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# EFFECTS OF LIMBIC LESIONS ON SOCIAL ATTRACTION IN RATS

A DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

by

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1975

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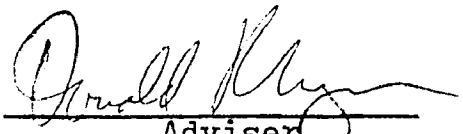

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# CHAPTER 1

## INTRODUCTION

There is considerable evidence that the limbic system is involved in the modification of basic behavior patterns such as approach to, avoidance of, and freezing in the presence of external stimuli. Lesions of the limbic system have been shown to result in increased (Kolb and Nonneman, 1975) or decreased (Blanchard and Blanchard, 1972) avoidance of innate fear stimuli, alterations in conspecific social behavior (Jonason and Enloe, 1971) and social postures (Enloe, MPA address, 1973) and in changes in emotional reactivity to external stimuli (Brady and Nauta, 1953; King and Meyer, 1958; Jonason and Enloe, 1975).

Jonason and Enloe (1971) first demonstrated that pairs of rats with lesions of the septal forebrain exhibited increases in social contacts, decreases in mobility, increases in the average length of a social contact, and decreases in the average distance maintained between subjects. This alteration in social behavior was shown to follow a transitory period of heightened emotional reactivity, lasting 3-5 days post-operative waith daily handling.

While it is clear that septal lesions in rats produce a dramatic increase in social cohesiveness, the basis of the altered behavior patterns is unknown. Because pairs of septal

subjects spend more time in physical contact than do normal-septal pairs, and both groups spend more time in physical contact than do pairs of normal rats, it may be that the septal preparations are emitting social cues that induce approach. Enloe (MPA address, 1973) has demonstrated that septal preparations emit more responses that are considered to be submissive than do normal rats, and that submissive gestures may enhance the probability of approach from another rat, especially if the other rat is a septal preparation.

Before accepting this hypothesis, it must be considered that normal rats, being more active and showing lower mean contact times than septal subjects (Jonason and Enloe, 1971), will necessarily reduce the total time spent in contact by a septal-normal pair below the level of a septal-septal pair. It is conceivable that a septal subject would spend as much time in contact with a normal rat as it spends with another septal subject if the normal rat were restrained from moving away and breaking social contact. Experiment I was designed, in part, to determine whether septal preparations spend as much time in contact with a tethered normal rat as might be expected if the tethered rat was a septal subject. This would dismiss the hypothesis that septal preparations approach conspecifics as a function of the percentage of submissive postures displayed. Secondly, the enhanced social

cohesiveness typical of septal preparations might generalize to species other than rats. In Experiment I, septal subjects are given the opportunity to approach a mouse, a rabbit, and a cat, none of which would be expected to display any social cues that would be typical of a conspecific. A comparison with the approach tendencies of normal rats would determine whether a septal lesion produces a tendency of approach which is sufficiently powerful to overcome innate reactions, such as avoidance of a cat (Curti, 1935; Plotnik, Mollenauer, and Snyder, 1974).

Jonason and Enloe (1971) demonstrated a behavioral reciprocity between septal and amygdaloid preparations in terms of the social cohesiveness tendencies of the lesion group toward conspecifics. Rats with amygdaloid lesions show increased mobility whether alone or paired with another rat (Corman, Meyer, and Meyer, 1967; Jonason and Enloe, 1971), less conspecific social cohesiveness than normal rats, and decreased average contact times for 12-14 days postoperative. Jonason, Enloe, Contrucci, and Meyer (1973) discovered that the amygdaloid lesion effect is unstable over time and that such preparations show normal levels of cohesiveness with rats after the recovery period. What has not been determined is whether amygdaloid

preparations, after the recovery of normal levels of conspecific social cohesiveness, will behave like normal rats in testing situations in which non-conspecifics serve as stimuli. Blanchard and Blanchard (1972) indicated that amygdaloid subjects approach and explore a cat more readily than do normal rats. This is consistent with the hypothesis advanced by Bunnell (1966) that amygdaloid behavios result from an increased threshold to aversive stimuli. In Experiment I, amygdaloid preparations are confronted with both aversive stimuli and woth non-aversive stimuli such as mice. If Bunnell's hypothesis is sufficient to describe all of the behavioral changes following an amygdaloid lesion, then an amygdaloid preparation should behave like a normal rat when confronted with non-aversive stimuli.

Enloe (1975) has investigated the effects of lesions of the anterior lateral hypothalamus, the best known region receiving inputs from both the septum and amygdala (Cowan, Raisman, and Powell, 1965; Driefuss and Murphy, 1968) which effects social behaviors in the rat. She has shown that LHA lesions result in rats which show long-term increases in emotionality, low social cohesiveness, decreased mobility, and a lack of interest in social behavior." Enloe reported that LHA's showed an increased

tendency for vocalization, defensive reactions, and avoidance when approached by another rat. Because the LHA region receives a major efferent input from the medial septum (Miller and Morgenson, 1972) which has been shown to be the critical region of the septum related to changes in social cohesiveness (Poplawsky and Johnson, 1973) it was expected that the LHA preparations might show changes in social behavior similar to those of septal or amygdaloid preparations.

It is possible that LHA subjects might show a recovery of social cohesion tendencies, as do amygdaloid preparations, if a postoperative testing period was used, which is longer than the 15-day period employed by Enloe (1975). In Experiment I, the attraction and cohesiveness tendencies of LHA subjects are evaluated following a 21-day recovery period and a partial attenuation of the heightened emotional reactivity which typifies the early postoperative period. The social attraction tendencies of the LHA group, for a wide variety of stimulus classes, can be compared to the behavior patterns of rats with lesions of the nuclei contributing major inputs to the LHA region.

# CHAPTER II

# METHODS

## Subjects and Apparatus

The subjects were 38 male Long-Evans rats, 90-120 days of age at the beginning of the experiment. Following selection, the rats were housed individually in a room which was isolated from the housing facilities for rabbits and cats, and were maintained on an *ad lib* food and water schedule.

The apparatus was the same circular open field used by Jonason and Enloe (1971). The field, which was 1.23 m in diameter and surrounded by a 48.6 cm wall, was painted glossy white and was divided by black lines into 49 numbered sections of approximately equal area. A wedge of the field, enclosing three-eighths of the total area, was designated as the approach zone and contained a hook for attachment of a tether to restrain a stimulus animal. The remaining five-eighths of the field was divided into a neutral zone (half of the total area of the field) and an avoidance zone (one-eighth of the total field area). The avoidance zone was located in the area of the field which was physically furthest from the approach zone.

A screen was used to cover the apparatus and to prevent the animals being tested from escaping. A 40-watt bulb suspended 51.2 cm above the center of the field provided the only illumination in the testing room. The luminance in the center of

the field was 80 candelas/$m^2$ and was 50 candelas/$m^2$ at the periphery of the field. The field was washed with vinegar, alcohol, and water after every testing trial to minimize odor-related cues.

Surgical Procedure

After 5 days of individual housing, each rat was assigned to one of four surgical groups. Surgery was carried out under clean but not sterile conditions after intraperitoneal injection of pentobarbital sodium anesthesia and atropine sulfate. Septal (S), amygdaloid (A), and anterior lateral hypothalamic (LHA) lesions were accomplished stereotaxically with the anodal electrolytic lesions being produced by means of a unipolar electrode insulated except for 0.5 mm at the tip.

