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SYNERGIES AND RECIPROCITIES IN THE BEHAVIORAL EFFECTS OF COMBINATORIAL ABLATIONS OF THE SEPTAL AND AMYGDALAR COMPONENTS OF THE LIMBIC SYSTEM OF THE RAT.

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

Jacqueline Conner Bresnahan, B.A., M.A.

*****

The Ohio State University
1973

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FIELDS OF STUDY

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vii
Introduction

The septal and amygdaloid nuclei appear to have a major role in the control or modulation of hypothalamic activity (Fried, 1972; Egger, 1973). Dreifuss and Murphy (1968), who recorded from neurons in the lateral and tuberal hypothalamus, found 49 which were responsive to stimulation of both the septum and amygdala, with 41 showing similar effects from stimulation of either area, and 8 showing opposite effects. Behavioral studies give similar indications of convergence. Lesions of the septum in the rat produce a transient rage phenomenon (Brady and Nauta, 1953) similar to the more persistent rage observed after lesions of the ventromedial hypothalamus (Hetherington and Ranson, 1942), but the addition of an amygdaloid lesion attenuates the septal effect (King and Meyer, 1958; Schwartzbaum and Gay, 1966; Jonason, Enloe, Contrucci, Meyer and Meyer, 1973), if there is a recovery interval between the surgeries (Kleiner, Meyer and Meyer, 1967; Jonason, et al, 1973). The decrease in spontaneous activity evident following lesions of the ventromedial hypothalamus (Hetherington and Ranson, 1942) is also observed following lesions of the septum, whereas lesions of the amygdala produce the opposite effect (Schwartzbaum and Gay, 1966; Anderson, 1966; Corman, Meyer and Meyer, 1967; Jonason and Enloe, 1971). With combined lesions, the septal hypoactivity is
reversed by the amygdaloid lesion (Schwartzbaum and Gay, 1966; Jonason, et al., 1973).

The present study was designed as an attempt to delineate the interrelationships of the major subdivisions of the septum and amygdala as these are reflected in changes in behaviors that are known to be altered by manipulations of hypothalamic processes. Accordingly, food and water intake, weight regulation, emotional behavior, spontaneous activity, and sensorimotor capacity were investigated after lesions of the medial and lateral septal nuclei, medial and basolateral amygdaloid nuclei, as well as after combinations of these lesions.
Procedure

Subjects. Seventy-two male, Long-Evans hooded rats served as the subjects of this study. All subjects were between 90 and 120 days of age at the beginning of the experimental procedure.

Treatments. The rats were first consecutively numbered and eight were randomly assigned to each of nine different surgical groups. The animals of four of these groups were then subjected to bilateral lesions of the lateral septal nucleus (LS), the medial septal nucleus (MS), the basolateral amygdaloid nuclei (LA), and the medial amygdaloid nucleus (MA). Rats of four additional groups were subjected to combinatorial ablations of the lateral septal and the basolateral amygdaloid nuclei (LSLA), the medial septal and medial amygdaloid nuclei (MSMA), the lateral septal and medial amygdaloid nuclei (LSMA) and the medial septal and basolateral amygdaloid nuclei (MSLA). The ninth group was a conglomerate control group of rats of which two each were subjected to the lowering of an inactive electrode into the lateral septum, the medial septum, the basolateral amygdala, or the medial amygdala. The latter group was not included as the principal control group of the study, but rather as a means of estimating the extent to which the different measures were affected by non-specific, incidental surgical trauma. The
comparisons of primary interest were between groups sustaining com­binatorial lesions of the brain, and groups which sustained the individual lesions of which the combinatorial ablations were composed.

