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ALTERATIONS IN SOCIAL BEHAVIOR FOLLOWING SEPTAL AND  
AMYGDALOID LESIONS IN THE RAT

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the  
Degree of Doctor of Philosophy in the Graduate  
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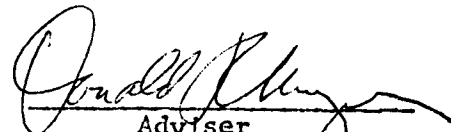
By

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1970

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## INTRODUCTION

The limbic system consists of a highly-interconnected group of phylogenetically old cortical and subcortical structures, characterized by strong connections with the olfactory system, which have been implicated in the mediation of motivation and emotion. Most classification systems include in this system the olfactory bulb and tubercle, the area of the diagonal band of Broca, the septal area, the cingulate gyrus, the hippocampus, the pyriform cortex, and the amygdaloid complex. Because of the interconnections of these structures with the olfactory system, early systematists (Kölliker, 1896) referred to them collectively as the rhinencephalon or nose brain.

This term has proved to be unfortunate, however, as it implied a primary functional involvement of limbic-system structures in olfaction, an implication which has been contradicted by many kinds of experimental evidence. Thus, Swann (1934, 1935) found that rats retained the ability to perform olfactory discriminations following lesions of the amygdala, hippocampus, pyriform cortex, lateral or medial olfactory stria, or the septal area, while Allen (1940, 1941) demonstrated that dogs were still able to perform olfactory discriminations after lesions to the hippocampus, amygdala, or to the pyriform cortex.

Present-day theoretical and experimental interest in the functions of limbic-system structures can be traced to Papez's (1937) now-classic theory. Papez suggested that limbic-system structures, acting in concert with the hypothalamus, formed a circuit which was critically involved in mediating emotional experience and responsiveness. Papez's hypothesis was subsequently given dramatic

experimental support by the results of Klüver and Bucy (1939), who noted that bilateral temporal lobectomy, an ablation which included the hippocampus, pyriform cortex, and amygdaloid nuclei, produced a large number of striking behavioral changes, one of which was a marked decrease in emotional reactivity. These two papers focused the attention of many subsequent investigators upon limbic-system structures, and results obtained in recent studies of the system have produced radical revisions of the concept of limbic system as the "olfactory brain."

Recent theoretical formulations of limbic-system functioning have emphasized the more general concept that these structures are critically involved in response modulation (McCleary, 1966) or the regulation of behavioral dispositions (Pribram, 1960; Thomas, Hostetter, and Barker, 1968). These concepts imply that limbic mechanisms might have either facilitatory or inhibitory modulating effects on homeostatically related behavioral dispositions. Both anatomical and physiological evidence can be cited to support the reasonableness of such a concept. Anatomical evidence indicates that the limbic system has strong interconnections with the hypothalamus (Nauta, 1960) a structure importantly implicated in the arousal, execution, and satiation of affective and motivated behavior sequences (Hess, 1949; Stellar, 1954, 1960; Valenstein, Cox, and Kakolewski, 1970), and so is in a good anatomical position to alter such behavior patterns, while Kaada (1951, 1960) has provided physiological evidence that stimulation of limbic-system structures may have either excitatory or inhibitory effects on on-going responses, thus demonstrating the

existence of functional circuits for response modulation.

Thomas et al. (1968) have more specifically suggested that limbic-system structures are critically involved in mediating "species-specific" behavioral dispositions, a formulation which would lead to the prediction that these structures might be involved in mediating the social interactions of organisms. In the current investigations an assessment was made of the effects of lesions of two limbic regions--the septum and the amygdaloid complex--upon several measures of the social responsiveness of rats.

#### Review of the Behavioral Effects of Septal Lesions

Emotionality Among the most consistent results of septal lesions in rats is a marked, but transitory, increase in emotional reactivity. Brady and Nauta (1953) observed a post-operative increase in the magnitude of both emotional reactivity and startle responses following septal lesions in rat ♂s, thus supporting earlier findings of Spiegel, Miller, and Oppenheimer (1940), who noted a similar increase in the incidence of rage reactions following septal lesions in cats. Subsequent investigators (King, 1958; King and Meyer, 1958; Kriekhaus, Sinmons, Thomas, and Kenyon, 1964; Yutzey, Meyer, and Meyer, 1967; Corman, Meyer, and Meyer, 1967) have confirmed the hyperemotionality of septal rats, and further demonstrated that the increased reactivity disappears rapidly with time and with handling (Yutzey et al., 1967; Corman et al., 1967).

Subsequent attempts to establish the cross-species generality of the increased emotionality following septal lesions have not, however, been uniformly successful. McCleary and his coworkers

(McCleary, 1966; Moore, 1964) reported that the "septal rage" syndrome is seldom seen in cat preparations, while Buddington, King and Roberts (1967) found no evidence of a rage response in septally-lesioned monkeys. Additionally, recent investigators (Lauber, 1969; Turner, 1970) have suggested that the hyperreactivity noted in rat Ss may not occur as a function of lesions in the septal nuclei per se, but rather may be related to damage to either the nucleus or the tract of the stria terminalis.

Avoidance Behavior King (1958) found that rats which had sustained septal lesions learned a two-way active avoidance task more rapidly than did either operated or unoperated control Ss, a result subsequently replicated using rats (Kriekhaus et al., 1964; Kenyon and Kriekhaus, 1965; Schwartzbaum, Green, Beatty, and Thompson, 1967; VanHoesen, MacDougall, and Mitchell, 1969), monkeys (Buddington et al., 1967), and cats (McCleary, 1961; Fox, Kimble, and Lickey, 1964; Zucker, 1965).

The active avoidance task is a fear-motivated learning paradigm in which an experimental S learns to move from one compartment to the other of a shuttle box upon presentation of an auditory or visual CS to avoid shock. King (1958) who explained the facilitated acquisition in terms of the hyperemotionality of septal Ss, proposed that highly fearful septal Ss should be expected to perform better on a fear-motivated avoidance task. More recent results have, however, made King's interpretation seem unlikely. First, Brady and Nauta (1953, 1955) found that septal lesions had the effect of attenuating a pre-operatively learned conditioned emotional response (CER) which

consisted of withholding a bar press for food in the presence of a CS signaling unavoidable shock, a result which has been replicated by Harvey, Lints, Jacobson, and Hunt (1965). Such a result is obviously difficult to explain in terms of increased fearfulness. It is also the case that the improved active avoidance performance occurs in both cats and monkeys, species which seldom display the overt signs of hyperemotionality seen in septal rats (McCleary, 1966; Buddington et al., 1967) and in rats tested after sufficiently long post-operative intervals for their hyperreactivity to have dissipated (Krieckhaus et al., 1964). Krieckhaus et al. (1964) have suggested that their results, taken in concert with results demonstrating a decrement in the acquisition of a CER, indicate that septal lesions may have the effect of reducing the probability of occurrence of the species-specific response of freezing in the presence of noxious stimuli--a response which would obviously interfere with the rapid acquisition of an active avoidance response.

Finally, McCleary (1961) found that septally lesioned cats displayed a large impairment on a passive avoidance task, a result repeatedly obtained in both cats (Zucker and McCleary, 1964; Lubar, 1964; Fox et al., 1964) and rats (Kaada, Rasmussen and Kveim, 1962; McNew and Thompson, 1966; Schwartzbaum and Spieth, 1964; VanHoesen et al., 1969). The passive avoidance paradigm consists of training an experimental S to obtain food or water reinforcement as a function of some instrumental response, then shocking the S while in the process of eating or drinking. The test consists of measuring the tendency of the S to return to the goal box where he has been shocked, a return

being scored as a failure to passively avoid. The passive avoidance deficit displayed by septally lesioned Ss is certainly inconsistent with a "fear" interpretation of the facilitated active avoidance learning, as "fearful" septal Ss should be expected to learn a passive avoidance task even more rapidly than do normal Ss.

Perseverative Overresponding The improved active avoidance behavior, retarded acquisition of a CER, and deficient passive avoidance performance are all specific examples of a more general tendency of septal Ss to overrespond, often perseveratively. Schwartzbaum, Kellicutt, Spieth, and Thompson (1964) found that septal rats displayed an increased rate of response in the presence of the negative stimulus in an operant discrimination task, a prolonged period of extinction of a food-reinforced response, and an increased number of perseverative errors in a simultaneous brightness discrimination task. Similar examples of overresponding have been obtained using other operant paradigms. Septal rats have been demonstrated to respond at higher rates on both continuous reinforcement schedules (Lorens and Kondo, 1969; Mothersall, Johnson, and Collen, 1970) and fixed interval schedules (Ellen and Powell, 1962; Schwartzbaum and Gay, 1966; Lorens and Kondo, 1969). Mothersall et al. (1970) additionally found that rats which had sustained septal lesions could be shaped to bar-press more easily than could control Ss, and would continue to work under much higher fixed ratio requirements (up to 800:1) than would control Ss. Septal rats have also been shown to overrespond under conditions of differential reinforcement of low rates (Ellen, Wilson, and Powell, 1964; Burkett and Bunnell, 1966;

MacDougall, VanHoesen, and Mitchell, 1969), a situation in which increased response rates are clearly maladaptive. Examples of perseverative responding by septally lesioned Ss include deficits in spatial reversal problems (Zucker and McCleary, 1964) and on the first reversal of an object reversal problem (Zucker, 1965).

Motivational Changes Harvey and Hunt (1965) have suggested an increased level of motivation as an explanation for the noted overresponding of septal Ss for food and water reinforcement. Septal rats have been found to display an increased water consumption (Harvey et al., 1965; Harvey and Hunt, 1965; Carey, 1967; Singh and Meyer, 1968), an increase in food consumption (Simmons and Thomas, 1961; Singh and Meyer, 1968) and an increase in sucrose consumption (Beatty and Schwartzbaum, 1968). Such an argument, while reasonable, is limited in that it cannot explain the increased responding by septal Ss in the non-appetitive avoidance conditioning experiments, the perseverative tendencies of septal Ss in spatial alternation tasks, nor the overresponding on DRL schedules. Additionally, Singh and Meyer (1968) noted that their septal rats, while hyperphagic, were finicky eaters, while Hothersall et al. (1970) have suggested that a motivational concept is inadequate to explain their results, as normal rats, even when severely deprived, never approach the response rates noted in their septal rats working on high ratio requirements.

Finally, Grossman and his coworkers have provided evidence that the tendencies of septal Ss to perseverate and overrespond may be mediated by different septal systems than the increased thirst motivation. Thus, stimulation of the septum with atropine, a cholinergic

blocking agent, reduced water consumption while improving active avoidance performance (Grossman, 1964), producing a passive avoidance deficit, and increasing resistance to extinction of an avoidance response (Hamilton, McCleary, and Grossman, 1968).

Evaluation McCleary (1966) has used a more general concept to explain the many behavioral changes which have been noted following septal lesions. He suggests that the septum normally performs a response-inhibitory function, and that the effect of septal lesions is to disinhibit responses which have a high probability of occurrence within a given experimental context. Such an explanation is notably consistent with Kaada's (1951) demonstration of inhibition of ongoing motor responses by stimulation of the septal area, and fits the large body of experimental evidence just reviewed showing various forms of perseveration and overresponding by septal Ss.

McCleary's theoretical position might be extended, then, to generate predictions as to the normal function of the septal area in mediating behavior. Such an inhibitory system might function to inhibit ongoing response sequences in the presence of altered environmental contingencies, an ability clearly lacking in experimental Ss which have been subjected to septal lesions. Thus, septally lesioned Ss perseverate in responding for food in a passive avoidance situation even when the response becomes maladaptive as a function of the introduction of shock in the goal box. Similarly, septal Ss display increased trials to extinction and perseverative responding in spatial alternation tasks, deficits which both clearly reflect an inability to alter responses as a function of changes in response-reinforcement contingencies. Similar arguments in terms of response disinhibition



could be used to explain the failure of septal Ss to develop a CER as rapidly as normals and the overresponding of septal Ss in various operant situations.

The one consistent effect of septal lesions which cannot be easily fitted within this theoretical framework is the hyperemotionality of septal Ss, an effect which is probably independent of the other behavioral alterations. This behavioral change disappears rapidly over time, in contradistinction to other effects of septal lesions, is not consistently found across species, and is probably mediated by extra-septal neural structures (Lauber, 1969; Turner, 1970).