The stereotaxic coordinates for the lesions were computed using the atlas of deGroot (1959) and were: Group S: AP +7.8, L $\pm$0.5, DV +1.0, current 2 ma. for 18 sec., Group A: AP +4.2, L $\pm$5.0, DV -3.0; AP +5.0, L $\pm$ 4.5, DV -3.0; AP +5.8, L $\pm$4.5, DV -2.5, current 2 ma. for 20 sec., Group LHA: AP +6.8, L $\pm$1.3, DV -2.0, current 1 ma. for 10 sec. Sham-operative rats (Group C) were anesthetized and were subjected to an incision of the skin over the midline. Following surgery, all rats were administered a broad-band antibiotic and were returned to their home cages for a 21-day recovery period.

Postoperative procedure

On post-operative days 4, 6, 8, 10, 12, 14, 16, and 18 the rats were emotionality rated using the procedures and scale described by King (1958), and used by Jonason and Enloe (1971). Using this six-component scale, each rat was scored according to (1) reaction to a visually presented pencil, (2) reaction to light pencil tapping on the back, (3) resistance to capture, (4) resistance to handling, (5) vocalization, (6) urination and defecation. Each subject was given a score of from 1-5 points on each of Categories 1-4, and from 0-5 on Category 5, and from 0-2 on Category 6. The mean sum of the category scores assigned by two independent raters became the daily emotionality score for a given subject. The emotionality score averages are presented for the subjects from both Experiment I and Experiment II combined in Figure 2.

On postoperative days 16-21, each subject was placed individually in the open field for 5 minutes per day. Following the six days of adaptation, the experimental rats were tested for 300 seconds per day for 36 days with various classes of stimulus animals tethered in the approach zone. The stimulus classes were:

(1) 5 normal hooded rats weighing approximately 400-500 g. each which were tethered with a wide rubber band that was attached around the chest. The rat stimuli were all male, as were all other stimuli used.

(2) 5 albino mice which were tethered with a small rubber band attached around the chest

(3) 3 albino and 2 pigmented rabbits weighing approximately 4.0 kg and tethered with a neck collar

(4) 5 adult cats weighing approximately 5.0 kg and tethered with a neck collar

At the beginning of each of the social behavioral observations, a stimulus animal was tethered in the approach zone. The experimental rat was placed in a circular wire starting cage which was placed in the center of the open field, but just outside the approach zone. After 5 seconds, the wire cage was lifted away and a 300 second timer was started. Three clocks were used to record (1) the number of seconds the experimental rat spent in the approach zone, (2) the number of seconds the rat spent in the approach zone and within 15 cm of the stimulus animal (close approach zone), and (3) the number of seconds the rat spent in the avoidance zone. The number of times each of the above events occurred was also recorded which made it possible to calculate mean numbers of seconds for each of the above events.

The order of presentation of the stimulus classes was constant across all experimental groups, and is listed in Table 1. Each class of stimulus animals described above contained five members, and the order of pairing individual stimulus animals with experimental rats was counterbalanced across each group. For purposes of testing the reliability of the testing

TABLE 1. Order of presentation of stimulus animals in Experiment I.

| STIMULUS ANIMAL | NUMBER OF DAYS |
|---|---|
| RAT - 1 | 3 DAYS |
| RABBIT | 3 DAYS |
| RAT - 2 | 3 DAYS |
| CAT-1 | 3 DAYS |
| RAT - 3 | 3 DAYS |
| REST PERIOD | 6 DAYS |
| RAT - 4 | 3 DAYS |
| MOUSE | 3 DAYS |
| RAT - 5 | 3 DAYS |
| CAT - 2 | 3 DAYS |
| RAT - 6 | 3 DAYS |

procedure and for determining if previous experience in the open field influenced later social behaviors, an individual experimental rat was always repaired with the same member of a stimulus class during repeated measures.

Histological Procedure

Upon completion of postoperative testing, the subjects were deeply anesthetized and then were perfused intracardially with 0.9% saline followed by 10% formalin. The brains were then removed and sectioned at 35μ. The sections were mounted on slides, stained with cresyl violet, and examined for the extent of the lesion. The lesions were reconstructed, with outcomes as shown in Figure 1.

Septal lesions. As in the experiment of Jonason and Enloe (1971), the lesions were large and included both pre- and post-commissural components of the septum. The structures involved included the lateral and medial septal nuclei, the nucleus of the tract of the diagonal bands, the anterior commissure, the columns of the fornix, the triangular septum, and the nucleus septalis fimbrialis. Damage also occurred in some subjects to the pars anterior of the hippocampus, nucleus interstitialis striae terminalis, stria medullaris thalami, preoptic region of the hypothalamus, and the nucleus paratenialis.

Amygdaloid lesions. Amygdaloid lesions were large and included: nucleus basalis, pars medialis; nucleus lateralis, pars anterior; nucleus centralis, nucleus corticalis, nucleus medialis, massa intercalatam, and stria terminalis. Extra-amygdaloid damage frequently occurred to: caudatus, putamen, entorhinal cortex, fimbria hippocampi, hippocampus, and the

Figure 1. Brain reconstructions for Groups S, A, and L from Experiment I.