**Surgical and histological procedure.** The subjects were anaesthe­tized with a combination of sodium pentobarbital and methoxyfluo­ride. Electrolytic lesions were made in the appropriate regions of the brain using unipolar electrodes uninsulated .5 mm at the tip, the circuit being completed via an anal electrode. The coordinates for the LS, MS, and LA lesions were determined from the deGroot atlas (1959) and were as follows: lateral septal nuclei, AP + 7.8, DV + 2.0, lateral + 1.0, with a current of 1 ma passed for 7 sec.; medial septal nucleus, AP + 7.8, DV + 1.5, lateral 0 with a current of 1 ma passed for 10 sec.; basolateral amygdaloid nuclei, AP + 4.5, + 5.0, + 5.8, DV - 2.6, - 2.4, - 2.4, lateral + 5.0, + 5.5, + 5.1, with a current of .5 ma passed for 10 sec. The medial amygdaloid coordinates were as follows: mouthbar -1, the electrode carrier was tilted 3° toward the midline, AP - 2.0 from bregma, DV - 8.5 from the surface of the cortex, lateral +4.3, with a current of 1 ma passed for 7 sec. Postsurgically, a broad band antibiotic was administered.

Upon completion of behavioral testing, the subjects were given a lethal dose of sodium pentobarbital and perfused intracardially with 0.9% saline followed by 10% formalin. The brains were removed from the skulls, either embedded in celloidin or frozen, and
sectioned at 30µm. The sections were stained with cresyl violet, and examined to determine the locations and extents of the lesions.

**Behavioral methods.** All of the behavioral procedures were conducted by experimenters who had no knowledge of the group to which any given subject was assigned. Food and water intake was measured as in the experiment of Singh and Meyer (1968). The subjects were placed on a cyclic food-deprivation schedule four days prior to surgery, which continued for 22 days post-operatively. Water was available at all times but food was presented on alternate days for 24 hr. periods. The food was dry mash and was presented in a cup that was covered except for a central hole, 1 in. in diameter. Spilled food was caught on waxed paper and weighed. The water was supplied through calibrated bottles equipped with conventional drinking tubes.

Emotional reactivity or responsiveness was measured for four days before and six days after surgery using the procedures and scale described by King (1958) and by Jonason and Enloe (1971). Using this six-component scale, each rat was evaluated on (A) reaction to presentation of a pencil close to the snout, (B) reaction to light tapping on the back with a pencil, (C) resistance to capture, (D) resistance to handling, (E) vocalization during capture and handling, and (F) urination and defecation in reaction to handling. Each subject was given a score of from 1 to 5 points on each of categories A through D, from 0-5 on category E, and from 0 to 2 on category F. The mean sum of the category scores assigned
by two independent raters represented the subject's emotional reactivity score for a given day.

Activity was measured with Quartec RWM-2 counters. The animals were placed in plastic cages, 48 cm long \times 26 \text{ cm wide} \times 16 \text{ cm high}, on the platform of one of the counters for a ten min. period on each of the four preoperative and 21 postoperative days. Placement of the animals on each of the four activity counters was systematically varied. The counters, which detected activity by measuring changes in capacitance associated with the animals' movements in the cage, were calibrated by moving a long object over all four counters simultaneously, and then setting the sensitivity so that each counter gave the same reading.

Capacity for localization of a stimulus was measured by delivering a 1-ma shock with a small probe to different regions of the body which had been shaved at the time of surgery. There were five stimulation points on each side of the body: the shoulder, the forearm, the mid-side, the back and the hindleg. The probe was brought up to the subject from the rear to minimize responding to visual cues, and the placements of the electrode were determined by counterbalanced orders within sessions, between sessions, and between groups. The testing was conducted on a small unstable platform which was raised above a table to reduce the amount of movement by the subject. Two presentations were delivered to each stimulation point in each session, and the sessions were conducted on post-operative days 1, 3, 6, 10, 15, and 21. If a localization response was not made after 10 sec. of shock, the stimulus was
terminated. Two types of localization responses were recognized: specific and non-specific. A specific localization response was recorded if in response to the stimulus, the subject turned its head to the point of stimulation, bit the electrode, or wiped the stimulus away with a paw. A non-specific localization response was recorded if the rat attempted to escape the stimulus by moving away or withdrawing a limb, or, if the rat turned its head to the side of stimulation. Stimulus localization as measured by the second category is clearly not as precise as that indicated by the specific localization responses. The non-specific responses, however, do indicate an ability to respond to stimulation with respect to its position on the body.
Results