#### Behavioral Effects of Amygdaloid Lesions

Experimental interest was importantly focused on deep temporal lobe structures by Klüver and Bucy's (1939) description of the behavioral effects of bilateral temporal lobectomy. These investigators found that the removal of the temporal lobes produced a remarkable complex of behavioral changes including visual discrimination deficits, decreased emotionality, hypersexuality, oral compulsiveness, and hyperactivity. While the visual discrimination deficits have subsequently been observed to occur as a function of temporal cortical removals (Blum, Chow, and Pribram, 1950; Riopelle and Ades, 1953; Mishkin, 1954; Mishkin and Pribram, 1954), other elements of the "Klüver-Bucy Syndrome" have repeatedly been obtained after lesions restricted to the amygdaloid complex (Brady, Schreiner, Geller, and Kling, 1954; Schreiner and Kling, 1956; Masserman, Levitt, McAvoy, Kling, and Pechtel, 1958; Green, Clemente, and DeGroot, 1957). Exceptions to this generalization exist, however, in reports by

Meyer (1958) and by Akert, Gruesen, Woolsey and Meyer (1961) who observed most of the Klüver-Bucy effects, including oral compulsive behaviors and decreased emotionality, following temporal cortical removals which spared subcortical structures.

Sexual Behavior The hypersexuality noted by Klüver and Bucy following temporal lobectomies has been observed after amygdaloid lesions in cats (Brady et al., 1954; Schreiner and Kling, 1956; Green et al., 1957), in monkeys (Masserman et al., 1958; Orbach, Milner, and Rasmussen, 1960) and in rats (Wood, 1958). Schreiner and Kling (1956) have described in detail the hypersexuality noted in cats following amygdectomy. The sexual behavioral alterations take the form of increased sexual activity, attempted copulations with inanimate objects, attempted copulations with both males and females of other species, and homosexual activities by male cats, including tandem mounting by groups of males. Interestingly, amygdaloid hypersexuality is often not seen in female preparations (Green et al., 1957).

The increased sexual behavior after amygdaloid lesions typically occurs only after a relatively long latent period of several weeks (Schreiner and Kling, 1956; Gloor, 1960), a fact which may account for some of the instances in the literature (Thompson and Walker, 1951; Weiskrantz, 1956; Kling and Schwartz, 1961; Michael, 1965) in which amygdaloid hypersexuality was not found. Additionally, in most of the experiments in which hypersexuality has been found, there was partial or total involvement of the pyriform cortex. Green et al. (1957) have, in fact, suggested that it is the pyriform cortical

damage which produces the changes in sexual behavior.

Emotionality Researchers subsequent to Klüver and Bucy have consistently, though not in every case, replicated the decrease in emotionality noted in temporal lobectomized monkeys with lesions restricted to the amygdaloid nuclei. Anand and Brobeck (1952) observed a decrease in emotional responsivity following amygdectomy in both rats and cats, a result replicated in cats (Brady et al., 1954; Schreiner and Kling, 1956; Green, Clemente and DeGroot, 1957), in monkeys (Weiskrantz, 1956; Orbach, Milner, and Rasmussen, 1960), and in rats (Woods, 1956; King, 1958; King and Meyer, 1958). This altered emotional reactivity typically takes the form of a failure to respond appropriately to fear and aggression eliciting stimuli.

Mirror-image results have, however, been obtained. Spiegel, Miller, and Oppenheimer (1940) and Bard and his coworkers (Bard and Mountcastle, 1948; Bard, 1950) have noted dramatic changes in the direction of increased rage reactions following amygdectomy in cats. These rage reactions occurred, however, only after fairly long post-operative intervals, and subsequent investigators (Green, Clemente, and DeGroot, 1957) have attempted to explain the discrepancy in terms of hippocampal involvement in the lesions of hyperemotional amygdaloid preparations, with associated seizure activity.

Avoidance Behavior The decreased emotionality of amygdaloid preparations would lead to the prediction that such preparations would be impaired in the acquisition of fear-motivated learning tasks, a prediction supported by experimental evidence. King (1958) found that amygdectomized rats had significantly longer response latencies

in an active avoidance task, although there were no statistically significant differences in the number of trials required to reach criterion. Robinson (1963), however, found that amygdaloid rats were impaired in the acquisition of an active avoidance task, a result replicated by Goddard (1964b) using continuous, low-intensity electrical stimulation to disrupt the amygdala. The active avoidance deficit following amygdectomy has also been obtained in cats (Brady et al., 1954; Horvath, 1963; Ursin, 1965) and in monkeys (Weiskrantz, 1956). Weiskrantz (1956) additionally found that amygdectomized monkeys required fewer trials to extinguish an avoidance response than did control ss.

Impaired passive avoidance learning has also been found following amygdaloid lesions, a result which is also consistent with the decreased emotionality of such preparations. Horvath (1963) demonstrated a small, but statistically significant passive avoidance deficit in amygdectomized cats, while Ursin (1965), using more discrete lesions, noted a passive avoidance decrement, but no active avoidance deficit following lesions to medial amygdaloid structures in cats, and an active avoidance decrement in the absence of a passive avoidance deficit following lateral amygdaloid lesions. Ursin's data are consistent with Kaada's demonstration of motor inhibitory effects of stimulating the medial amygdaloid area and a concomitant motor excitatory effect of stimulating the lateral amygdaloid area. This functional localization of the avoidance deficits is not, however, clearly established as Pellegrino (1968) using rat ss found a small passive avoidance deficit with corticomедial amygdaloid lesions,

but an even larger deficit following lesions in the basolateral region of the amygdala. Pellegrino (1965) has also obtained a passive avoidance deficit in rats subjected to low-level stimulation of the amygdala, while Goddard (1969) found a similar deficit following carbachol injections placed in the amygdaloid nuclei of rats.

An additional example of an amygdaloid deficit in the acquisition of a fear-motivated task is the impaired learning of a conditioned emotional response, a result obtained in both rats (Kelicut and Schwartzbaum, 1963) and monkeys (Weiskrantz, 1956). This deficit in the acquisition of a CER has also been obtained during electrical stimulation of the amygdala (Goddard, 1964b) and following injection of carbachol into the amygdaloid complex (Goddard, 1969). While it is tempting to explain the deficits in the acquisition of fear-motivated tasks noted after amygdalectomy in terms of a decreased responsiveness to fear provoking stimuli (Brady et al., 1954; Goddard, 1964), evidence has accumulated (Kaada, 1951; Ursin, 1965; Goddard, 1969) that there may be two response-modulatory systems within the amygdala, one involved in response suppression, the other a response facilitatory system. Thus, Kaada (1951) found both motor excitatory and motor inhibitory effects of amygdaloid stimulation, while Ursin (1965) noted an anatomical dissociation of the active and passive avoidance deficits occurring after amygdaloid lesions. Additionally, Goddard (1969) found that cholinergic stimulation of the amygdala selectively disrupted passive avoidance and CER acquisition while having no effect on the acquisition of an active avoidance task.

Since low-intensity electrical stimulation of the amygdala disrupts active avoidance (Goddard, 1964b), as well as passive avoidance learning (Pellegrino, 1965) and the acquisition of a CER (Goddard, 1964b), Goddard (1969) suggests that his result represents the selective disruption of a system involved in response suppression in fear-motivated tasks.

Exploratory Behavior Klüver and Bucy's temporal-lobectomized monkeys also exhibited oral compulsive behaviors, which consisted of repeated oral examination of objects in their environment, and hyperactivity. One or both of these patterns of behavior have been frequently seen in experimental Ss subjected to amygdectomy (Brady et al., 1954; Schreiner and Kling, 1956; Weiskrantz, 1956; Wood, 1958; Schwartzbaum, Wilson, and Morrissette, 1961; Schwartzbaum and Gay, 1966; Corman, Meyer, and Meyer, 1967), and probably reflect a general increase in the tendency of amygdectomized Ss to repetitively explore their environment. Schwartzbaum et al., (1961) have suggested that the phenomenon is not one of an initial increase in activity, but rather reflects a failure of amygdectomized Ss to habituate their exploratory responses to environmental novelty. Thus, the differences between their amygdaloid and control monkeys were not reflected in peak activity scores, but rather, represented a failure of the amygdaloid preparations to parallel the tendency of control Ss to reduced locomotor activity over sessions. Additional evidence for this position was obtained by Schwartzbaum (1964), who found that amygdectomized monkeys failed to display the reduced rate of bar pressing for visual reinforcement across sessions noted in control Ss.

Eating Behavior Amygdaloid lesions often produce a transitory period of markedly reduced food intake (Brady et al., 1954; Schreiner and Kling, 1956; Weiskrantz, 1956; Wood, 1958). This initial hypophagia probably reflects a general period of depression often occurring immediately following amygdaloid lesions which is characterized by a cataleptic-like state, lethargy, refusal to eat and groom, and depressed body temperature (Gloor, 1960; Goddard, 1964a). More chronic amygdaloid preparations have, on the other hand, been reported to gradually develop a hyperphagia (Green, Clemente, and DeGroot, 1957; Morgane and Kosman, 1957; Wood, 1958; Schwartzbaum, 1961).

Schwartzbaum (1960 a, b, 1961) has, however, provided evidence that the amygdaloid hyperphagia does not reflect an increase in food motivation. Thus, amygdalectomized monkeys were found to be relatively unresponsive to the effects of prolonged deprivation and failed to display within-sessions performance decrements associated with satiation (Schwartzbaum, 1961), failed to respond normally to within-sessions shifts in incentive value (Schwartzbaum, 1960a), and failed to display the normally augmenting effect of extinction on subsequently reinforced behavior (Schwartzbaum, 1960b). Additionally, Schwartzbaum, Thompson, and Kellicutt (1964) found that amygdalectomized rats displayed an increase in response rate to the negative stimulus in an operant discrimination task with no concomitant increase in the rate of response to the positive stimulus.

Evaluation Most theoretical attempts to explain amygdaloid functioning have emphasized the role of that structure in modulating motivated response sequences. Such a position was formally proposed

by Gloor (1960) who suggested that amygdaloid lesions disrupt motivational mechanisms which normally function in the selection of behaviors which are appropriate within a given situational context. This view is consistent with the large body of literature just reviewed, demonstrating that amygdaloid ss are unable to differentiate between appropriate and inappropriate sexual objects, fail to respond normally to fear-eliciting contingencies and objects, and fail to respond to altered reinforcement contingencies. What seems to be missing in amygdaloid preparations, then, is the ability to respond in a normal fashion to environmental contingencies, a deficit which implies a difficulty in utilizing information concerning stimulus and reinforcement parameters.

#### Functional Reciprocity of Septal and Amygdaloid Nuclei

Several examples can be cited of mirror-image effects of septal and amygdaloid lesions upon post-operative behavior. Septal lesions, for example, increase the emotional reactivity of rat ss while amygdaloid lesions reduce emotionality; septal lesions facilitate the acquisition of active avoidance tasks, while amygdaloid lesions retard the acquisition of such a task. King and Meyer (1958) put such a septal-amygdaloid reciprocity concept to a direct experimental test through the use of sequential lesions to the two structures, and found that the hyperreactivity noted after septal lesions in rats was attenuated by the addition of an amygdaloid lesion. Schwartzbaum and Gay (1966) replicated this result, and found additional evidence for a functional reciprocity between the two structures in mediating open field activity levels. These investigators noted that amygdaloid



lesions increased the activity levels of rats, that septal lesions decreased activity levels, and that the addition of an amygdaloid lesion reversed the typical pattern of septal hypoactivity.

Such a reciprocity principle must, however, be viewed with caution. First, it is notable that in some seemingly-similar behavioral situations septal and amygdaloid lesions produce very similar effects. Thus, both preparations have been found to be impaired in learning a passive avoidance task, retarded in the acquisition of a CER, and both have been found to display increased food intake. Additionally, Schwartzbaum and Gay (1966) found that amygdectomy did not counteract the increased response rates of septal SS working on a fixed interval schedule. Finally, even in cases in which the two lesions do alter behavior in opposite directions, there is evidence that the effects are not strictly reciprocal. The increased emotionality following septal lesions is of very short duration, while the flattened affect of amygdaloid preparations persists over time. Similarly, Cornan, Meyer, and Meyer (1967) found that while the increased activity of amygdaloid SS disappeared rapidly with time, the decrease in activity noted after septal lesions persisted over time.

