teleostean forebrain. In Ingle, D. (Ed.) The central nervous system and fish behavior. Chicago: Univ. Chicago Press, 1968.

Beach, F.A. Importance of progesterone to induction of sexual receptivity in spayed female rats. Proc. Soc. Exper. Biol. Med., 1942. 50-51, 369-371.

Beach, F.A. A review of physiological and psychological studies of sexual behavior in mammals. Physiol. Rev., 1947. 27, 240-307.

Beach, F.A., & Jaynes, J. Studies on maternal retrieving in rats: II. Effects of practice and previous parturitions. Am. Naturalist, 1956. 90, 103-109.

Bermant, G., & Taylor, L. Interactive effects of experience and olfactory bulb lesions in male rat copulation. Physiol. & Beh., 1969. 4, 13-17.

Berry, C.M., Hagamen, W.D., & Hinsey, J.C. Distribution of potentials following stimulation of olfactory bulb in the cat. J. Neurophysiol., 1952. 15, 139-148.

Birch, H.G., Levels, categories, and methodological assumptions in the study of behavioral development. In Tobach, E., Aronson, L.R., & Shaw, E. (Eds.) The biopsychology of development. New York: Academic Press, 1971.

Bolles, R.C., & Woods, P.J., The ontogeny of behaviour in the albino rat. Anim. Behav., 1964. 12, 427-441.

Brodal, A. The hippocampus and the sense of smell: a review. Brain, 1947. 70, 179-222.

Bronson, F.H. Rodent Pheromones. Biol. Reprod. 1971. Suppl. 3.

Bruce, H.M. & Parker, A.S. Hormonal factors in exteroceptive block to pregnancy in mice. J. Endocrin., 1960. 20, 219-30.

Bruce, H.M., & Parrot, D.M.V. Role of olfactory sense in pregnancy block by strange males. Science, 1960. 131, 1526.

Carr, W.J., Loeb, L.S., & Dissinger, M.L. Responses of rats to sex odors. J. Comp. Physiol. Psychol., 1965. 59, 370-377.

Carr, W.J., Loeb, L.S., & Wylie, M.R. Responses to feminine odors in normal and castrated male rats. J. Comp. Physiol. Psychol., 1966. 62, 336-338.

Carr, W.J., Martorano, R.D. & Kramer, L. Responses of mice to odors associated with stress. J. Comp. Physiol. Psychol. 1970. 71, 223-228.

Chapman, V.M., Desjardin, C., & Whitten, W.K. Pregnancy block in mice: changes in pituitary LH and LTH and plasma progestin levels. J. Reprod. Fertil., 1970. 21, 333-337.

Cooper, G.P. Receptor origin of the olfactory bulb response to ionizing radiation. Am. J. Physiol., 1968. 215, 803-806.

Crozier, W.J., & Pincus, G. Photic stimulation of young rats. J. Gen. Psychol., 1937. 17, 105-111.

Detwiler, S.R. Experimental Observations upon the developing rat retina. J. Comp. Neurol., 1932. 55, 473-492.

Didiergeorges, F., Vergnes, M., & Karli, P. Privation des afférences olfactives et agressivité interspécifique du rat. Comptes Rendus de la Société de Biologie (Paris), 1966. 160, 866-868.

Didiergeorges, F., Vergnes, M. & Karli, P. Sur le mode d'action d'une influence inhibitrice d'origine olfactive s'exercant sur l'aggressivité interspécifique du rat. Comptes Rendus de la Société de Biologie (Paris), 1968. 162, 267-270.

Dominic, C.J. The inhibition of the olfactory block to pregnancy in mice by the administration of exogenous progesterone. Zeitschrift fuer Naturwissenschaften, 1966. 12, 310-311.

Donovan, C.A. Some clinical observations on sexual attraction and deterrence in dogs and cattle. Vet. Med., 1967. 62, 1047-1051.