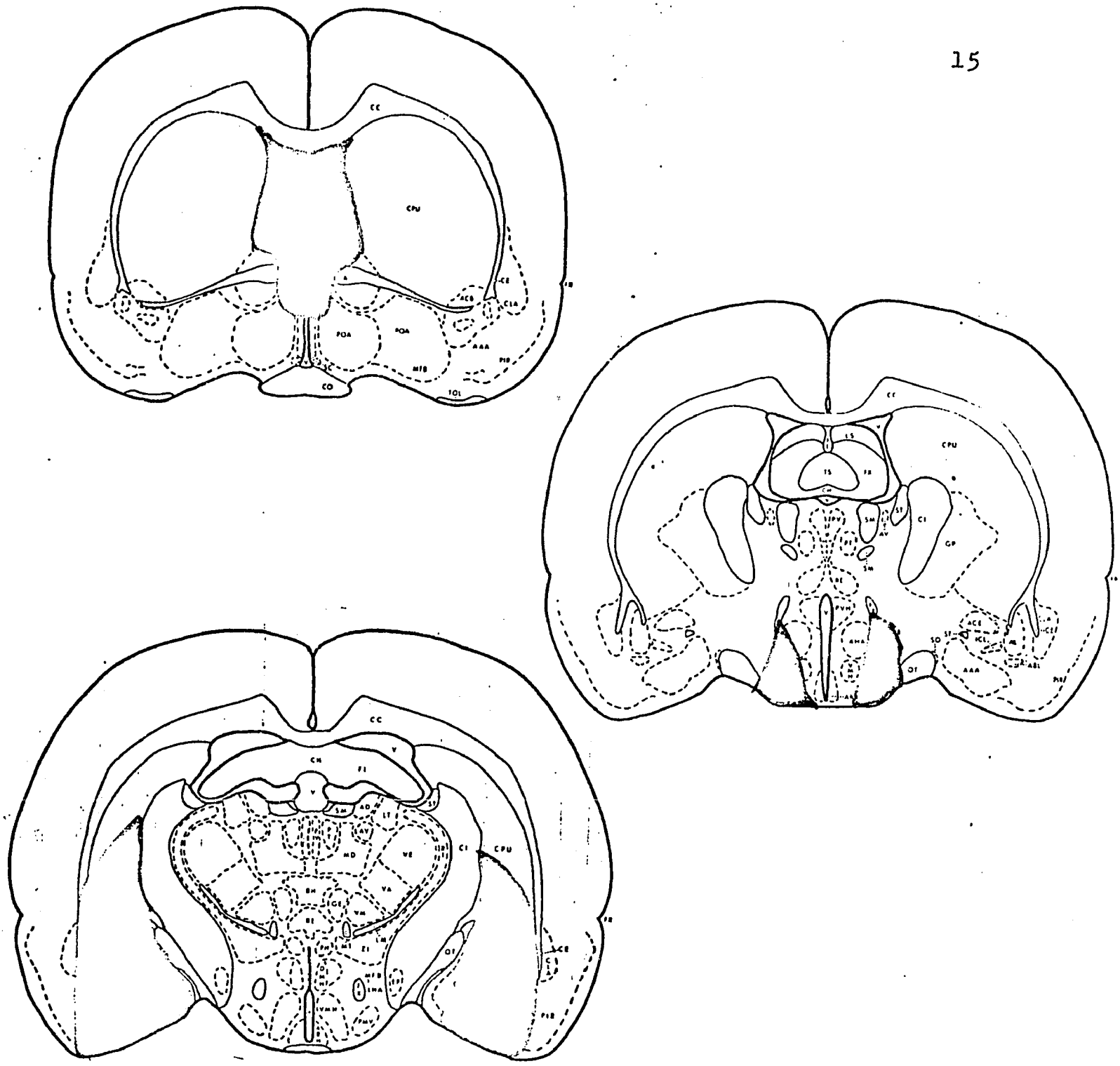



Figure 1. Reconstructions of typical lesions from (a) Septal Group (b) LHA Group (c) Amygdaloid Group. Diagrams from deGroot (1959).

internal capsule.

Anterior lateral hypothalamic lesions. As intended, the LHA lesions were anterior to the region typically associated with eating disorders, and the rats experienced no abnormal postoperative weight loss. The damage typically included: nucleus lateralis hypothalami, the medial forebrain bundle, and the columns of the fornix. Frequent damage also occurred to the dorsal supraoptic commissure, and to the anterior hypothalamic nucleus.

# CHAPTER III

## RESULTS

The mean emotionality ratings for the four experimental groups (septal (S), amygdaloid (A), anterior lateral hypothalamus (L), and sham normal (N)), combined across Experiments I and II, are presented graphically in Figure 2. Postoperative ratings indicated that both septal and LHA groups showed a dramatic increase in emotionality, while the amygdaloid group showed a lesser increase. Septal preparations recovered to normal levels after 6-8 postoperative days with handling, but LHA subjects remained more reactive than normals even after 18 postoperative days.

A one-way ANOVA performed between groups on the postoperative emotionality data indicated a highly significant effect of lesions on emotionality during the 18 day postoperative rating period ($F=75.12$, $df=3,624$, $p$ less than .01). A Newman-Keuls comparison between group means, the results of which are listed in Table 2, indicated that while septal and amygdaloid subjects were more emotional than normal rats during the rating period, all three groups were significantly less emotional than LHA subjects. A t-statistic on the emotionality data for the last day of rating indicated that LHA preparations were more emotional than the amygdaloid group which showed the highest mean of the remaining three experimental groups ($t=2.75$, $df=38$, $p$ less than .01).

Figure 2. Mean emotional reactivity scores by postoperative days for rats in Experiments I and II combined.

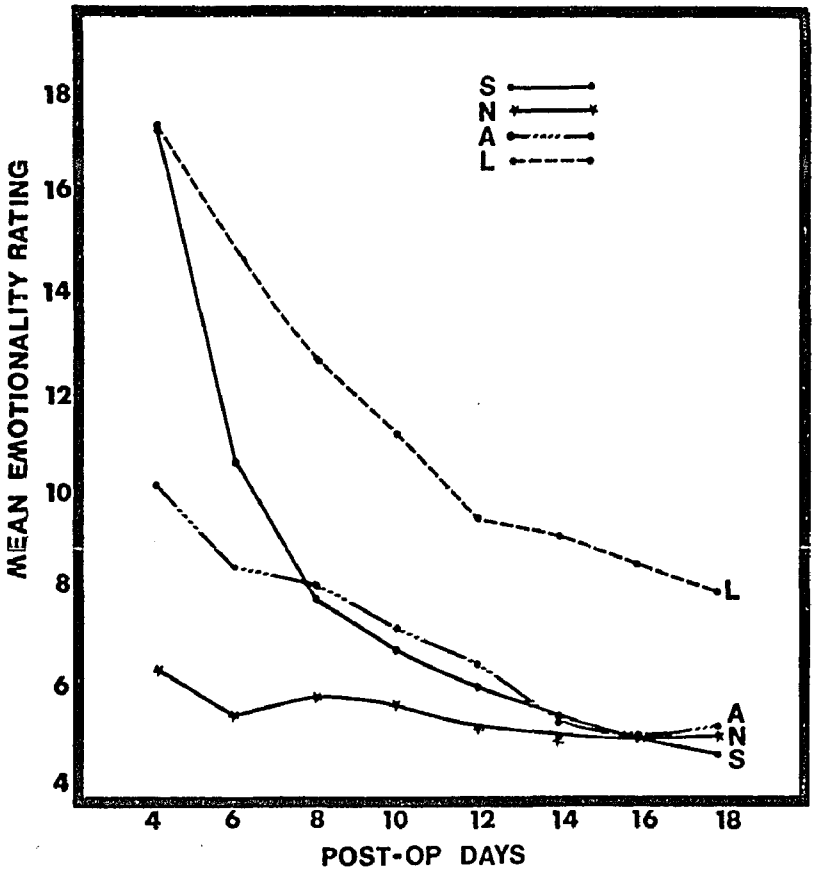

S
N
A
L
MEAN EMOTIONALITY RATING
18
16
14
12
10
8
6
4
4
6
8
10
12
14
16
18
POST-OP DAYS
L
A
N
S

TABLE 2

Newman-Keuls tests for differences in postoperative emotionality between experimental groups.

| Group | p |
|---|---|
| N-A | .01 |
| N-S | .01 |
| N-L | .01 |
| A-S | ns |
| A-L | .01 |
| L-S | .01 |

The distance maintained between the experimental rat and the tethered stimulus animal was assumed to reflect the attractiveness of the stimulus to the subject. The number of seconds, out of a possible 300 per testing period, that the subjects spent in the approach zone, in the close approach zone, and in the avoidance zone was taken to represent respectively the tendencies of the rats to approach, contact, or avoid the stimulus animal. The percentages of time spent by experimental rats in the approach, close approach, avoidance, and neutral zones when confronting rats, cats, rabbits, and mice are shown graphically in Figure 3. It can be seen that rats spend a very small amount of time in the neutral zone, which constitutes one-half of the total field area, and tend to actively approach or avoid any of the living stimuli tested.

A multivariate ANOVA indicated that lesions, stimulus animals, and lesion x stimulus animals were all significant for each of the three measures of attraction or avoidance with probabilities less than .002. The values of F for the MANOVA are listed in Table 3.

The close approach measure, indicating that there was no more than 15 cm between the stimulus and subject, was chosen for further analysis because it is the measure

TABLE 3

Values of F and related probabilities for measures of attraction to stimulus animals by experimental rats in Experiment I.