#### Social Behavior

Septal and amygdaloid lesions have been demonstrated to critically alter the nature of intra-species social interactions (Rosvold, Mirsky, and Pribram, 1954; Fuller, Rosvold, and Pribram, 1957; Brady and Nauta, 1953; Bunnell, 1966; Bunnell, Bemporad, and Flesher, 1967a). Rosvold et al. (1954) demonstrated that monkeys subjected to bilateral amygdectomy displayed a dramatic

loss of social dominance. Similar results were obtained by Fuller et al. (1957), who found that dogs which had sustained amygdaloid lesions were less dominant in competition for bones than they had been preoperatively. Further evidence of the generality across species of the loss of social dominance following destruction of the amygdala was provided by Bunnell (1966), who found that such lesions altered the dominance-subordination relationships of hooded rats in the direction of decreased dominance.

The observed alteration in dominance after amygdaloid lesions has generally been explained in terms of a lowered responsiveness to aversive and social stimuli rather than in terms of a decrease in aggressiveness per se (Fuller et al., 1957; Bunnell, 1966). Thus, Fuller et al. (1957) report that while their amygdalectomized dogs had a higher threshold for aversive stimuli, these animals, once aroused, would fight fiercely. Similarly, Bunnell (1966) suggests that his amygdalectomized rats were simply less reactive to attacks by other animals even though they often won confrontations when sufficiently aroused.

Septal lesions have generally been found to alter social responsiveness in a direction opposite to that noted after amygdaloid lesions (Brady and Nauta, 1953; Bunnell et al., 1967). Brady and Nauta (1953) found that septal rats placed in group cages exhibited increased aggressiveness, fighting vigorously and continuously for long periods, and Bunnell et al. (1967) found that septal lesions increased the social dominance of hooded rats in a competitive situation. Bunnell et al. (1967) suggest that the altered dominance of septally-lesioned

Ss may not be due simply to an alteration in aggressiveness. Their septal rats, though dominant in a competitive situation, seldom initiated competitive interactions, a result which indicates that the behavior of septal rats in a non-competitive social situation might be completely different.

Most previous investigations of the effects of limbic-system lesions on social behavior have centered on dominance relationships in competitive situations. In the current study, investigation was made of the effects of septal and amygdaloid lesions on another aspect of social behavior, social attraction or "gregariousness," using quantitative techniques developed by Latané<sup>1</sup> (1970) who measures social attraction between pairs of rats in an open field in terms of the number and duration of physical contacts, and in terms of the mean distance which paired rats maintain between themselves.

Thomas et al. (1968) have suggested that limbic-system structures are involved in mediating "species-specific" behavior patterns, and that the specific effects of limbic-system lesions should be evaluated in terms of the dispositional tendencies of the organism under investigation. The Latané<sup>1</sup> (1970) technique seemed to be a promising one for investigating the mediation of social interaction by limbic structures as it offered the advantage of having associated with it a set of empirically defined behavioral tendencies by which the results could be evaluated. Using this procedure, Latané<sup>1</sup> (1970) has found that rats are strongly attracted to each other, and that paired rats have a strong, mutual fear reducing effect. Latané<sup>1</sup> and Glass (1968) have demonstrated that such rat-rat social attractions

are limited to "social objects", such that rats are only slightly attracted to anesthetized rats, and not at all to either moving or stationary non-living objects. Latané and his coworkers (1967) have further demonstrated that "gregariousness" increases as a function of familiarity with the test environment, and that social deprivation increases the social attraction of rats for each other. Alterations in such rat-rat interactions as a function of limbic-system lesions should give, then, some insight into the role which that system plays in mediating social dispositions.

## METHOD

### Subjects

The Ss used in this experiment were 144 male, hooded, Long-Evans rats which were 90-120 days old at the beginning of the experiment. The Ss were arbitrarily assigned to pairs on the basis of order of selection, the first member of each pair being painted red with a marking pen for the purpose of identification. The marking procedure seemed justified by the fact that Latané<sup>1</sup>, Joy, Meltzer, and Cappell (1970) had previously demonstrated that dying one of a pair of rats had no effect on the rats' social interactions in the open field.

### Apparatus

The apparatus, a circular open-field similar to the one described by Latané<sup>1</sup> (1970), is shown schematically in Figure 1. The field, which was 4 feet in diameter and surrounded by a 19 in. wall, was painted glossy white, and divided by black lines into 49 numbered sections of approximately equal area. A 40-watt light, suspended 20 in. above the floor, was used to illuminate the open field.

### Pre-operative Procedure

Following selection, all Ss were housed individually 4-5 days before testing was begun. On test days 1-6, Ss were rated for emotionality using the procedures and scale described by King (1958) and by Yutzey, Meyer, and Meyer (1967). Using this 6-component scale, each S was scored according to: (1) reaction to a visually presented pencil, (2) reaction to light tapping on the back with a pencil, (3) resistance to capture, (4) resistance to handling, (5) vocalization during handling, and (6) urination and defecation.

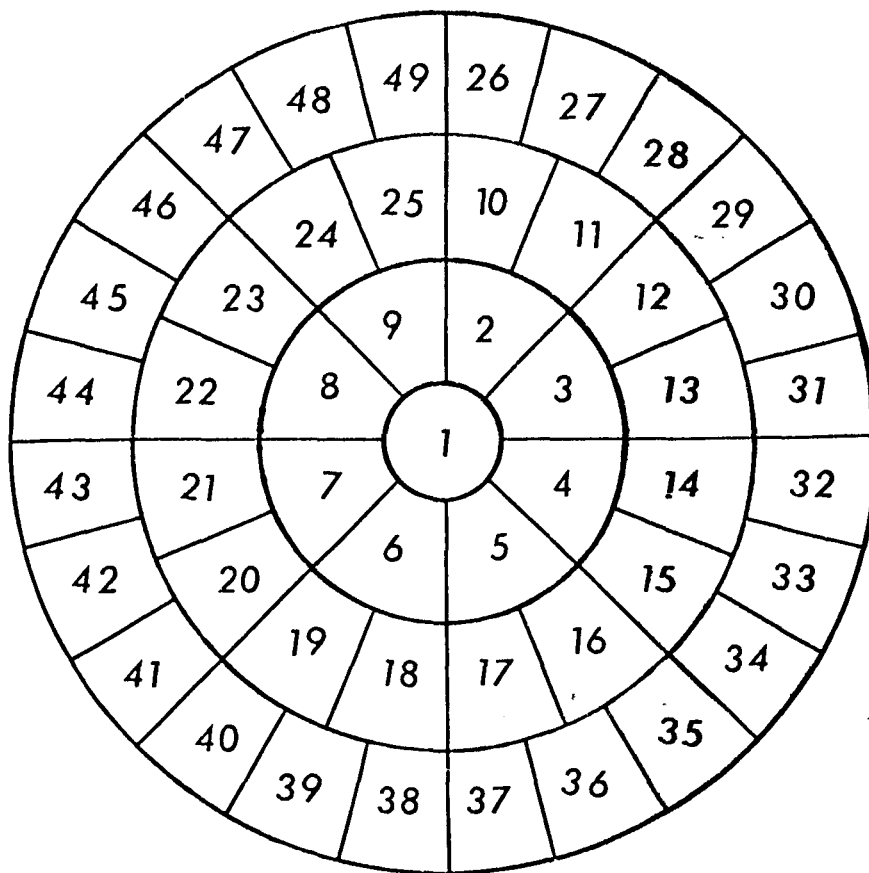


Figure 1. Schematic diagram of the apparatus.

Each S was given a score from 1-5 points on each of categories 1-4, 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 S.

Following each daily emotionality-rating session, Ss were placed by pairs into the open field for a 5-minute testing period. Records were taken of the location of both rats at 10-second intervals during the testing period, and, on the basis of these locations, the mean distance which the two rats maintained between themselves was computed. The positional recordings were also used to compute a mobility measure for each rat based on the straight-line distance between the numbered maze segments occupied by the rats at each 10-second position recording. An immobility index was computed based on the number of times during the 5-minute testing period that a rat remained in the same maze segment during the 10-second inter-recording interval.

In addition to these position-related measures, records were kept of the percentage of time in each of the 5-minute testing periods which was spent by the rats in direct contact, and of the total number of discrete contacts made. Finally, a count was taken at the end of each testing period of the number of fecal boluses left in the maze by each rat pair.

#### Surgical Procedures

After completion of pre-operative testing, rat-pairs were assigned to one of 6 experimental groups of 12 pairs each, the groups being matched on the basis of the contact time measure. The 6

experimental groups are shown in Table 1. Both members of each

Table 1  
Experimental Groups

Pair member Group	1	2
SS	septal	septal
SN	septal	sham
AA	amygdaloid	amygdaloid
AN	amygdaloid	sham
NN	sham	sham
SA	septal	amygdaloid

rat-pair in group SS received septal lesions. The first member of each pair in Group SN received a septal lesion, while the second member received a sham operation. Similarly, both Ss in each pair of AA animals were subjected to an amygdalectomy. The first member of each group AN pair was subjected to an amygdalectomy, and the second to a sham procedure. Both members of group NN pairs were subjected to sham-operative procedures. Finally, the first member of each SA pair received a septal lesion, while the second received an amygdalectomy.

On the day following completion of training, each S was subjected to the appropriate surgical procedure. Surgery was carried out under a combination of sodium pentobarbital and metafane anesthesia. Rats were first given .5 cc/kg body weight of 60 mg/cc sodium pentobarbital, with metafane--administered by means of a nose cone--used to complete anesthesia. Septal and amygdaloid lesions were accomplished stereotaxically, electrolytic lesions being produced by means of a unipolar electrode, insulated except for .5 mm at the



tip. A ground was established by means of an anal electrode. The stereotaxic coordinates for the two types of lesions, which were computed using the stereotaxic atlas by deGroot (1959), are shown in Table 2. The current parameters for each of the two septal burns were 2 ma for 15 sec., while 2 ma for 20 sec. was used at each of the 6 electrode sites for the amygdaloid lesions. Sham procedures consisted of making a midline incision, and removing a section of each sham-operate's calvarium by means of a trephine. Following surgery Ss were administered a broad-band antibiotic and returned to their home cages.

Table 2

Lesion Coordinates			
Coordinates Lesion	Anterior-Posterior	Lateral	Dorsal-Ventral
septal	+ 7.8	± .5	+ 1.0
amygdaloid	+ 4.2	± 5.0	- 3.0
	+ 5.0	± 4.5	- 3.0
	+ 5.8	± 4.5	- 2.5

#### Post-operative Procedure

Following a two-day recovery period, Ss were tested in the open field and rated for emotionality on 12 successive days using procedures identical to those used pre-operatively.

The two-day recovery period was selected on the basis of the expectation that the altered emotional reactivity of Ss with septal lesions might importantly affect the nature of their social interactions. The hyperreactivity of septally-lesioned Ss has been demonstrated to disappear rapidly with time and with handling (Yutzey et al.,

1967; Corman et al., 1967), and so the short recovery period was chosen to maximize the reactivity of septal Ss.

Similar considerations concerning the time-dependency of altered activity levels following limbic lesions also seemed to indicate the advantage of a short recovery period. Corman et al. (1967) found that the increased activity of amygdalotomized Ss disappeared very rapidly with time, while the decrease in activity noted after septal lesions persisted over time, and was independent of the hyper-emotionality of these Ss.

#### Histological Procedure

Upon completion of post-operative training Ss were anesthetized, then perfused with 0.9% saline followed with 10% formalin. The brains were then embedded in celloidin, and sectioned at 30 micra. Each brain was then stained, mounted on slides, and examined for location and extent of lesion.

Reconstructions of the lesions of each of the experimental groups are shown in Figures 2 and 3. A section mid-way through the lesion was drawn for each septal S, while an anterior, middle, and posterior section was drawn for each amygdaloid S. Septal lesions were large, involving both pre- and post-commissural components of the septum. Structures involved in the septal lesions were: nucleus septi lateralis, nucleus septi medialis, nucleus tractus diagonalis (Broca), tractus diagonalis (Broca), nucleus interstitialis striae terminalis, stria terminalis, tractus septohypothalamicus, fornix precommissuralis, and fornix superior. Occasional damage also occurred to the nucleus caudatus, cingulate cortex, corpus callosum, and nucleus accumbens.