Donovan, C.A. Canine anal glands and chemical signals (pheromenes). J.Am.Vet.Med. Ass., 1969. 155, 1995-1996.

Douglas, R.J., Isaacson, R.L., & Moss, R.L. Olfactory lesions, emotionality, and activity. Physiol. & Beh., 1969. 4, 379-381.

Fleming, A.S. & Rosenblatt, J.S. Role of olfaction in maternal behavior in the rat. Papaer presented at A.P.A., 1971, Washington D.C.

French, R.L. A method of studying olfactory discrimination in the white rat. Psychol. Bull., 1939. 36, 643-644.

Gandelman, R., Zarrow, M.X., Deneberg, .H., & Myers, M. Olfactory bulb removal eliminates maternal behavior in the mouse. Science, 1971. 171, 210-211.

Gibson, J.J. Visually controlled locomotion and visual orientation in animals. Brit. J. Psychol., 1958. 49, 182-194.

Gibson, J.J. and Gibson, E.J. Perceptual learning: differentiation or enrichment? Psychol. Rev. 1955. 62, 32-41.

Glickman, S.E. Effects of peripheral blindness on exploratory behavior in the hooded rat. Canad. J. Psychol., 1958. 12, 45-51.

Gottlieb, G. Prenatal behavior of birds. Quart. Rev. Biol., 1968. 43, 148-174.

Gottlieb, G. Ontogenesis of sensory function of birds and mammals. In Tobach, E., Aronson, L.R. & Shaw, E. (Eds.) The biopsychology of development. New YorkL Academic Press, 1971.

Grosvenor, C.E. & Mena, F. Effect of auditory, olfactory, and optic stimuli upon milk ejection and suckling-induced release of prolactin in lactating rats. Endocrinology, 1967. 80, 840-846.

Hall, C.D., Garcia, J. Buchwald, N.A., Dubrowsky, B., & Feder, B.H. Role of olfactory system in arousal to X-ray. Nature, 1965. 205, 627-628.

Halliday, M.S. Exploration and fear in the rat. Symp. Zool. Soc. London, 1966. 18, 45-59.

Ham, A.W. Histology. Philadelphia: J.B. Lippincott, 1965.

Harris, D.B. The development of human behavior: theoretical considerations for future research. In Tobach, E., Aronson, L.R., & Shaw, E. (Eds.) The biopsychology of development. New York: Academic Press, 1971.

Hebb, D.O. The organization of behavior. New York: John Wiley & Sons, 1949.

Heimer, L., & Larsson, K. Mating behavior of male rats after olfactory bulb lesions. Psychol. & Beh., 1967. 2, 207-209.

Helson, H. Adaptation-level theory. New York: Harper & Row, 1964.

Herrick, C.J. J. Comp. Neurol., 1921. 32, 429-438.

Hogg, I.D., & Bryant, J.W. The development of sensory innervation in the mouth and pharynx of the albino norway rat. J.Comp. Neurol., 1969. 136, 33-56.

Howard, W.E., Marsh, R.E., & Cole, R.E. Food detection by deer mice using olfactory rather than visual cues. An.Beh., 1968. 16, 13-17.

Hull, E.M., Anosmia and mouse killing by rats: a non-sensory limbic role for the olfactory bulbs. Paper presented at Society for Neuroscience, 1972. Houston.

Kappers, C.U.A. Huber, G.C., & Crosby, E.C. The comparative anatomy of the nervous system of vertebrates, including man, Vol. II. New York: Macmillan, 1936.

Kennedy, R.F. Address at the University of Capetown, June, 1966. Cited by Birch, H.G. Levels, categories, and methodological assumptions in the study of behavioral development. In Tobach, E., Aronson, L.R., & Shaw, E. (Eds.) The biopsychology of development. New York: Academic Press, 1971.

Klein, D., & Brown, T.S. Exploratory behavior and spontaneous alteration in blind and anosmic rats. J. Comp. Physiol. Psychol., 1969. 68, 107-110.