AVOIDANCE

| Variable | F | df | p |
|---|---|---|---|
| L | 86.21 | 3,360 | .001 |
| S | 19.62 | 9,360 | .001 |
| LxS | 6.29 | 27,360 | .001 |

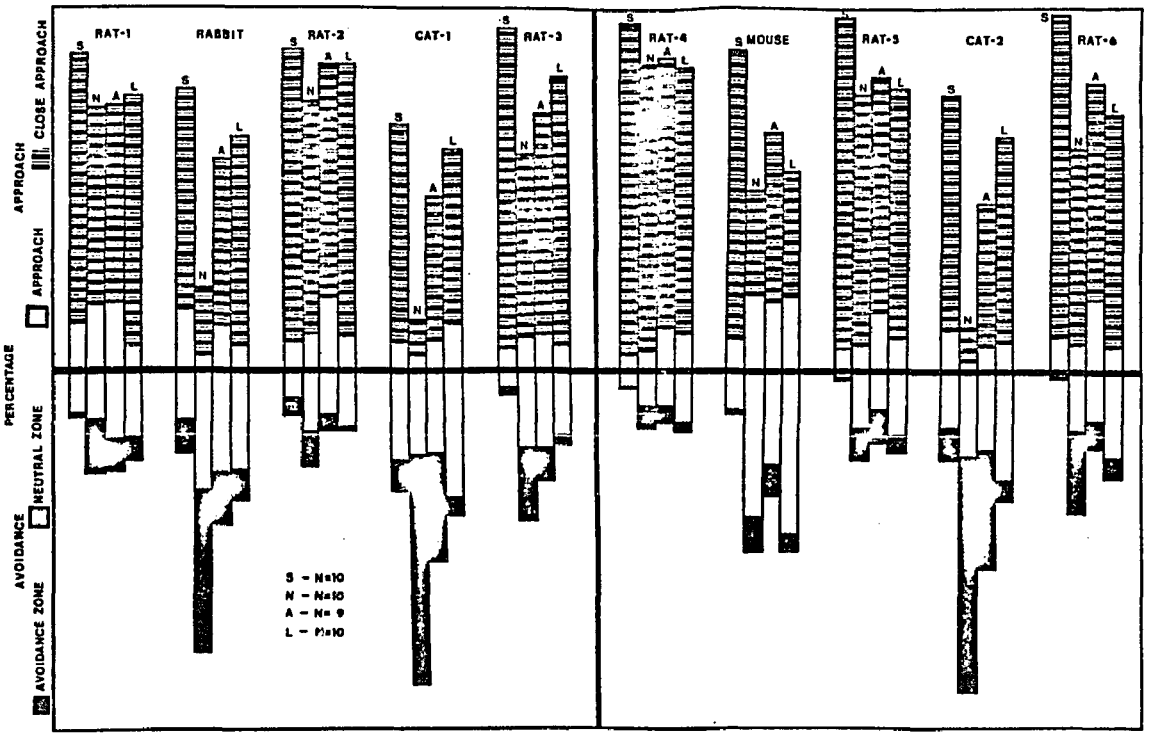
APPROACH

| Variable | F | df | p |
|---|---|---|---|
| L | 44.21 | 3,360 | .001 |
| S | 17.62 | 9,360 | .001 |
| LxS | 2.31 | 27,360 | .001 |

CLOSE APPROACH

| Variable | F | df | p |
|---|---|---|---|
| L | 46.00 | 3,360 | .001 |
| S | 18.83 | 9,360 | .001 |
| LxS | 2.051 | 27,360 | .002 |

Figure 3. Percentages of the testing periods spent in the close approach, approach, avoidance, and neutral zones by rats in Experiment I as a function of the class of stimulus animal in the approach zone.


RAT-1
RABBIT
RAT-2
CAT-1
RAT-3
RAT-4
MOUSE
RAT-5
CAT-2
RAT-6
S
N
A
L
APPROACH
CLOSE APPROACH
APPROACH
PERCENTAGE
NEUTRAL ZONE
AVOIDANCE
AVOIDANCE ZONE
S - N=10
N - N=10
A - N= 9
L - N=10

that most closely resembles the mean contact measure used by Jonason and Enloe (1971), and considered by those authors to be their most sensitive index of social cohesiveness and attraction.

Next, one-way ANOVA's were calculated for each experimental group comparing close approach times for each of the six presentations of the conspecific stimulus. This was necessary to determine if the fixed sequential order of presentation of the stimulus animal classes introduced a bias into the social attraction behaviors of the experimental rats, which would influence conspecific cohesiveness over repeated presentations of the rat stimulus. Septal, amygdaloid, and LHA groups showed a consistent level of conspecific cohesiveness across all six presentations of the rat stimulus, regardless of the intervening stimulus animals. The ANOVA for the normal group, however, revealed a significant difference ($F = 2.94$, $df = 5,54$, $p$ less than .05) across presentations which appeared by inspection to be related to the sharply decreased conspecific cohesiveness which followed presentation of the cat. A Newman-Keuls test indicated that the only significant difference between conspecific means occurred between means for the first conspecific presentation which followed presentation of the cat (C - 1), and the subsequent conspecific presentation

(p less than .05). As had been anticipated, the trauma of the first presentation of the cat had apparently suppressed normal cohesiveness tendencies following the presentation of the predator stimulus. The six-day rest interval, inserted between the third and fourth presentations of the conspecific, was apparently sufficient to restore a normal level of conspecific cohesiveness to the normal subjects as the mean close approach times for rat presentations 4, 5, and 6 were not significantly different from those for presentations 1 and 2.

Although approach tendencies to conspecifics was not effected, except for those in the normal group, by intervening stimulus presentations it must next be determined whether approach tendencies to non-conspecific stimuli are equally stable. The predator stimulus was presented on two occassions to test the notion that approach to a docile, tethered cat might not be stable with repeated presentations of that stimulus which never resulted in predatory attack. A one-way ANOVA comparing the close approach times to the cat between groups for the first and second cat presentations indicated that habituation to that stimulus did not occur in any group, including normal rats.

For the purposes of conducting Newman-Keuls post-hoc analyses of the cell means related to approach times

to the four classes of stimuli employed, the data from the six presentations of rats was collapsed into one mean close approach time per subject, as was the data from the two presentations of the cat. The results of the Newman-Keuls tests are presented in Table 4.

Rats with septal lesions showed significantly higher close approach times to all species tested than did any of the other experimental groups, with one exception. LHA subjects, which behaved most like septal preparations, showed an approach tendency to rabbits which was not significantly different from that of septals, although the LHA close approach mean was lower. The septal lesion was the only lesion to produce a long-term increase in conspecific cohesiveness as compared to levels exhibited by normal rats. Septal preparations also showed a high degree of attraction to mice, which were only minimally attractive to LHA, amygdaloid, or normal subjects. The mouse stimulus elicited as much approach from the septal subjects as did a conspecific stimulus. Through the entire duration of Experiments I and II, the author recorded only two cases of muricide, both by amygdaloid subjects, and an increased drive to approach and kill mice does not seem to be related to the increased cohesiveness with mice by the septal group.