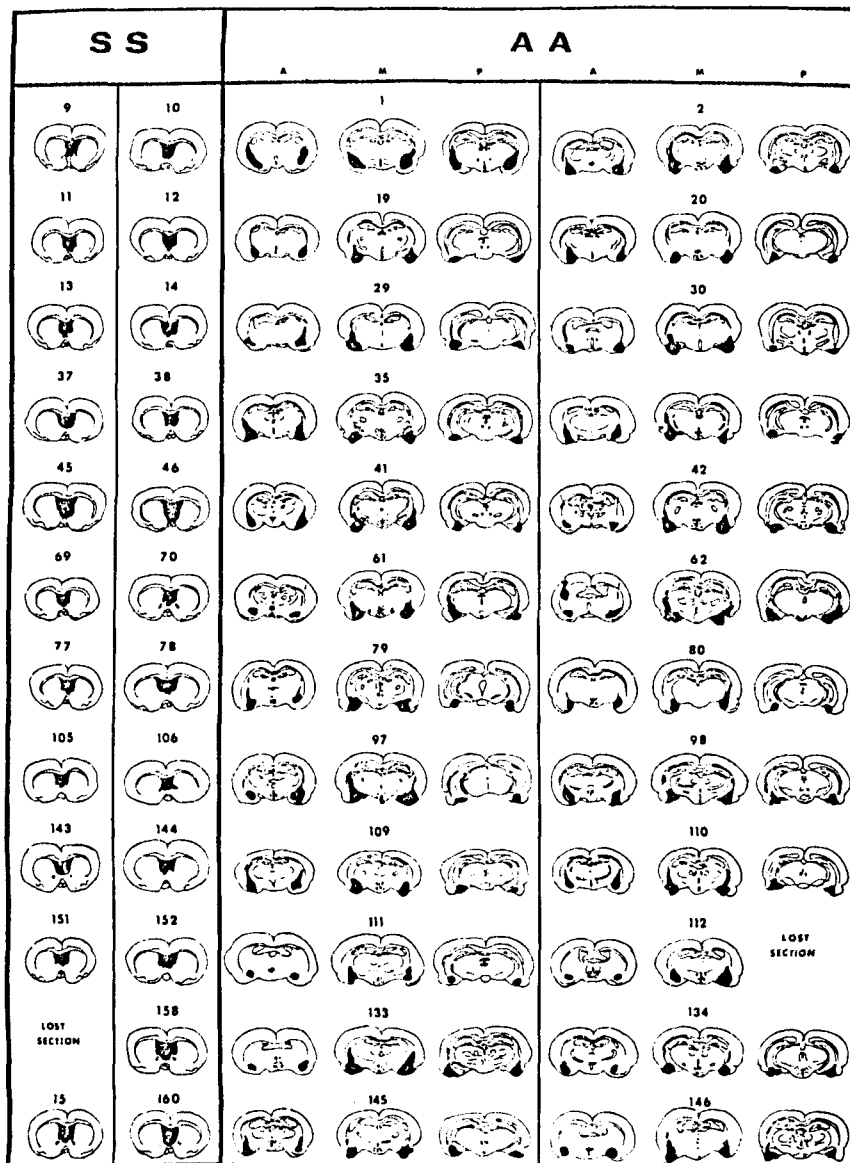


Figure 2. Brain reconstructions for groups SS and AA.



Figure 3. Brain reconstructions for groups SN, AN, and SA.

Amygdaloid lesions were also large, including the following structures: Nucleus amygdaloideus basalis, pars lateralis, nucleus amygdaloideus basalis, pars medialis, nucleus amygdaloideus lateralis, pars posterior, nucleus amygdaloideus lateralis, pars anterior, nucleus amygdaloideus centralis, nucleus amygdaloideus corticalis, nucleus amygdaloideus medialis, massa intercalata, and stria terminalis. Extra-amygdaloid damage frequently occurred to: nucleus caudatus putamen, cortex entorhinalis, fimbria hippocampi, hippocampus, and the internal capsule.

## RESULTS

The primary results of the experiment are shown graphically in Figure 4 in which the mean daily time spent by rat-pairs in direct physical contact is plotted. Pre-operatively, all groups displayed a marked increase in the time spent in contact over the first 3 days of testing before reaching a reasonably stable contact time score of approximately 170 sec., or slightly more than 50% of the total daily test period.

Post-operative testing revealed that septal lesions produce a dramatic and persistent increase in the social cohesiveness of rat-pairs as measured by the total time spent in contact, while amygdaloid lesions produce an equally dramatic reduction in contact times. The reciprocity of the effects of the two lesions is further demonstrated by the fact that when a rat which has sustained a septal lesion is paired with an amygdalectomized rat (Group SA) their contact time is almost identical to that of paired sham-operate rats (Group NN). Thus, it would seem that the increased approach tendencies of Ss which have sustained septal lesions is almost exactly offset by the concomitant decrease in the approach tendencies of amygdaloid preparations. Septal-Sham pairs spend slightly more time in contact than do Sham-Sham pairs, while Amygdaloid-Sham pairs spend less time in contact than do Sham-Sham pairs.

Separate analyses of variance performed on the pre- and post-operative contact time data are summarized in Tables 3 and 4. Pre-operatively there was no significant difference between groups ( $F = .09$ ,  $df = 5, 66$ ). The between-days effect was highly significant

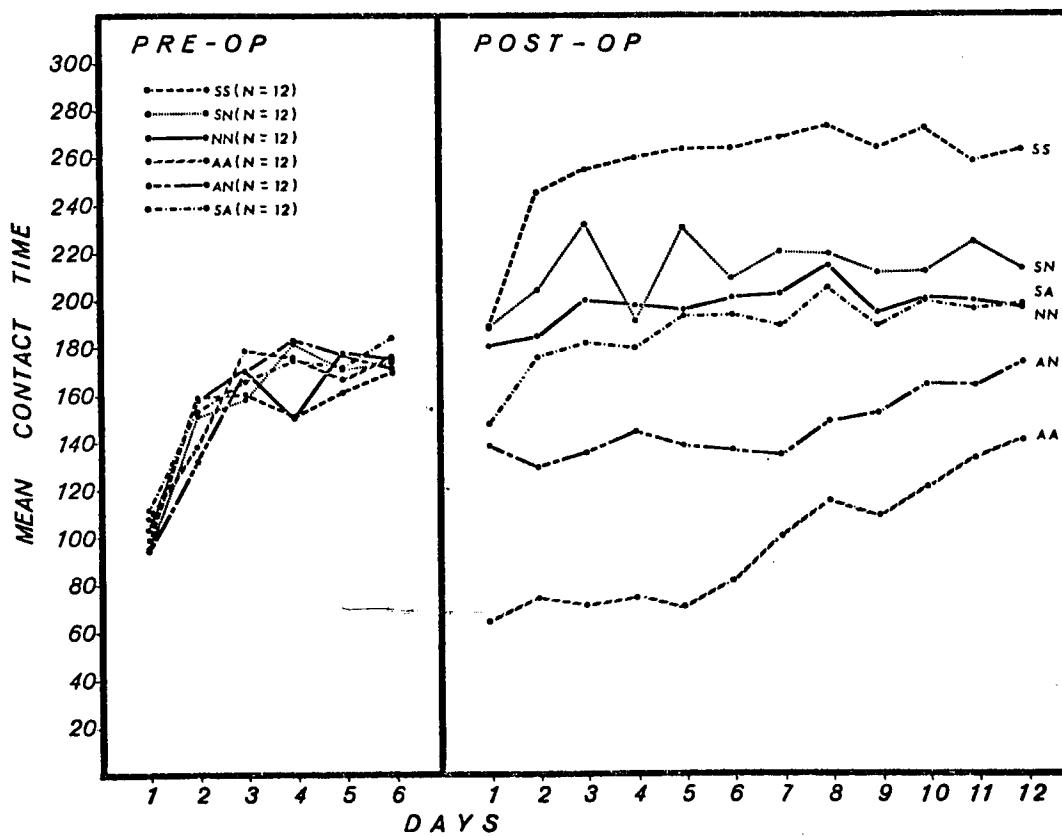


Figure 4. Mean contact times by days.

Table 3

Analysis of Variance of Pre-operative Within  
and Between Groups Differences in Contact Time

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	.71			
Lesion	5	695.9	.09	NS
Subj. w. groups	66	7651.0		
<u>Within Subjects</u>	360			
Days	5	55,014.4	51.7	.01
Lesion x Days	25	899.3	.84	NS
Days x Subj. w. groups	330	1,064.5		



Table 4

Analysis of Variance of Post-operative Within  
and Between Groups Differences in Contact Time

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	5	435,078.9	47.9	.01
Subj. w. groups	66	9,080.3		
<u>Within Subjects</u>	792			
Days	11	12,516.1	15.26	.01
Lesion x Days	55	1,835.0	2.24	.01
Days x Subj. w. groups	726	819.7		

( $F = 51.7$ ,  $p < .01$ ,  $df = 5$ , 330) reflecting the increasing contact times across days. There was no significant Groups x Days interaction ( $F = .84$ ,  $df = 25$ , 330).

The analysis of variance conducted on the post-operative data revealed a highly significant Groups effect ( $F = 47.9$ ,  $p < .01$ ,  $df = 5$ , 66). There was also a significant Days effect ( $F = 15.26$ ,  $p < .01$ ,  $df = 11$ , 726), reflecting a general increase in contact times over days, and a significant Groups x Days interaction ( $F = 2.24$ ,  $p < .01$ ,  $df = 55$ , 726), reflecting a differential change over days by the various experimental groups. Thus, reference to Figure 4 indicates that experimental groups containing septal Ss (Groups SS, SN and SA) reach near-asymptotic contact times by at least Day 3, that Group NN Ss have contact times which are relatively consistent over days, and that Groups AA and AN display relatively stable contact times over the first 6 days, after which they display a marked increase over the last 6 test days.

Results of Scheffe' (1959) tests for differences between individual experimental groups are summarized in Table 5. All comparisons

Table 5

Scheffe' Tests for Differences in Contact Times  
Between Individual Groups

Groups	p	Groups	p
SS - SN	.05	SN - SA	NS
SS - AA	.01	AA - AN	.01
SS - AN	.01	AA - NN	.01
SS - NN	.01	AA - SA	.01
SS - SA	.01	AN - NN	.01
SN - AA	.01	AN - SA	.05
SN - AN	.01	NN - SA	NS
SN - NN	NS		

between experimental groups yield statistically significant differences except for the comparisons between Groups NN and SA, Groups NN and SN, and the comparison between Groups SN and SA.

Results from the other Latané index of social cohesiveness, the mean-distance measure, are shown in Figure 5 and closely parallel the results obtained from the analysis of contact times. Pre-operatively, all groups maintain increasingly small mean distances between themselves over the first 3 days before a stable level is attained. Post-operatively, Group SS pairs maintain very small distances between themselves, while Group AA ss show a marked increase in mean distance scores. Rats in Group AN have mean distance scores which are intermediate between those of Group AA and Group NN. There is, however, very little difference between the mean distance scores of Groups SN and NN, or between Groups SA and NN.

Results from analyses of variance performed on the mean-distance data are summarized in Tables 6 and 7. The pre-operative analysis of variance indicated that there were no significant Group differences ( $F = .20$ ,  $df = 5$ , 66); that there was a highly significant Days effect ( $F = 44.02$ ,  $p < .01$ ,  $df = 5$ , 330), reflecting the systematic decrease in mean distance scores over days; and that there was no significant Groups x Days interaction ( $F = .92$ ,  $df = 25$ , 330). Post-operatively, there was a significant Groups effect ( $F = 23.5$ ,  $p < .01$ ,  $df = 5$ , 66), a significant Days effect ( $F = 20.3$ ,  $p < .01$ ,  $df = 22$ , 726), and a significant Groups x Days interaction ( $F = 2.2$ ,  $p < .01$ ,  $df = 55$ , 726).