Kling, A. Effects of rhinencephalic lesions on endocrine and somatic development in the rat. Am. J. Physiol., 1964. 206, 1395-1400.

Kumadaki, N., Hitomi, M. & Kumada, S. Effect of psychotherapeutic drugs on hyperemotionality of rats in which the olfactory bulb was removed. Jap. J. Pharm., 1967. 17, 659-667.

Kuo, Z. The need for coordinated efforts in developmental studies. In Aronson, L.R., Tobach E., Lehrman, D.S., & Rosenblatt, J.S. (Eds.) Development and evolution of behavior. San Francisco: W.H. Freeman, 1970.

Karlson, P., & Luscher, M. Pheromone. Nature, 1959. 183, 4653.

Larue, C. & Le Magnen, J. Effect of removal of olfactory bulbs upon hyperphagia and obesity induced in rats by VMH lesion. Physiol. & Beh., 1970. 5, 509-514.

Le Gros Clark, W.E. & Meyer, M. The terminal connexions of the olfactory tract in the rabbit. Brain, 1947. 70, 304-328.

Le Magnen, J. Etude des phénomènes olfacto-sexuels chez le rat blanc. Comptes Rendus de la Société de Biologie de Paris, 1951. 145, 851-860.

Le Magnen, J. Les phénomènes olfacto-sexuels chez le rat blanc. Archives des Sciences Physiologiques, 1952. 6, 295-331.

Leon, M.A.& Moltz,H.Discrimination of a maternal pheromone by pre-weanting albino rats. Paper presented at EPA, 1971. New York.

Leonard, C.M. Reproductive behavior of the female golden hamster after neonatal olfactory bulbectomy. Paper presented at EPA, 1971, New York.

Levitsky, D.A. & Barnes, R.H. Nutritional and environmental interactions in the behavioral development of the rat: long term effects. Science, 1972. 176, 68-71.

Long, C.J. & Tapp, J.T. An apparatus for the assessment of the reinforcing properties of odors in small animals. J. Exp. Anal. Beh., 1968. 11, 49-51.

Mac Lean, P.D. Some psychinatric implications of physiological studies on the frontotemporal portion of the limbic system. Electroenceph. Clin. Neurophysiol., 1952. 4, 407-418.

Macrides, F. & Chorover, S.L. Olfactory bulb units: activity correlated with inhalation cycles and odor quality. Science, 1972. 175, 84-87.

Mainardi, D., Marsen, M., & Pa quali, A. Causation of sexual preference of the house mouse, the behavior of mice reared by parents whose odour was artificially altered. Societa Italiano ce Scienze Naturali, Milano, Att 1965. 104, 325-338.

Marks, H.E., Seago, J.D. & Remley, N.R. The effect of anosmia on taste preference behavior as a function of deprivation conditions. Psychon. Sci., 1971. 23, 9-11.

Marr, J.N. & Gardner, L.E., Jr. Early olfactory experience and later social behavior in the rat. J. Genet. Psychol., 1965. 107, 167-174.

Marr, J.N. & Lilliston, L.G. Social attachment in rats by odor and age. Behaviour, 1969. 33, 277-282.

Moltz, H. Maternal behavior of primiparous and multiparous rats. J. Comp. Psychol., 1965. 60, 417-421.

Morrison, R.R., & Ludvigson, H.W. Discrimination by rats of conspecific odors of reward and nonreward. Science, 1970. 167, 904-905.

Moulton, D.G., and Beidler, L.M. Structure and function in the peripheral olfactory system. Physiol. Beh., 1967. 47, 1-52.

Mueller Velton. H. Ueber den Angstgeruch bei der Hausmaus (Mus musculus L.). Zeitschrift fuer vergleichende Physiologie, 1966. 52, 401-429.

Munn, N.L. Handbook of psychological research in the rat. Boston: Houghton Mifflin, 1950.