TABLE 4

Newman-Keuls tests for differences in mean close approach times.

| Comparison | p |
|---|---|
| N(R) X N(L) | .01 |
| N(R) X N(C) | .01 |
| N(R) X N(M) | .01 |
| N(L) X N(C) | ns |
| N(L) X N(M) | ns |
| N(C) X N(M) | ns |
| S(R) X S(L) | .01 |
| S(R) X S(C) | .01 |
| S(R) X S(M) | ns |
| S(L) X S(C) | ns |
| S(L) X S(M) | .01 |
| S(C) X S(M) | .01 |
| A(R) X A(L) | .01 |
| A(R) X A(C) | .01 |
| A(R) X A(M) | .01 |
| A(L) X A(C) | .01 |
| A(L) X A(M) | ns |
| A(C) X A(M) | ns |
| L(R) X L(L) | .01 |
| L(R) X L(C) | .01 |
| L(R) X L(M) | .01 |
| L(L) X L(C) | .05 |
| L(L) X L(M) | .01 |
| L(C) X L(M) | .01 |
| N(R) X S(R) | .01 |
| N(R) X S(L) | ns |
| N(R) X S(C) | ns |
| N(R) X S(M) | .01 |
| N(L) X S(R) | .01 |
| N(L) X S(L) | .01 |
| N(L) X S(C) | .01 |
| N(L) X S(M) | .01 |
| N(C) X S(R) | .01 |
| N(C) X S(L) | .01 |
| N(C) X S(C) | .01 |
| N(C) X S(M) | .01 |
| N(M) X S(R) | .01 |
| N(M) X S(L) | .01 |
| N(M) X S(C) | .01 |
| N(M) X S(M) | .01 |

| Comparison | p |
|---|---|
| N(R) X A(R) | ns |
| N(R) X A(L) | .01 |
| N(R) X A(C) | .01 |
| N(R) X A(M) | .01 |
| N(L) X A(R) | .01 |
| N(L) X A(L) | .01 |
| N(L) X A(C) | .01 |
| N(L) X A(M) | .01 |
| N(C) X A(R) | .01 |
| N(C) X A(L) | .01 |
| N(C) X A(C) | .01 |
| N(C) X A(M) | .01 |
| N(M) X A(R) | .01 |
| N(M) X A(L) | .01 |
| N(M) X A(C) | .01 |
| N(M) X A(M) | .01 |
| N(R) X L(R) | ns |
| N(R) X L(C) | .05 |
| N(R) X L(L) | ns |
| N(R) X L(M) | .01 |
| N(L) X L(R) | ns |
| N(L) X L(L) | .01 |
| N(L) X L(C) | .01 |
| N(L) X L(M) | .01 |
| N(C) X L(R) | .01 |
| N(C) X L(L) | .01 |
| N(C) X L(C) | .01 |
| N(C) X L(M) | .01 |
| N(M) X L(R) | .01 |
| N(M) X L(L) | .01 |
| N(M) X L(C) | .01 |
| N(M) X L(M) | ns |
| S(R) X A(R) | .01 |
| S(R) X A(L) | .01 |
| S(R) X A(C) | .01 |
| S(R) X A(M) | .01 |
| S(L) X A(R) | ns |
| S(L) X A(L) | .01 |
| S(L) X A(C) | .01 |
| S(L) X A(M) | .01 |
| S(C) X A(R) | ns |
| S(C) X A(L) | .01 |

| Comparison | p |
|---|---|
| S(C) X A(C) | .01 |
| S(C) X A(M) | .01 |
| S(M) X A(R) | .01 |
| S(M) X A(L) | .01 |
| S(M) X A(C) | .01 |
| S(M) X A(M) | .01 |
| S(R) X L(R) | .01 |
| S(R) X L(L) | .01 |
| S(R) X L(C) | .01 |
| S(R) X L(M) | .01 |
| S(L) X L(R) | ns |
| S(L) X L(L) | ns |
| S(L) X L(C) | ns |
| S(L) X L(M) | .01 |
| S(C) X L(R) | ns |
| S(C) X L(L) | ns |
| S(C) X L(C) | .01 |
| S(C) X L(M) | .01 |
| S(M) X L(R) | ns |
| S(M) X L(L) | .01 |
| S(M) X L(C) | .01 |
| S(M) X L(M) | .01 |
| A(R) X L(R) | ns |
| A(R) X L(L) | ns |
| A(R) X L(C) | ns |
| A(R) X L(M) | .01 |
| A(L) X L(R) | .01 |
| A(L) X L(L) | .01 |
| A(L) X L(C) | ns |
| A(L) X L(M) | .01 |
| A(C) X L(R) | .01 |
| A(C) X L(L) | .01 |
| A(C) X L(C) | .01 |
| A(C) X L(M) | .01 |
| A(M) X L(R) | .01 |
| A(M) X L(L) | .01 |
| A(M) X L(C) | ns |
| A(M) X L(M) | .01 |

Amygdaloid subjects, while showing a normal level of conspecific cohesiveness, showed higher than normal levels of close approach with rabbits, cats, and mice. In each case, however, the close approach times were lower than comparable scores for the septal group. It is obvious that if experimental groups show a normal level of cohesiveness with conspecifics, this does not necessarily indicate that they will behave like normal rats when confronting other living stimuli.

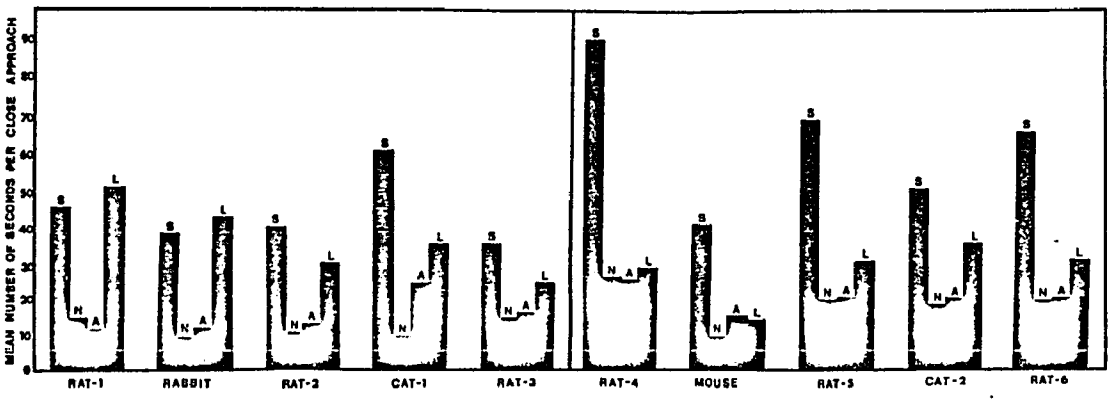
LHA subjects, while showing normal levels of cohesiveness with both conspecifics and mice, showed approach tendencies to rabbits and cats which were higher than those for either normal or amygdaloid subjects. As was previously mentioned, the close approach tendencies of septal and LHA subjects toward rabbits were not significantly different.

Normal rats were significantly more cohesive with conspecifics than with cats, rabbits, or mice, which were all approached to a low degree. Rabbits and cats elicited equally low approach tendencies and an inspection of the avoidance zone data in Figure 3 indicates that normal rats not only fail to approach, but actively avoid, both rabbits and cats, while they tend to ignore mice, neither approaching

nor avoiding that stimulus.

Changes that occurred postoperatively in the average duration of close contact were assumed to represent important consequences of the lesions administered. Average close contact times, presented in Figure 4, were calculated by dividing the total close approach times by the number of times the subjects entered the close approach zone. An ANOVA performed on close approach mean durations between groups and stimulus classes indicated that lesions ($F + 38.79$, $df = 3, 337$, $p$ less than .001) and stimuli ($F = 3.135$, $df = 3, 135$, $p$ less than .001) were significant but the interaction was non-significant ($p$ less than .511). As a consequence, mean close approach times were compared between experimental groups using a Newman-Keuls test. Both septal and LHA groups showed statistically equal average close approach times ($p$ less than .05), and both of these groups were significantly higher on this measure than either normal or amygdaloid subjects ($p$ less than .01 for S, and $p$ less than .05 for L). Normal and amygdaloid subjects exhibited statistically equal mean approach times, which were significantly lower than the mean close approach times for septal or LHA subjects. It is interesting to note that while the close approach times for septal versus LHA groups were quite different between mice and

Figure 4. Mean numbers of seconds spent in the close approach zone by rats in Experiment I as a function of the class of stimulus animal in the approach zone.