Scheffé' comparisons of differences between individual groups are summarized in Table 8. These results suggest that the mean-

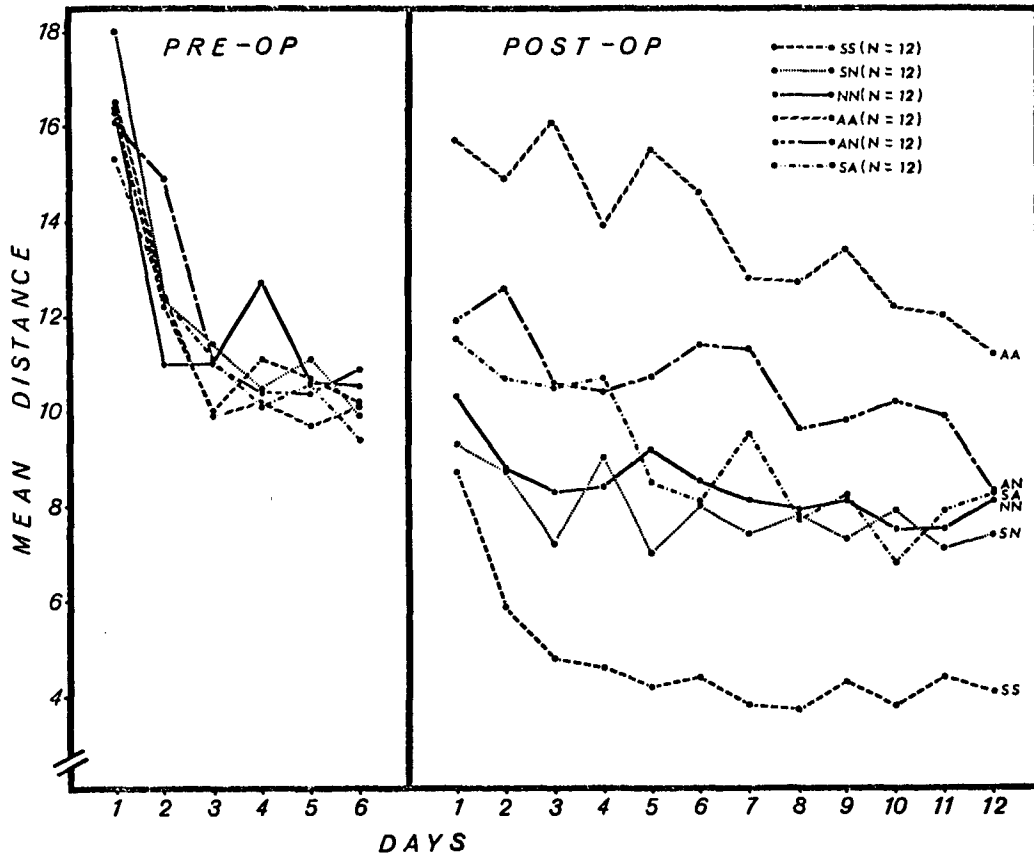


Figure 5. Mean distance scores by days.

Table 6

Analysis of Variance of Pre-operative Within and  
Between Groups Differences in Mean Distance Scores

SOURCE OF VARIANCE	df	MS	F	P
Between Subjects	71			
Lesion	5	9.34	.20	NS
Subj. w. groups	66	47.04		
<u>Within Subjects</u>	360			
Days	5	411.18	44.02	.01
Lesion x Days	25	8.56	.02	NS
Days x Subj. w. groups	330	9.34		

Table 7

Analysis of Variance of Post-operative Within and  
Between Groups Differences in Mean Distance Scores

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	5	1284.4	23.5	.01
Subj. w. groups	66	54.6		
<u>Within Subjects</u>	792			
Days	11	73.2	20.3	.01
Lesion x Days	55	7.8	2.2	.01
Days x Subj. w. groups	726	8.6		

distance measure is not as sensitive to Group differences in social cohesiveness as is the contact time measure. Thus, while all of the homogeneous groups are significantly different from one another, there is no statistically reliable difference between either the SN or AN groups and the NN control group. Failure of the AN, NN difference to attain significance may, however, reflect the use of the conservative Scheffé' test, as the difference between these groups is both consistent over days and fairly large.

Table 8

Scheffé' Tests for Differences in Mean Distance Scores  
Between Individual Groups

Groups	p	Groups	p
SS - SN	.05	SN - SA	NS
SS - AA	.01	AA - AN	.05
SS - AN	.01	AA - NN	.01
SS - NN	.01	AA - SA	.01
SS - SA	.01	AN - NN	NS
SN - AA	.01	AN - SA	NS
SN - AN	NS	NN - SA	NS
SN - NN	NS		

While Group SS mean-distance scores are substantially higher on the first post-operative day, this can be related almost exclusively to the time required by these Ss to make their first contact. The typical first reaction of these hyperreactive Ss when placed into the maze was an explosive retreat to opposite edges of the maze. Subsequently, septal Ss cautiously approached each other until contact was established. Having made this initial contact, these Ss spent virtually the entire remaining test session in direct physical contact. These observations are shown graphically in Figure 6 in which the

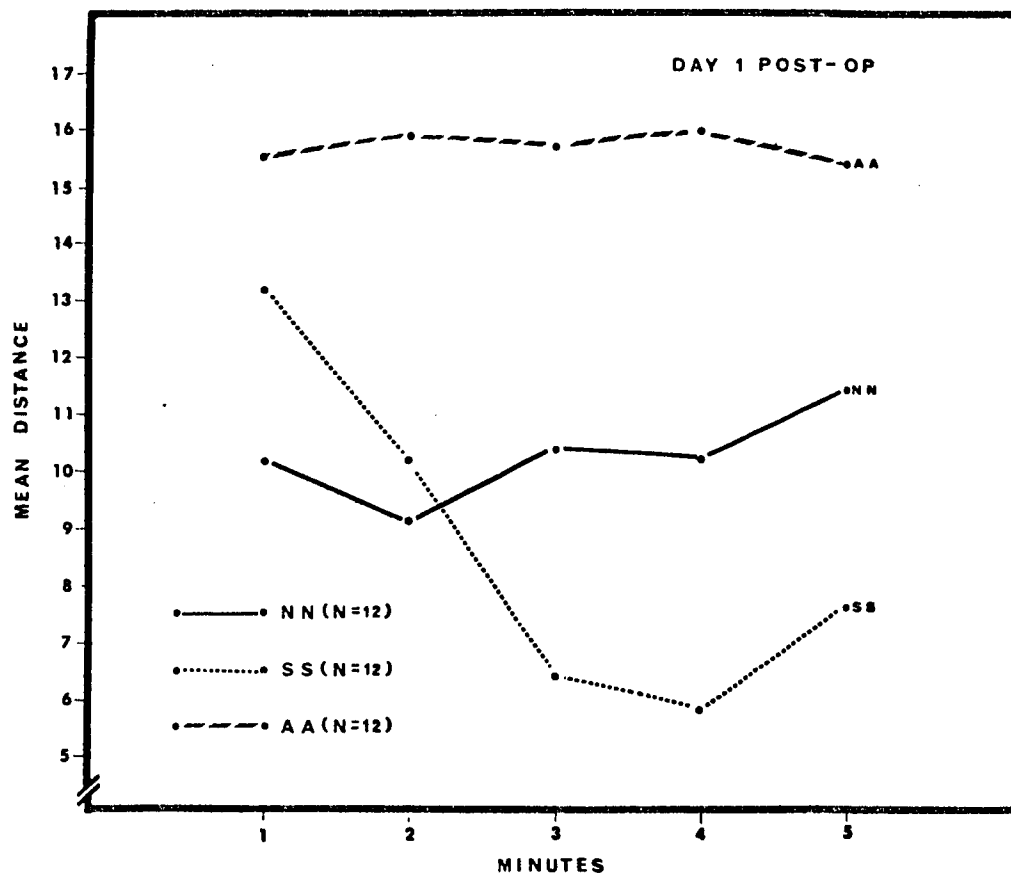


Figure 6. Mean distance scores by minute on the first post-operative day.



mean distance scores by minute are plotted for the 3 homogeneous groups on the first post-operative day. While Group NN and Group AA Ss display fairly constant mean distance scores over minutes, septal pairs show a very large decrease over the first two minutes spent in the maze.

The mean emotionality ratings for the three lesion types (septal, amygdaloid, and sham), combined across experimental groups, are shown graphically in Figure 7. Pre-operative emotionality-scale scores display a systematic reduction over days. Post-operative rating revealed that septally lesioned Ss display a marked, but transitory increase in emotionality, while amygdalectomized Ss show a small, but consistent, increase in reactivity when compared either with pre-operative levels or with the scores of sham Ss.

Analyses of variance performed on the emotionality data are summarized in Tables 9 and 10. There were no significant differences between groups pre-operatively ( $F = .99$ ,  $df = 2, 69$ ). There was a highly significant Days effect ( $F = 147.3$ ,  $p < .01$ ,  $df = 5, 345$ ), reflecting the general decrease in reactivity over days, but no significant Groups x Days interaction ( $F = .31$ ,  $df = 10, 345$ ). Post-operative comparisons revealed a significant Groups effect ( $F = 18.34$ ,  $p < .01$ ,  $df = 2, 141$ ), a highly significant Days effect ( $F = 205.9$ ,  $p < .01$ ,  $df = 11, 1551$ ), as well as a significant Groups x Days interaction ( $F = 77.7$ ,  $p < .01$ ,  $df = 22, 1551$ ).

Scheffé' comparisons between groups are summarized in Table 11. There was a significant difference between the emotionality scores of septal and sham Ss, a significant difference between the scores

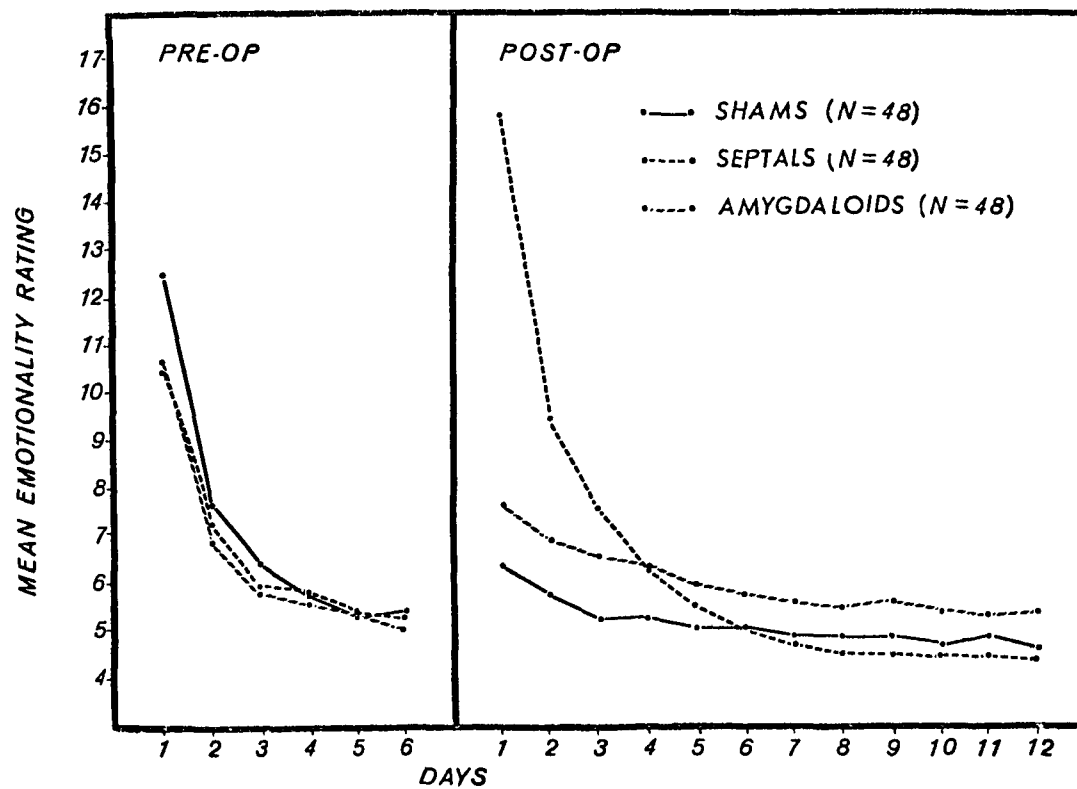


Figure 7. Mean emotionality scores by days.

Table 9

Analysis of Variance of Pre-operative Within  
and Between Groups Differences in Emotionality

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	2	16.17	.99	NS
Subj. w. groups	69	16.43		
<u>Within Subjects</u>	360			
Days	4	704.24	147.33	.01
Lesion x Days	10	1.52	.31	NS
Days x Subj. w. groups	345	4.78		

Table 10

Analysis of Variance of Post-operative Within  
and Between Groups Differences in Emotionality

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	143			
Lesion	2	257.48	18.24	.01
Subj. w. groups	141	14.11		
<u>Within Subjects</u>	1584			
Days	11	339.80	205.93	.01
Lesion x Days	22	128.19	77.69	.01
Days x Subj. w. groups	1551	1.65		

of amygdaloid and sham Ss, but no statistically significant differences in the scores of septal and amygdaloid Ss. Failure of the difference between the reactivity of septal and amygdaloid Ss to attain statistical significance reflects the significant Groups x Days interaction. Thus, while the reactivity levels of septal Ss were substantially higher than those of amygdaloid Ss for the first 3 days of testing, septal scores dropped below those obtained by amygdaloid Ss on Days 4-12.