Murphy, M.R. Olfaction and territorial behavior of the caged golden hamster. Paper presented at E.P.A., 1971, New York.

Murphy, M.R., & Schneider, G.E. Olfactory bulb removal eliminates mating behavior in the male golden hamster. Science, 1970. 167, 302-304.

Navakova, V. & Dlouha, H. Effect of severing the olfactory bulbs in the intake and excretion of water in the rat. Nature, 1960. 186, 638-639.

Negus, V. Comparative anatomy of the nose and paranasal sinuses. London: Livingstone, 1958.

Nieuwenhuys, R. Comparative anatomy of olfactory centres and tracts. In Zotterman, Y. (Ed.) Progress in Brain Research, Vol. 23. Amsterdam: Elsevier Publishing Co., 1967.

Nyakas, C. & Endroczi, E. Olfaction guided approaching behaviour of infantite rats to the mother in maze box. Acta Physiol. Acad. Sci. Hung., 1970. 38, 59-65.

Orbach, J., & Kling, A. Effect of sensory deprivation on onset of puberty, mating, fertility, and gonadal weights in rats. Brain Res., 1966. 3, 141-149.

Ottoson, P. Generation and transmission of signals in the olfactory system. In Zotterman, Y. (Ed.) Olfaction and taste. New York: Macmillan, 1963.

Papez, J.W. A proposed mechanism of emotion. Arch. Neurol. Psychiat., 1937. 38, 725-743.

Pfaff, D., & Pfaffmann, C. Behavioral and electrophysiological responses of male rats to female rat urine odors. In Pfaffmann, C. (Ed.) Olfaction and taste, III. New York: Rockefeller Univ. Press, 1969.

Phillips, D.S. Effects of olfactory bulb ablation on visual discrimination Physiol. & Beh., 1970. 5, 13-15.

Powell, T.P.S., Cowan N.M., & Raisman, G. The central olfactory connexions. J. Anat., 1965. 99, 791-813.

Raisman, G. An experimental study of the projection of the amygdala to the accessory olfactory bulb and its relationship to the concept of a dual olfactory system. Exp. Brain Res., 1972. 14, 395-408.

Rehmer, H. Variabilitat der Form und Grosse der Bulbus olfactorius der erwachsenen weissen Laborratte. J. Fuer Hirnforschung, 12, 113-122.

Reiter, R.J. Sorrentino, S. Jr., & Ellison, N.M. Interaction of of photic and olfactory stimuli in mediating pineal-induced gonadal regression in adult female rats. Gen. Comp. Endocr., 1970. 15, 326-333.

Riss, W., Halpern M., & Scalia, F. Anatomical aspects of the evolution of the limbic and olfactory systems and their potential significance for behavior. Ann.N.Y.Acad.Sci., 1969. 159, 1096-1111.

Roparts, P. The relation between olfactory stimulation and aggressive behavior in mice. Anim.Behav., 1968. 16, 97-100.

Ropartz, P. Mise en evidence d'une augmentation de l'activite locomotrice des groupes de souris femelles en reponse a l'odeur d'un groupe de males etranges. Comptes Rendus de l' Academie des Sciences de Paris, 1968. 267, 2341-2343.

Rose, G.H. The development of visually evoked electrocartical responses in the rat. Develop. Psychobiol., 1968. 1, 35-40.

Rosenblatt, J.S. Views on the onset and maintenance of maternal behavior in the rat. In Aronson, L.R., Tobacg E., Lehrman, D.S., & Rosenblatt, J.S. (Eds.) Development and evolution of behavior. San Francisco: W.H. Freeman, 1970.

Rosenblatt, J.S., & Lehrman, D.S. Maternal behavior of the laboratory rat. In Rheingold, H.L. (Ed.) Maternal behavior in mammals. New York: John Wiley & Sons, 1963.