MEAN NUMBER OF SECONDS PER CLOSE APPROACH
S
N
A
L
RAT-1
RABBIT
RAT-2
CAT-1
RAT-3
RAT-4
MOUSE
RAT-5
CAT-2
RAT-6

conspecifics, the mean close approach times were equivalent. Similarly, while amygdaloid subjects showed higher close approach times to rabbits and cats than did normal subjects, the mean close approach times were nevertheless equivalent.

# CHAPTER IV

## EXPERIMENT II

### INTRODUCTION

Experiment II is designed to determine the preferential approach behaviors of limbic-lesioned and normal rats when two classes of living stimuli are simultaneously presented. This procedure will first allow a determination of preferences which might occur between stimulus classes which, when presented individually in Experiment I, elicited equal degrees of approach from the experimental rats. Second, this procedure will allow the determination of whether the approach behavior and mobility of a group of experimental rats changes when more than one living stimulus is simultaneously present in the environment.

An interesting observation was made during the testing of a group of normal rats at the beginning of the procedures for Experiment II. Rats which had been housed in a hallway outside the housing facilities for rabbits and cats showed no avoidance of rabbits or cats when presented with those stimuli. Subsequent use of rats which were housed in an isolated area of the laboratory resulted in behaviors by the normal rats which matched the behaviors of rats presented with a cat in Experiment I. Access to olfactory cues was thus shown to radically alter reactions which are considered to be innate in rats.

# CHAPTER V
# METHODS

## Subjects and Apparatus

The subjects were 40 male Long-Evans rats, 90-120 days of age at the beginning of the experiment. Selection, housing, and feeding conditions were identical to those conditions used in Experiment I.

The apparatus was a Y-shaped preference box, with three identical arms separated by $120^{\circ}$. Each arm was 76 cm. long, 60 cm. high, and 60 cm. wide, and was joined to a triangular-shaped starting area which was 60 cm. on each side. The corners at the end of each arm were rounded with pieces of white vinyl plastic having radii of curvature of 30 cm. The apparatus was painted with glossy white enamel, except for the covers over the arms which were constructed of clear plexiglas. A 25-watt bulb suspended 70 cm. above the center of the box provided the only illumination in the testing chamber. The luminance in the center of the apparatus was 50 candelas/$m^2$ and was 20 candelas/$m^2$ at the ends of the arms.

Each arm contained a hook to which a tether attached to a stimulus animal could be fastened. The length of the tether could be adjusted so that the head of the stimulus animal could not break the plane formed at the intersection of the apparatus arm and the start area. The apparatus was washed after every testing trial as in Experiment I.

Surgical Procedure

Surgical procedure and surgical groups were identical to those described in Experiment I.

Postoperative Procedure

As in Experiment I, the rats were tested for emotional reactivity on postoperative days 4, 6, 8, 10, 12, 14, 16, and 18, and were adapted to the apparatus on postoperative days 16-21 for five minutes per day. Upon completion of the adaptation period, the rats were tested for preferences in the Y-shaped choice apparatus for 300 seconds per day for 9 days, with various combinations of the stimulus animal classes described in Experiment I.

During the first three days of the behavioral testing sequence, all experimental rats were tested for preferences with a tethered rat in one arm of the apparatus, a tethered rabbit in another arm, and the third arm of the apparatus containing no stimulus animal. On the next three days, post-operative days 25-27, all rats were tested for preferences between a rat, a cat, and an empty arm, and on the final three days of the sequence the rats were tested for preferences between a rabbit, a cat, and an empty arm. Preference behavior was measured as the number of seconds, out of a possible 300 seconds per day, that the experimental rat spent in each arm of the apparatus. The number of times a rat entered each arm of the apparatus was also measured, and the mean length of an approach to any stimulus could be calculated.

The order of presentation of the pairs of stimulus animal classes was always fixed, but each class of stimulus animals contained three different members chosen from the pool of five animals per stimulus class used in Experiment I. Each experimental group of rats experienced all members of each class during the course of the experiment, and the order of presentation was counterbalanced.

A given experimental rat would be presented with the same stimulus animals during any three day testing period, but would experience other members of the same stimulus classes during subsequent testing periods employing the same stimulus classes. During a three day testing period, each stimulus animal would appear for one day in each of the three arms of the apparatus. To minimize the effects of residual odor cues, a given class of stimulus animals would always be presented in the same arm of the apparatus for all experimental rats tested on a specific day, but would be consistently presented in another arm the following day.

To begin a daily testing session, two stimulus animals from different stimulus classes, such as a rat and a cat, would be tethered in two arms of the apparatus while the third arm would contain no stimulus. The experimental rat would be held in the center of the apparatus such that both stimulus animals would simultaneously be visible, and the empty arm

was behind the experimental rat's head. The rat was then released, and the number of seconds it spent in each arm of the apparatus was recorded. At the conclusion of testing each rat was sacrificed and perfused, and the brains removed so that lesion could be examined histologically.

Histological Procedure

Histological procedures were identical to those described in Experiment I. The outcomes of reconstruction of the lesions in Experiment II are shown in Figure 5.

Figure 5. Brain reconstructions for Groups S, A, and LHA from Experiment II.