Table 11

Scheffé' Tests for Differences in Emotionality  
Between Individual Groups

Groups	p
SS - AA	NS
SS - NN	.01
AA - NN	.01

Bolus counts have frequently been used as a measure of the open-field emotionality of rat Ss. The mean number of boluses per day left in the maze by each of the homogeneous groups is shown in Figure 8. These results, while not completely clear, suggest that the bolus-count measure is not a valid indicant of emotional reactivity. First, there was no systematic reduction pre-operatively in the number of boluses left in the field over days, even though there was a large drop during this period in emotionality scale scores. Second, while septal Ss display a marked increase in emotionality scale scores, they produce a much smaller number of fecal boluses, and while their bolus counts are highest on the first two post-operative days when their emotionality scores are highest, the

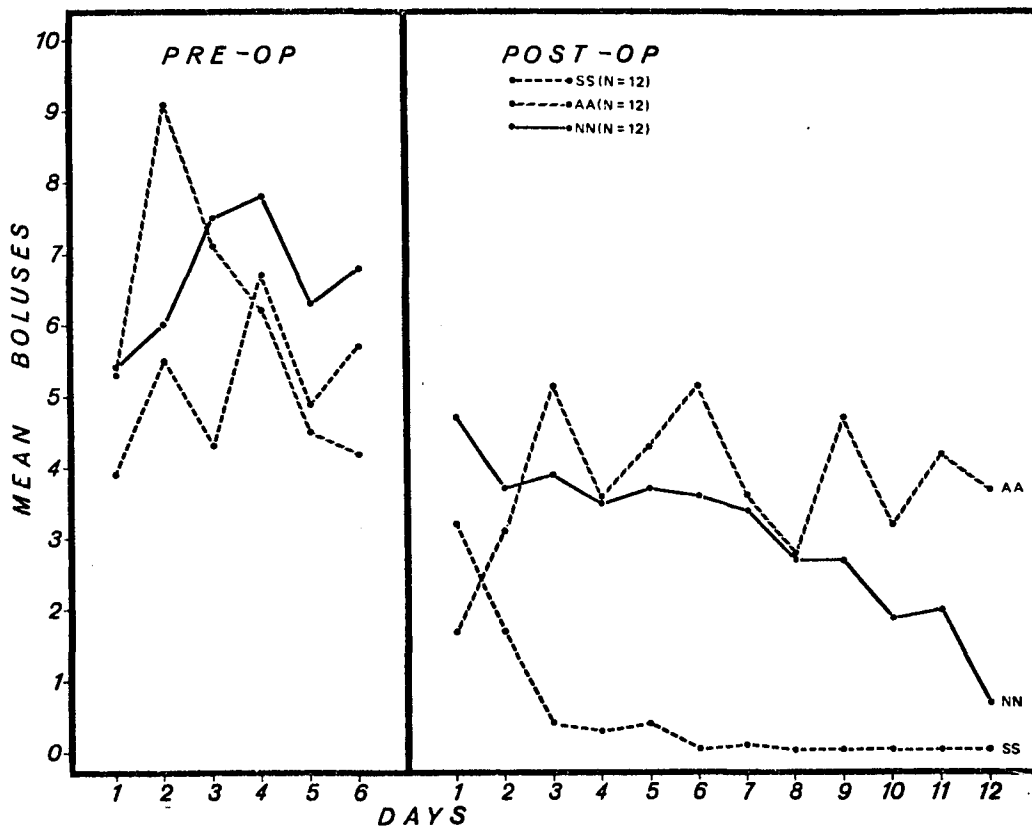


Figure 8. Mean boluses by days.

bolus counts of septal Ss are never as high as those of sham-operate Ss.

A Kruskal-Wallis Analysis of Variance was performed on both the pre-operative and post-operative bolus data. There were no significant differences among groups pre-operatively, but there was a significant difference between groups post-operatively ( $p < .02$ ). Subsequent comparisons between individual groups using a Mann-Whitney U Test revealed a significant difference between septals and shams ( $p < .004$ ) but a non-significant difference between septals and amygdaloid preparations ( $p < .10$ ).

Data from the immobility index for the three homogeneous groups are shown in Figure 9. This measure, based upon the number of times an animal remained in the same field segment during the 10 sec. observational period, was presumed to be closely and inversely related to the animal's tendency to explore his environment. Rats have a strong tendency to explore a novel environment, a tendency which should be strongest on Day 1 when their pre-operative immobility scores are lowest. As exploratory behavior drops out, the immobility scores increase. The subsequent drop in immobility scores after Day 3 is not so easily explained, as all other measures--contact times, mean distance, and emotionality--have reached stable levels by that time. The post-operative immobility scores of septal Ss are greatly elevated in comparison to those of sham pairs who in turn have higher scores than do amygdaloid Ss. These scores parallel very closely the differential tendencies of the various groups to engage in exploratory behaviors.

The analyses of variance performed on the immobility data are

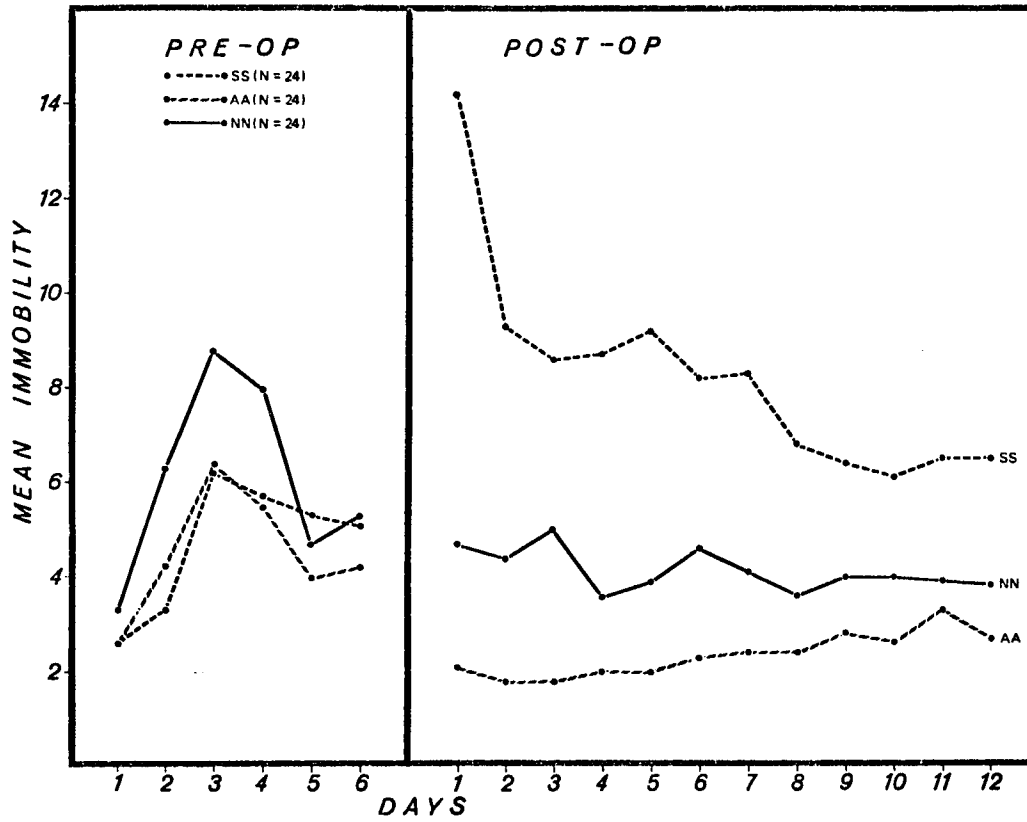


Figure 9. Mean immobility by days.



summarized in Tables 12 and 13. The only factor to attain statistical significance pre-operatively is the Days factor ( $F = 16.0$ ,  $p < .01$ ,  $df = 5$ , 345). Post-operative comparisons revealed a significant Groups factor ( $F = 38.6$ ,  $p < .01$ ,  $df = 2$ , 69), a significant Days factor ( $F = 5.2$ ,  $p < .01$ ,  $df = 11$ , 759), and a significant Groups x Days interaction ( $F = 5.8$ ,  $p < .01$ ,  $df = 22$ , 759). Scheffé<sup>1</sup> tests for differences among the three groups which are summarized in Table 14 show all groups to be significantly different from each other.

Table 14

Scheffé<sup>1</sup> Tests for Differences in Immobility  
Between Individual Groups

Groups	p
SS - AA	.01
SS - NN	.01
AA - NN	.01

Results for the mobility measure, based upon the mean distance moved per 10 sec. interval, are summarized in Figure 10. These data are, in general, inversely parallel to the immobility data. Thus, there is a pre-operative decrease in movement over the first 3 days of testing, followed by a slight increase during the final 3 days. Post-operative comparisons reveal a decrease in movement by septal SS, almost no change in the movement scores obtained by shams, and a marked increase in the mobility scores obtained by amygdaloid preparations. These scores are again assumed to reflect the tendency of SS to engage in exploratory activities.

The analyses of variance performed on the data are summarized in Tables 15 and 16. There is, unfortunately, a significant Groups

Table 12

Analysis of Variance of Pre-operative Within and  
Between Groups Differences in Immobility Scores

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	2	102.6	1.95	NS
Subj. w. groups	69	52.7		
<u>Within Subjects</u>	360			
Days	5	163.3	16.0	.01
Lesion x Days	10	11.2	1.1	NS
Days x Subj. w. groups	345	10.2		

Table 13

Analysis of Variance of Post-operative Within  
and Between Groups Differences in Immobility Scores

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	2	2624.5	4.98	.01
Subj. w. groups	69	67.9		
<u>Within Subjects</u>	792			
Days	11	39.2	2.34	.01
Lesion x Days	22	43.4	1.97	.01
Days x Subj. w. groups	759	7.4		

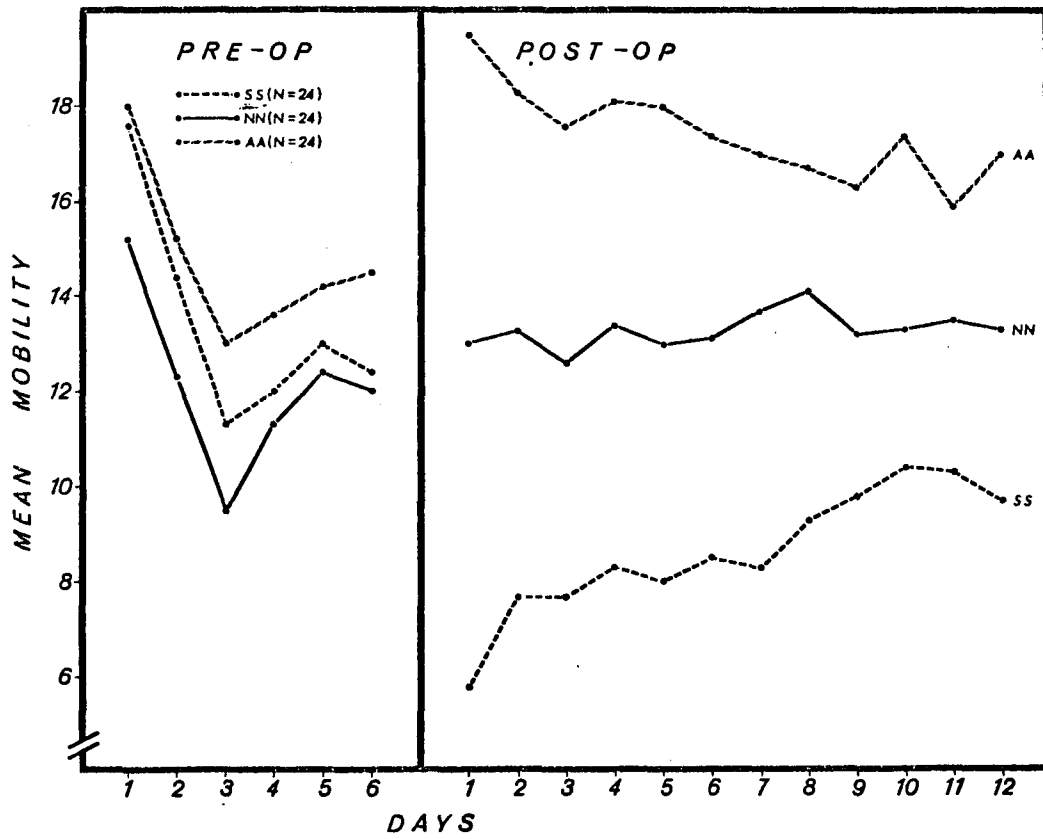


Figure 10. Mean mobility by days.