Rosenblatt, J.S., Turkewitz, G., and Schnierla, T.C. Development of suckling and related behavior in neonate kittens. In Bliss, E.L. (Ed.) Roots of behavior. New York: Harper & Bros., 1962.

Rouger, Y., Tobach, E., & Schneirla, T.C. Development of olfactory function in the rat pup. Amer. Zool., 1967. 7, 792-793.

Rowe, F.A. & Edwards, D.A. Olfactory bulb removal: influences on rhe aggressive behaviors of male mice. Physiol. & Beh., 1971. 7, 889-892.

Salas, M. Schapiro, S., & Tugman-Flores, C. Development of olfactory bulb discrimination between maternal and food odors. Physiol. & Beh., 1970. 5, 1261 - 1264.

Satinder, K.P. Effects of odor trails on open-field behavior in the rat. Psychol. Reports, 1969. 25, 115-116.

Schapiro, S., & Salas, M. Behavioral response of infant rats to maternal odor. Physiol. & Behav., 1970. 5, 815-818.

Scherrer, J. Electrophysiological aspects of cortical development. Progr. Brain Res., 1968. 22, 480-489.

Schneirla, T.C. Levels in the psychological capacities of animals. In Sellars, R.W., McGill, V.J. & Farber, M. (Eds.) Philosophy for the future. New York: Macmillan, 1949.

Schneirla, T.C. The concept of development in comparative psychology. In Harris, D.B. (Ed.) The concept of development. Minneapolis, Minn.: Univ. of Minn. Press, 1955.

Schneirla, T.C. & Rosenblatt, J.S. Behavioral organization and genesis of the social bond in insects and mammals. Amer. J. Orthopsychiat., 1961. 31, 223-253.

Schneirla, T.C. Behavioral development and comparative psychology. Quart. Rev. Biol., 1966. 41, 283-302.

Scott, J.W., & Pfaff, D.W. Behavioral and electrophysiological responses of female mice to male urine odors. Physiol. & Beh., 1970. 5, 407-411.

Scott, J.W. & Pfaffmann, C. Olfactory input to the hypothalamus: electrophysiological evidence. Science, 1967. 158, 1492-1594.

Segaar, J. Behavioral aspects of degeneration and regeneration in fish brain: a comparison with higher vertebrates. In Singer, M., and Schade, J.P. (Eds.) Progress in brain research, Vol. 14. New York: Elsevier, 1965.

Siegel, S. Nonparametric statistics. New York: McGraw-Hill, 1956.

Sinclair, J.G. Reflections on the role of receptor systems for taste and smell. Quart. Rev. Biol., 1971. 159-172.

Small, W.S. Notes on the psychic development of the young white rat. Am. J. Psychol., 1899. 11, 80-101.

Stern, J.J. Responses of male rats to sex odors. Physiol. & Beh., 1970. 5, 519-524.

Stone, C.P. Delay in the awakening of copulatory ability in the male albino rat incurred by defective diets. J. Comp. Physiol. Psychol., 1925. 5, 177-203.

Stone, C.P. A simple method for developing olfactory discrimination habits in rats. J. Genet. Psychol., 1941. 58, 419-421.

Stone, H. Effect of ethmoidal nerve stimulation on olfactory bulbar electrical activity. In Pfaffmann, C. (Ed.) Olfaction and taste, III. New York: Rockefeller Univ. Press, 1969.

Tapp, J.T., & Long, C.J. Reinforcing properties of odors for the albino rat. Psychon.Sci., 1967. 7, 17-18.

Thorne, B.M. & Linder, L.H. No change in emotionality of rats following bulbectomy. Psychon. Sci. 1971. 24, 5.

Tobach, E. Introduction and discussion. In Mead, M., Dobzhansky, T., Tobach E., and Light, R.E. (Eds.) Science and the concept of race. New York: Columbia Univ. Press, 1968.