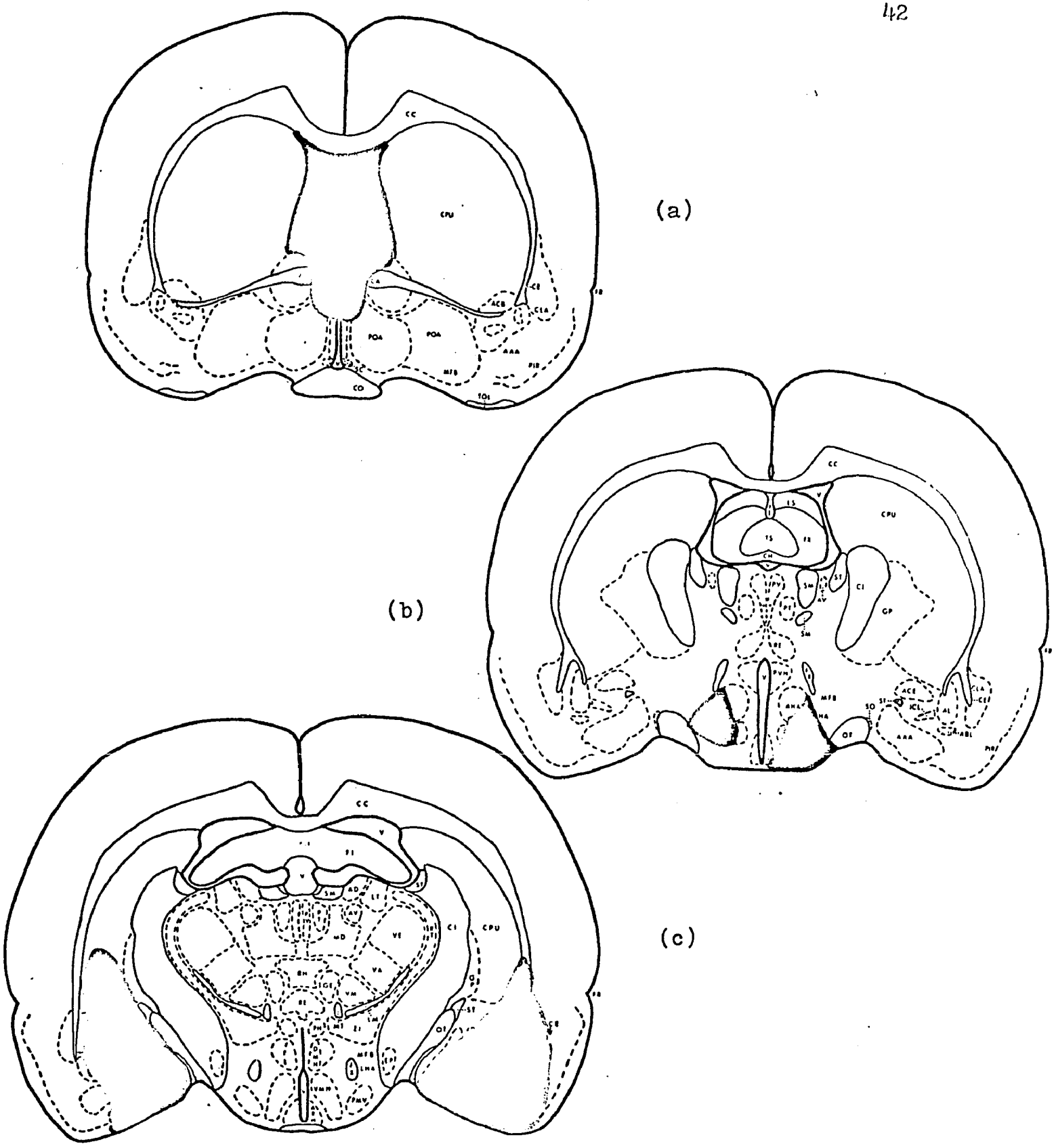



Figure 5. Reconstruction of a typical lesion from (a) Septal Group (b) LHA group (c) Amygdaloid Group Diagrams from deGroot (1959).

# CHAPTER VI
# RESULTS

The data collected during Experiment II was concerned with an examination of the preferential approach behaviors of septal, amygdaloid, LHA and normal subjects when two stimulus animal types were simultaneously presented in a Y-shaped apparatus.

The data related to preferential approach to rabbits, rats, cats, or an empty apparatus alley is presented graphically in Figure 6. While the data in that figure is expressed as percentages of total time spent approaching particular stimuli, statistical analyses were performed on the raw data expressed in numbers of seconds of approach. Because the preference data within groups is related, Wilcoxen matched pairs, signed rank tests were performed to compare preferences within groups for each of the three combinations of stimulus animals that were presented. The results of the Wilcoxen tests are presented in Table 5, with the following abbreviations: A - amygdaloid; S - Septal; L - LHA; N - Normal; R - rat; C - cat; L - rabbit; 0 - no stimulus.

Septal preparations showed a clearcut preference for conspecifics over either rabbits or cats, although the three stimulus classes were approached to an approximately equal degree when only one stimulus was present in the open field in Experiment I. When no conspecific was present, the septal

Figure 6. Percentages of the testing periods spent in the various arms of the testing apparatus as a function of the combinations of classes of stimulus animals presented to rats in Experiment II.

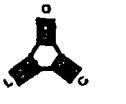
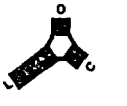
| GROUP | R-RAT<br>L-RABBIT<br>C-CAT<br>O-EMPTY | | |
|---|---|---|---|
| **S**<br>N:10 | | | |
| **N**<br>N:10 | | | |
| **A**<br>N:10 | | |  |
| **L**<br>N:10 | | |  |

TABLE 5

Wilcoxen tests for differences between approach times to alleys of the testing apparatus containing a specific stimulus animal or containing no stimulus, for three combinations of stimuli.

| COMPARISON | SEPTAL | NORMAL | AMYGDALOID | LHA |
|---|---|---|---|---|
| R X L | .01 | .01 | ns | ns |
| L X 0 | ns | ns | ns | ns |
| R X 0 | .01 | .025 | ns | ns |
| R X C | .01 | .01 | ns | .01 |
| C X 0 | ns | ns | ns | ns |
| R X 0 | .05 | .05 | ns | .01 |
| L X C | ns | .01 | ns | .025 |
| L X 0 | ns | ns | ns | .01 |
| C X 0 | .01 | .01 | ns | ns |

preparations approached either a rabbit or a cat to an approximately equal degree, and generally preferred either stimulus to the alley containing no stimulus.

LHA subjects which, like septals, showed an above normal degree of approach to a rabbit or cat in Experiment I, exhibited no preference between conspecifics or rabbits in Experiment II, but showed a significantly greater degree of approach to either the rabbit or rat over the cat. The fact that LHA subjects prefer to approach non-predator stimuli when given a choice differentiates this group from septal or amygdaloid groups which also showed more approach to a cat than did normal rats in Experiment I. Normal rats avoided the rabbit or cat when a conspecific stimulus was present in the apparatus and, like septal or LHA groups, preferred to approach a conspecific over an empty apparatus alley. Interestingly, when a rabbit and cat were simultaneously presented, the normal rat showed significantly more approach to the rabbit than to the cat, but preferred the empty alley over either stimulus.

The amygdaloid group was unique among the experimental rats tested because this group showed no significant preference for any stimulus, or for approach to a stimulus versus entry into the alley containing no stimulus.

The average approach times to the stimuli used in Experiment II were examined to determine if a second living stimulus presented in the environments of the experimental rats would effect the lengths of average approaches to the stimuli used, as compared to the results from Experiment I for the average close approach measure. A second stimulus animal in the field might be expected to alter the expected average approach times if both stimuli elicited approach. The results of a comparison of average approach times between groups, based on mean numbers of seconds of approach, is presented graphically in Figure 7.

While no direct comparisons between the average approach times from Experiment II could be made with the mean close approach times from Experiment I, the average approach times to living stimuli could be compared between experimental groups. A one-way ANOVA was calculated to compare the mean approach times between groups, excluding scores of zero, to all living stimuli. The results indicated a significant lesion effect ($F = 16.02$, $df = 3, 205$, $p$ less than .01), and a Newman-Keuls test, the results of which are presented in Table 6, was conducted to test differences between experimental group means.

Figure 7. Mean number of seconds spent in the various arms of the apparatus per entry as a function of the combination of stimulus animals presented to rats in Experiment II.

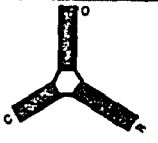
| GROUP | R-RAT<br>L-RABBIT<br>C-CAT<br>O-EMPTY | | |
|---|---|---|---|
| S | |  | |
| N | | | |
| A | | | |
| L | | | |

TABLE 5

Newman-Keuls tests for differences between the mean approach times to the stimuli used in Experiment I.

| COMPARISON | p |
|---|---|
| S X N | .01 |
| S X A | .01 |
| S X L | .01 |
| A X N | ns |
| A X L | ns |
| L X N | ns |

Septal subjects, as in Experiment I, exhibited significantly longer average approach times to living stimuli than did either amygdaloid or normal rats. Unlike Experiment I, however, septal subjects also showed significantly higher average approach times than did LHA preparations. LHA subjects could not be statistically differentiated from either normal or amygdaloid preparations on the basis of average approach times when two stimuli were simultaneously presented. Because LHA subjects exhibited lower average approach times than did septals when two stimuli were presented, it might be concluded that LHA subjects are alternating approaches between stimuli while septal subjects tend to remain more continuously in the vicinity of the first stimulus animal approached.