Table 15

Analysis of Variance of Pre-operative Within  
and Between Groups Differences in Mobility Scores

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	2	252.8	3.39	.05
Subj. w. groups	69	74.4		
<u>Within Subjects</u>	360			
Days	5	272.1	28.9	.01
Lesion x Days	10	5.9	.6	NS
Days x Subj. w. groups	345	9.4		

Table 16

Analysis of Variance of Post-operative Within  
and Between Groups Differences in Mobility Scores

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	2	5,582.2	45.0	.01
Subj. w. groups	69	124.0		
<u>Within Subjects</u>	792			
Days	11	6.17	.84	NS
Lesion x Days	22	31.50	4.3	.01
Days x Subj. w. groups	759	7.3		

effect pre-operatively ( $F = 3.39$ ,  $p < .05$ ,  $df = 2, 69$ ), and hence, post-operative differences must be interpreted with caution. These differences are, however, small relative to those noted in post-operative comparisons, and Scheffé<sup>1</sup> tests of the data showed no significant intergroup differences. There is also a statistically significant Days effect pre-op. ( $F = 28.9$ ,  $p < .01$ ,  $df = 5, 345$ ), reflecting the decrease, and subsequent increase in mobility scores over days. The Groups x Days interaction was not significant ( $F = 0.6$ ,  $df = 10, 345$ ). The Groups factor was highly significant in the post-operative comparison ( $F = 45.0$ ,  $p < .01$ ,  $df = 2, 69$ ). There was no significant Days effect ( $F = .84$ ,  $df = 11, 759$ ), although there was a significant Groups x Days interaction ( $F = 4.3$ ,  $p < .01$ ,  $df = 22, 759$ ), reflecting the tendency toward an increase in septal mobility over days as well as a tendency toward decreased mobility scores for amygdaloid ss. Scheffé<sup>1</sup> comparisons between groups, summarized in Table 17, indicated that all groups were significantly different from one another.

Table 17

Scheffé<sup>1</sup> Tests for Differences in Mobility  
Between Individual Groups

Groups	P
SS - AA	.01
SS - NN	.01
AA - NN	.01

Comparisons of the mobility of the various lesion groups as a function of the type of preparation with which they are paired, shown

in Figures 11, 12 and 13, demonstrate the context specificity of the mobility scores of both septal and sham preparations. Figure 11 is a plot of the mobility scores of Group SS septals compared with the mobility of septals when paired with sham preparations (Group SN) and when paired with amygdaloid Ss (Group SA). From this figure it can be seen that while septals when paired with each other have very low mobility scores, reflecting their tendency to engage in social interactions as opposed to exploratory activities, they have slightly higher scores when paired with shams, and much higher mobility scores--higher than those of sham-sham pairs--when paired with amygdaloids. These results demonstrate then, the fact that the increase in social cohesiveness displayed by septal Ss is an active phenomenon rather than a passive function of hypomobility. Thus septals when paired with a hypermobile, hyperexploratory amygdaloid preparation tend to pursue the other rat in an attempt to establish social contacts. In Figure 12, it can be seen that sham preparations also actively seek out social contacts, such that their mobility scores tend to reflect those of the preparations with which they are paired. Thus, sham mobility scores are higher when they are paired with hypermobile amygdaloids and lower when they are paired with normally hypoactive septals. Reference to Figure 13 demonstrates that the noted amygdaloid hypermobility has no relationship to pairing conditions, a result which reflects the unresponsiveness of amygdaloid preparations to social stimuli.

The mean number of discrete contacts made by each of the experimental groups is plotted in Figure 14. Both Group SS and Group SN



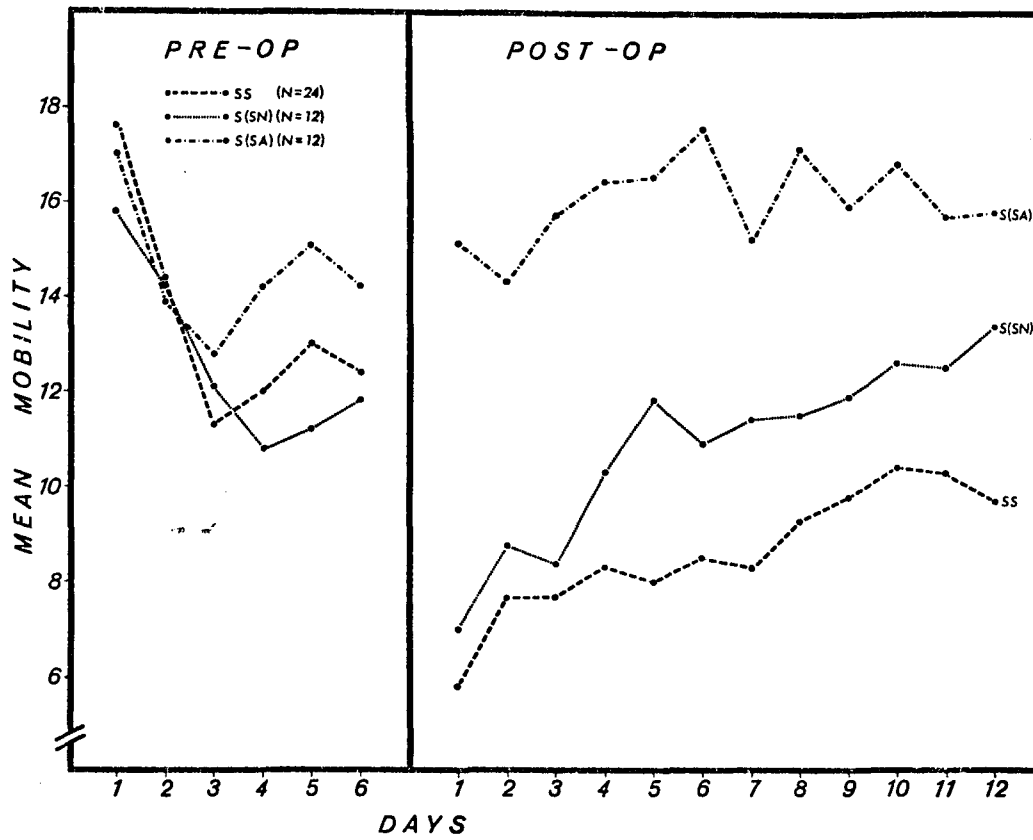


Figure 11. Mean mobility by days of septal Ss as a function of pairing condition.

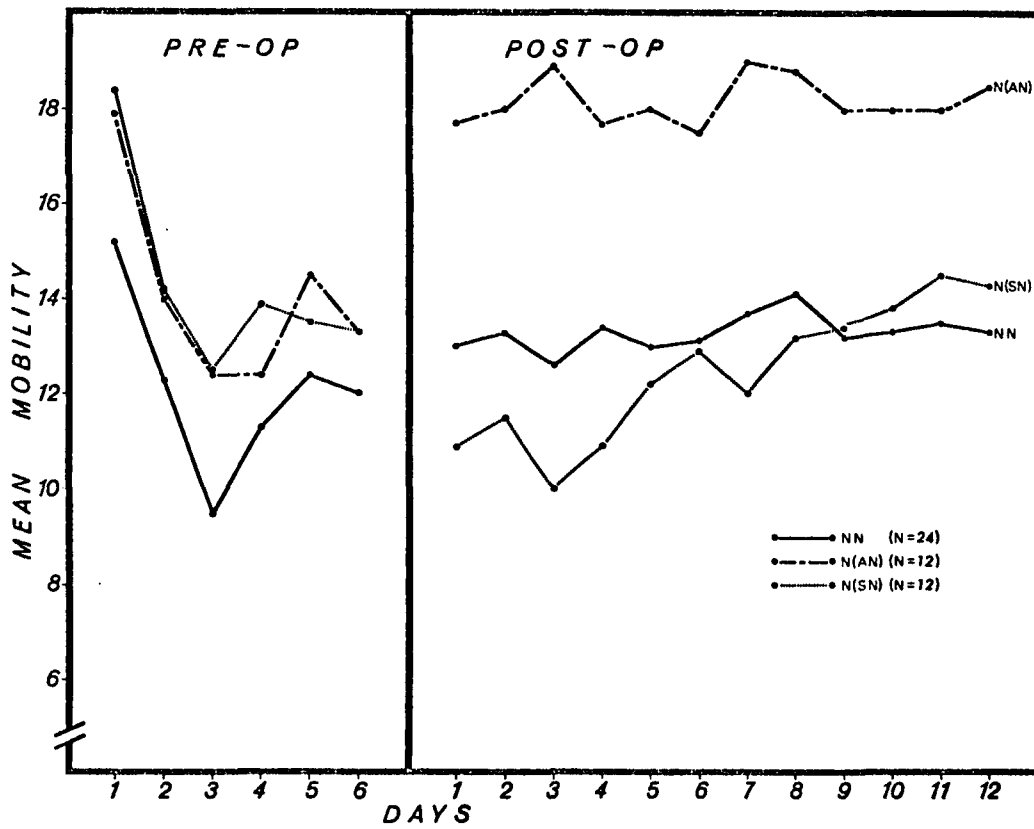


Figure 12. Mean mobility by days of sham Ss as a function of pairing condition.

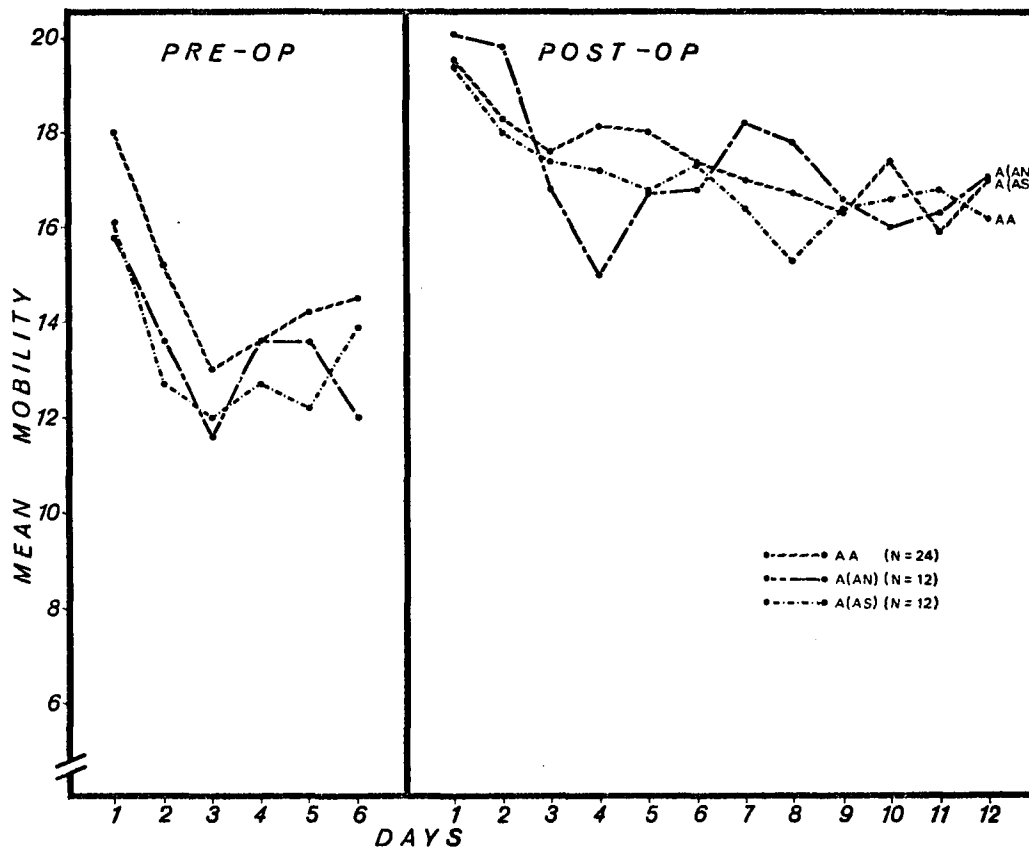


Figure 13. Mean mobility by days of amygdaloid Ss as a function of pairing condition.