Tobach, E. Photoreception and chemoreception: questions for the evolution and development of orientation. An. N.Y. Acad. Sci., 1971. 188, 194-202.

Tobach, E., Schneirla, T.C., Aronson, L.R., & Laupheimer, R. The ATSL: an observer-to-computer system for a multivariate approach to behavioural study. Nature, 1962. 194, 257-258.

Tobach, E. & Schneirla, T.C. Eliminative responses in mice and rats, and the problem of "emotionality." In Bliss, E.L. (Ed.) Rotts of behavior. New York: Harper, 1962.

Tobach, E. & Schneirla, T.C. The biopsychology of social behavior in animals. In Cooke, R.E. (Ed.) The biologic basis of pediatric practice. New York: Mc-Graw-Hill, 1968.

Tobach, E., Schnierla, T.C., Sang, B., Gold, P., Steel, K. and Wortis, R., Hopping behavior in mice of pre-weaning age. Anato. Rec., 1958. 131. 604.

Tobach, E., Singh, P.J., Lederhindler, I., De Santis, J.L. & Beckhorn, G. The effect of familiar and unfamiliar odors and substrates on normal and olfactorily bulbectomized rat pups. (Paper in preparation.)

Tobach, E., Turkewitz, L., Vroman, L. & Schneirla T.C. Long term effects of diffenretial preweaning experience in the wistar rat. Proc. Inter. Union Physiol. Sci., 1968. Vol. VII.

Tobach, E., Vroman, L., Turkewitz, G., and Schnierla, T.C. Infantile experience with specific visual stimuli as related to later differential approach responses in rats. Anat. Rec., 1960. 138, 385.

Tucker, A.M. & Shapiro, S. Procedure for sectioning the brains of small animals in situ. Psychol. Reports, 1971. 29, 563-568.

Turkewitz, G. The development of spatial orientation in relation to the effective perceptual environment in neonate rats. Doctoral dissertation. New York Univ., 1966.

Valenta, J.G. & Rigby, M.K. Discrimination of the odor of stressed rats. Science, 1968, 161, 599-601.

Valverde, F. Studies on the piriform lobe. Cambridge, Mass.: Harvard Univ. Press, 1965.

Ventis, W.L. Behavioral effects of olfactory bulbectomy in the albino rat, 1966. M.A. Thesis, University of Tennessee.

Vernet-Maury, E. & Chanel, J. Some methods for evaluating emotions in rats. Journal de Physiologie, 1967. 59, 526.

Vernet-Maury, E., Le Lagnen, J., & Chanel, J. Comportement émotif chez le rat; influence de l'odeur d'un predateur et d'un nonpredateur. Comptes Rendus de l' academie des Sciences (Paris), 1968. 267, 331-334.

Volokhov, A.A. Comparative studies of the functional development of analyzer systems in animals in the process of ontogenesis Progr. Brain Res., 1968. 22, 527-540.

Wada, T. Anatomical and physiological studies on the growth of the inner ear of the albino rat. Amer. Anat. Mem., 1923. 10, 1-174.

Watson, J.B. Animal education: an experimental study on the psychical development of the white rat, correlated with the growth of its nervous system. Contrib. Philos., 1903. 4, 5-122. Cited by Sherwood, N.M., & Timiras, P.S. A stereotaxic atlas of the developing rat brain. Berkeley: Univ. of Calif. Press, 1970.

Winer, B.J. Statistical principles in experimental design. New York: McGraw-Hill, 1962.

Winans, S.S., & Scalia, F. Amygdaloid nucleus: new afferent input from the vomeronasal organ. Science, 1970. 170, 330-332.

Wenzel, B. Olfactory sensation in the kiwi and other birds. An.N.Y. Acad. Sci., 1971. 188, 183-194.

Ziegler, H.P. Feeding behavior in the pigeon: a neurobehavioral analysis. In Proceedings of the Lashley Memorial Conference, II. West Virginia Univ., 1971.