# CHAPTER VII

## GENERAL DISCUSSION

First, this investigation has confirmed the observation of Jonason and Enloe (1971) that septal lesions enhance conspecific cohesiveness. This increased cohesiveness has been shown to be stable for at least 57 postoperative days, following a 1-2 day period at the beginning of testing during which time the subjects show a transient decreased cohesiveness tendency. Jonason and Enloe reported a similar transient decrease while using a much shorter recovery period. Although Kolb and Nonneman (1975) have challenged the validity of the septal cohesiveness effect, it should be noted that those authors tested their subjects for only two days and were, in all probability, observing the septal preparations only during the period of decreased social cohesiveness.

Second, the present study confirms a finding of Jonason, Enloe, Contrucci, and Meyer (1973) which indicates that the decreased cohesiveness which was observed by Jonason and Enloe (1971) to follow an amygdaloid lesion is a transient effect. Amygdaloid preparations, tested from 22-57 days postoperative in Experiment I, exhibited levels of conspecific cohesiveness which were indistinguishable from the cohesiveness of normal rats.

Third, this study has shown that rats subjected to LHA lesions exhibit normal or above normal levels of conspecific social cohesiveness following a 21-day recovery period. This fact contrasts with the finding of Enloe (1975) that LHA lesions result in decreased social cohesiveness and mobility during the first 15 postoperative days. The recovery of normal levels of cohesiveness in LHA subjects may be related to the substantial reduction in emotional reactivity which occurs during the first two postoperative weeks.

Lesion of the septum results in rats which approach all of the classes of stimuli tested, and which remain physically close to these stimuli for significantly longer average periods than do normal rats. Septal subjects demonstrate a markedly increased tendency to maintain social contacts, once established, even when a second stimulus animal is present in the apparatus. Septal subjects were the only rats in the experiment which showed a high degree of approach to mice, which are only mildly attractive stimuli for eliciting approach from normal rats.

The fact that septal rats approach all types of animals tested indicates that their increased social cohesiveness with conspecifics is not a function of an increased reactivity

to social cues which are specific to another rat. That septal preparations show a high degree of cohesiveness with cats and rabbits would indicate that conspecific social cues, including submissive posturing, are not necessary to elicit approach in the lesioned rats.

A possible explanation for the septal behavior pattern may be that septal subjects emit the same types and frequencies of approach behaviors as do normal rats, but that the lesioned rats continue the approaching behavior regardless of the type of stimulus animal. Even normal rats will approach aversive stimuli such as cats for short periods (Curti, 1935; Blanchard and Blanchard, 1972; Plotnik et. al., 1974), usually followed by a rapid retreat, which may not occur following a septal lesion.

Septal subjects were observed in this experiment to react to the mobility of the stimulus animal, and a moving tethered stimulus seemed to elicit more vigorous approach than did a more docile stimulus animal. Jonason and Enloe (1971) showed that the mobility of a septal animal in an open field is directly proportional to the mobility of the conspecific with which it is paired. It is highly likely that a free-moving cat and a septal subject would behave in much the same manner as a septal subject paired with a free-moving normal rat.

Septal subjects do not, however, approach social stimuli indiscriminantly in a two-choice situation. Rats with septal lesions reliably prefer a conspecific over a rabbit or a cat. Hence, the rats discriminate between conspecifics and non-conspecifics, but if no conspecific is present in the apparatus there is ahigh probability that the lesioned rat will approach another animal for an approximately equal period of time. The two choice data suggest that septal subjects are responsive to conspecific social cues, but that the septal cohesiveness effect is not a strong function of such cues.

Amygdaloid subjects, after a 14-16 postoperative recovery period, show normal levels of contact with single conspecifics. However, their behaviors are by no means otherwise normal even after long recovery periods. This study has confirmed the finding of Blanchard and Blanchard (1972) that amygdaloid subjects exhibit less freezing and more approach in the presence of a cat, than do normal rats. This is consistent with the notion of Bunnell (1966) that amygdaloid subjects have an increased threshold to aversive stimuli.

Bunnell's hypothesis may not, however, explain all of the postoperative changes in social attraction observed after amygdaloid lesions. In a two-choice situation, amygdaloid subjects entered empty alleys of the apparatus as often as alleys which contained stimulus animals, and showed

no preferences for rats over cats or for rabbits over cats. In Experiment I, amygdaloid subjects constituted the only group, beside the septal group, which showed a higher than normal level of approach to mice. The results first indicate that amygdaloid subjects are hyperexploratory, as their average approach times were not different from those of normal rats. Secondly, it is conceivable that the animals are not able to utilize the types of cues, both aversive and non-aversive, emitted by living animals that direct the approach or avoidance behaviors of normal rats in the testing situation.

The approach behaviors of the LHA subjects seem to be dependent upon whether one or two stimuli are present in the apparatus. When one stimulus was present the LHA subjects showed a clearcut increase over normal levels of cohesiveness. The LHA's were indistinguishable from septal preparations in terms of approach to rabbits, and were slighly lower in approach to the cat stimuli. The behaviors of the LHA subjects in response to stimulus animals were, however, different from those of septal rats in some respects. LHA subjects frequently groomed or bit at the legs, tail, or ears of the rabbits and cats, or crawled under the animal, while septal subjects were typically more passive when in the close approach zone.

Wheb two stimuli were present in the apparatus, as in Experiment II, a dramatic change occurred in the LHA behavior patterns. The subjects now showed average approach times which were not different from those of normal rats, and alternated

frequently between the stimuli, whereas the septal subjects tended to remain with a stimulus for a longer period of time. The tendency of the LHA subjects to remain with a stimulus for a shorter average approach time before beginning an approach to the other stimulus differentiated the animals from septals when confronting some stimulus classes. In the two choice situation in which cats were present, the rats tended to show greater approach tendencies for the rabbit or rat, a tendency which could not have been predicted from the results of Experiment I. Thus, the LHA subjects showed preferential behaviors for stimuli which had been equally attractive when presented alone in Experiment I.

Finally, the behaviors of normal rats used in the present study were shown to parallel expectations from previous reports. Normal rats demonstrated freezing and avoidance in the presence of rabbits, as well as cats, which seems to confirm the hypothesis of Blanchard, Mast, and Blanchard (1975), that it is the size and movement properties of a stimulus, and not olfactory cues, which trigger defensive reactions. There are two findings that perhaps make necessary a revision of that hypothesis. First, our experience, as described in the introduction to Experiment II, was consistent with the report of Plotnik, Mollenauer, and Snyder (1974) who showed that the expected avoidance of cats by normal rats does not occur if the species are housed together even when there is no opportunity for visual observation between rats and cats. Secondly, in the present study it was shown that rabbits

which are large furry animals of approximately the same weight as cats were apparently less aversive to normal rats than were cats when both species were used as stimuli. While normal rats were shown to avoid both cats and rabbits in Experiment I, normal rats more frequently approached the rabbit stimulus when a cat was also present in the apparatus than when a conspecific was the second stimulus animal. It must be concluded that while size and movement properties of a living stimulus are related to the eliciting of defensive reactions in the rat, some property of a non-visual nature is also important in the control of these reactions.

The limbic system might be viewed as functioning to identify stimuli which have positive or aversive components and then to direct the rat to approach, avoid, or freeze. The duration of a social contact or approach to a non-conspecific stimulus, the social postures emitted, and the emotional reactivity of the rat to external stimuli may also be related to a large degree to the limbic system.

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