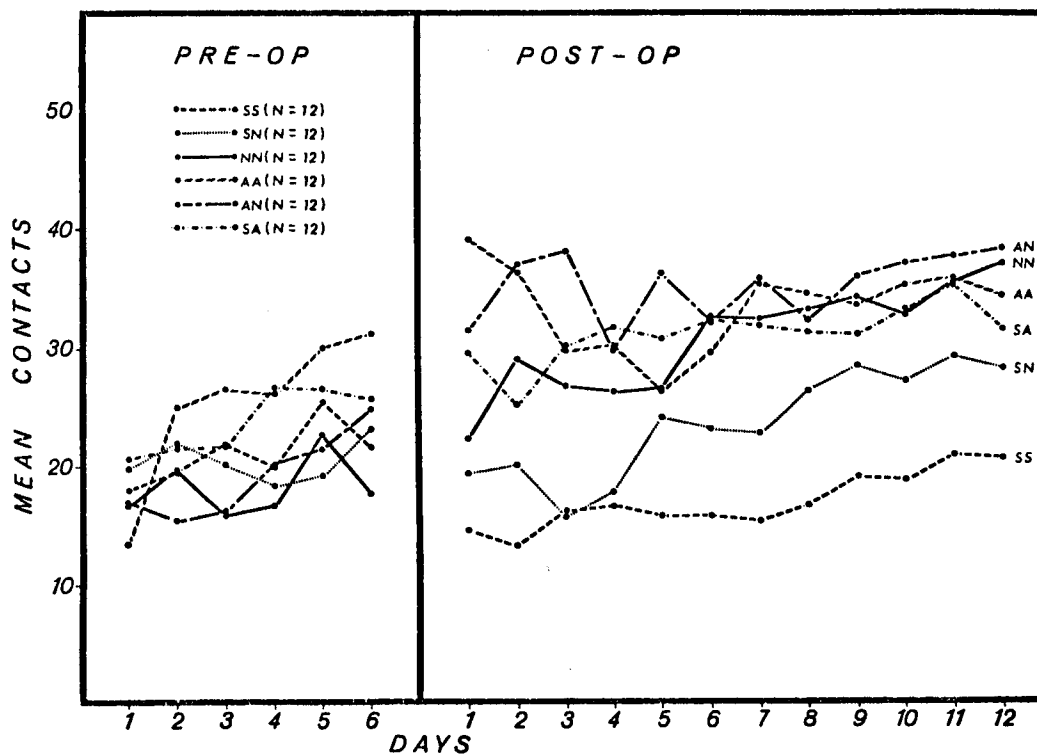


Figure 14. Mean contacts by days.

pairs displayed a reduced number of contacts in comparison with sham pairs, a reduction which reflects the increased duration of individual contacts maintained by these groups. Of interest, is the fact that the number of contacts made by amygdaloid preparations is, if anything, a bit higher than that of sham pairs. This would seem to reflect the fact that these ss don't maintain an active avoidance of other rats, but rather, fail to respond with continued contacts to social stimuli.

Results from the analyses of variance performed on the contacts data are summarized in Tables 18 and 19. Pre-operative comparisons revealed both a significant Groups factor ( $F = 4.53$ ,  $p < .01$ ,  $df = 5$ , 66) and Days factor ( $F = 6.24$ ,  $p < .01$ ,  $df = 5$ , 330) while the Groups x Days interaction was not significant ( $F = 1.12$ ,  $df = 35$ , 330). Scheffé tests performed on the pre-operative data, summarized in Table 20, indicate that the significant F ratio for the Groups factor can be attributed to significant differences between Groups SS and AN and between Groups AA and NN. Post-operative comparisons revealed a

Table 20

Scheffé Tests for Pre-operative Differences in the  
Number of Contacts Between Individual Groups

Group	p	Group	p
SS - SN	NS	SN - SA	NS
SS - AA	NS	AA - AN	.05
SS - AN	NS	AA - NN	.05
SS - NN	NS	AA - SA	NS
SS - SA	NS	AN - NN	NS
SN - AA	NS	AN - SA	NS
SN - AN	NS	NN - SA	NS
SN - NN	NS		

Table 18

Analysis of Variance of Pre-operative Within and  
Between Groups Differences in Number of Contacts

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	5	812.5	4.53	.01
Subj. w. groups	66	179.2		
<u>Within Subjects</u>	360			
Days	5	261.0	6.24	.01
Lesion x Days	25	47.0	1.12	NS
Days x Subj. w. groups	330	41.8		

Table 19

Analysis of Variance of Post-operative Within and  
Between Groups Differences in Number of Contacts

SOURCE OF VARIANCE	df	MS	F	P
<u>Between Subjects</u>	71			
Lesion	5	6966.0	13.1	.01
Subj. w. groups	66	530.3		
<u>Within Subjects</u>	792			
Days	11	383.0	6.50	.01
Lesion x Days	55	94.7	1.60	.01
Days x Subj. w. groups	726	58.9		

significant Groups effect ( $F = 13.1, p < .01, df = 5, 66$ ), a significant Days effect ( $F = 6.50, p < .01, df = 11, 726$ ), and a significant Groups x Days interaction ( $F = 1.60, p < .01, df = 55, 726$ ). Scheffe' tests performed on the post-operative data are summarized in Table 21. Group SS scores were significantly different from all other groups except Group SN. In addition, Group SN contact scores differed significantly from those of Group AA and Group AN.

Table 21

Scheffe' Tests for Post-operative Differences in the  
Number of Contacts Between Individual Groups

Group	P	Group	P
SS - SN	NS	SN - SA	NS
SS - AA	.01	AA - AN	NS
SS - AN	.01	AA - NN	NS
SS - NN	.01	AA - SA	NS
SS - SA	.01	AN - NN	NS
SN - AA	.05	AN - SA	NS
SN - AN	.01	NN - SA	NS
SN - NN	NS		



## DISCUSSION

The results of this experiment provide evidence for powerful and reciprocal effects of septal and amygdaloid lesions in altering the social cohesiveness of rats. Sham-operate Ss spent a mean of 64.3% of the post-operative testing sessions in direct contact. Septal lesions strongly augmented this normal tendency of rat Ss to engage in social interactions, increasing the mean time in contact to 85.4% of the testing sessions, while amygdaloid lesions had an equally strong effect in reducing the incidence of social responses, decreasing the mean time in contact to only 32.2% of the testing sessions. These alterations in response tendencies were essentially cancelled when a septal preparation was paired with an amygdalectomized rat such that the resulting mean of 62.3% of the post-operative testing sessions spent in contact was little different from that obtained by sham preparations.

The context specificity of the decreased mobility scores of septal Ss provides evidence that the noted increase in social interactions displayed by septal Ss is an active phenomenon rather than a passive function of hypomobility. While pairs of septals were hypomobile, a result consistent with previous results demonstrating hypoactivity in septal rats (Nielson, McIver, and Boswell, 1965; Schwartzbaum and Gay, 1966; Corman et al., 1967), their mobility scores were higher when paired with sham preparations, and septal Ss were actually hypermobile when paired with amygdaloid preparations. Thus, septal rats, when paired with hypermobile, hyperexploratory amygdaloid preparations, tended to pursue the other rat. As sham

preparations also display differential activity levels as a function of pairing condition, decreasing activity when paired with septals and increasing activity when paired with amygdaloid Ss, it would seem that the differences between the responses of septal and sham Ss are quantitative, rather than qualitative, and that septal lesions act by potentiating the normal rat's tendency to engage in social interactions.

It is significant to note that the hyperreactivity of septal Ss is not related in any simple manner to the increased social cohesiveness of these Ss. Thus, while the hyperemotionality of septals persists for 3 days, their contact times have reached near asymptotic levels by Day 2. The contact time and mean distance scores of septal pairs are substantially lower and higher respectively on the first post-operative day when their emotionality scale scores are highest, but this can be related almost exclusively to the time required by these Ss to make their first contact. Such a view is supported by the observation that septal Ss had attained near-asymptotic mean distance scores by the third minute of the first post-operative testing session. The typical first response of hyperreactive septal Ss when placed into the maze on the first post-operative day was an explosive retreat to opposite edges of the maze. Subsequently septal Ss cautiously approached each other until contact was established. Having made this initial contact, these Ss spent virtually the entire remaining test session, and all subsequent sessions in direct physical contact.

These results indicating that septal hyperemotionality and increased social cohesiveness are independent are notably consistent

with other results demonstrating a dissociation between septal hyper-reactivity and other behavioral changes occurring after septal lesions. Krieckhaus et al. (1964), for example, found that septal rats were facilitated in the acquisition of an active avoidance task even when tested after their hyperreactivity had disappeared, while Ahmad and Harvey (1968) found that increased shock-elicited fighting in septal rats was unrelated to the presence or absence of hyper-irritability. Similarly, Corman et al. (1967) noted a dissociation of septal hypoactivity and septal hyperemotionality. Such findings are consistent with results (Lauber, 1969; Turner, 1970) suggesting that the hyperemotionality of septal ss may be a function of damage to extra-septal structures.

The decrease in social cohesiveness noted after amygdaloid lesions probably does not reflect an active avoidance of social objects. Thus, while amygdalectomized rats had very low contact time scores and very high mean distance scores, they made at least as many discrete contacts with the other rat as did sham preparations. These rats, then, simply fail to respond to social stimuli with continued contacts.

There is evidence in the current study, then, that amygdaloid lesions produce a pronounced reduction in the rat's responsiveness to social stimuli. This position is supported both by the previously noted decrease in the duration of individual contacts, and by mobility data showing that the activity levels of amygdalectomized rats are unaffected by the behavior of the rat with which they are paired. Thus, while both septal and sham ss display an increased mobility

score when paired with hyperactive Ss and a decreased mobility score when paired with a hypoactive S, pairing condition had no effect on the mobility of amygdaloid Ss.

While septal and amygdaloid lesions were found to alter social responsiveness in opposite directions, the results of this study do not seem to support a strict principle of functional reciprocity between the two structures. The mirror-image of the tendency on the part of septal Ss to seek out social contacts would be an active avoidance of social contacts, but the large number of discrete contacts demonstrates that this does not describe the behavior of amygdaloid Ss in the present study. Rather, amygdaloid Ss simply didn't exhibit social behaviors, but engaged almost exclusively in non-social exploratory activities. Differences in the time course of the effects of the two lesions would also seem to argue against a reciprocity principle. Thus, while the contact times of septal Ss were relatively constant across sessions, amygdalectomized Ss showed a substantial increase in contact times across days.

## CONCLUSIONS

The effect of amygdaloid lesions in this experiment was that of dramatically reducing social interaction such that these Ss spent almost the entire test period in exploratory activities, a tendency reflected by the large increase in mobility and concomitant decrease in social contact times. This reduced responsiveness of amygdaloid Ss to social stimuli reflects the more general inability of such preparations to utilize information concerning stimulus and reinforcement parameters, as exemplified by deficits in discriminating between appropriate and inappropriate sexual objects (Schreiner and Kling, 1956), abnormal responses to fear-provoking stimuli (Brady et al., 1954; Weiskrantz, 1956), and a lack of responsiveness to changes in reinforcement values (Schwartzbaum, 1960a). This deficit is consistent with Gloor's (1960) view that the amygdala functions in the selection of behaviors which are appropriate within a given situational context.

The large increase in social cohesiveness after septal lesions noted in this experiment is consistent with McCleary's (1966) view that the septum normally performs a response inhibitory function, and that the effect of septal lesions is to produce an increase in the probability of occurrence of prepotent response sequences. Pre-operatively, rats displayed a strong tendency to engage in social interactions spending, on the average, over 50% of the last 3 pre-operative test sessions in direct physical contact. This response tendency was strongly augmented by septal lesions such that septal pairs spent almost all of each daily post-operative test session in

direct contact. McCleary's position is further supported by results obtained by Bunnell et al. (1967) with hamster Ss in which it was found that pre-operatively dominant animals displayed an increase in dominance-related behaviors following septal lesions, while pre-operatively submissive septals showed an increase in submission-related behaviors.

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