Histological findings. Figure 1 illustrates the maximal extent of the lesion for each of the experimental animals. The lateral septal lesions damaged the lateral septal nucleus bilaterally in all subjects. Very minimal damage to the medial septal nucleus unilaterally, the septohypothalamic tract, the caudate-putamen, the superior fornix, and the septofimbrial nucleus was also observed. The medial septal lesions damaged the medial septal nucleus bilaterally in all subjects, and the lesions were observed to occasionally involve slight damage to the lateral septal nucleus unilaterally, the superior fornix, the columns of the fornix, the diagonal bands, the triangular septal nucleus, and the septofimbrial nucleus. The basolateral amygdaloid lesions typically damaged the lateral amygdaloid nucleus bilaterally, the lateral division of the basal nucleus bilaterally, the central nucleus bilaterally, and the peri-amygdaloid cortex bilaterally. Less typically, damage was observed to invade the lateral portion of the cortical amygdaloid nucleus, the caudate-putamen and the medial portion of the basal amygdaloid nucleus. Occasional damage to the stria terminalis and the hippocampus was also evident. The medial amygdaloid lesions damaged the medial amygdaloid nucleus bilaterally in all subjects. The peri-
Figure 1. Brain reconstructions illustrating the maximal extent of the lesion for all subjects.
amygdaloid cortex was also damaged ventrally in a large proportion of the medial amygdaloid lesions. The medial extent of the cortical amygdaloid nucleus and the optic tract were damaged in several preparations, and the medial portion of the basal amygdaloid nucleus, the internal capsule and the hippocampus were also involved in a few lesions.

Behavioral findings. Figure 2 presents the mean food intakes for all nine groups as assessed preoperatively, and during the course of the animals' postoperative recovery. The functions suggested that the acute effects of surgery were over in about 9 days. Accordingly, the bulk of the data were collapsed and treated as measures of the effects obtained under relatively chronic conditions. The exceptions were the data for emotionality which were taken on the first post-operative day, and for responses to local stimulation which were measured periodically throughout the postoperative phase. The latter two measures were treated as they were because, on the basis of previous findings (Yutzey, Meyer and Meyer, 1967; Jonason, et al., 1973; Turner, 1973) notable effects were expected to be relatively transitory.

Tests for significance were carried out by means of analysis of variance. Single lesion groups, including the operated control group, were compared with each other, and each single-lesion group was compared with combinatorial groups that were subjected to ablations that included that lesion as one of its particular components. When over-all analysis resulted in F's beyond the .05
Figure 2. Average food intake for all groups during the experiment.
level of significance, comparisons between individual groups were made by the method of Newman and Kuels (Winer, 1971).

There were no significant intergroup differences in food intake. In general, however, there was a tendency for LS and MA subjects to eat more than the other single-lesion subjects, and for the rats with both lesions, i.e. LSMA's, to also show slightly greater food intake.

The outcomes of the other measures are summarized in Table 1. In each of its subtables, OC scores are given in the upper left hand corner, while single-lesion outcomes for LS and MS versus LA and MA are entered at the heads of the columns and the rows, respectively. The interiors of the tables give the mean scores for groups with combinatorial lesions and hence interactive effects can be observed as differences between the scores at heads of rows and columns and the scores at intersections between them.

Consider first the single-lesion outcomes. The findings with respect to emotionality suggest that either an LS or LA lesion modestly enhances the King index. This is supported by an over-all test ($F = 4.15$, $df = 4, 35$, $p < .01$) and Newman-Kuels tests ($p < .05$ for all LA and LS comparisons except for LS versus LA, and LS versus OC which did not reach significance). However, neither treatment yielded what could be regarded as a full-blown effect. Most investigators who have used the procedure regard 12+ as the cut-off for rage. Notably, the MS and MA groups had scores that were essentially normal and within one point of that for OC subjects.
The findings with respect to the effects of single lesions on body weight were insignificant under both conditions of food availability. In general, the chronic body weights fell between 6 and 9 percent on days when food was withheld. The trends for the LS and MA groups parallel the slightly higher food intake for these groups. Water intake when food was present, likewise did not yield over-all significance. There were, however, very large changes in drinking as a function of some of these single-lesions when food was not present ($F = 2.91$, df = 4/35. $p < .05$). Water intake by the LS group was over twice that of the MS and the LA ($p < .05$ in both cases) and nearly twice that of the operated controls ($p < .05$). The MA animals also showed an elevation of about 50% over the LS, LA and OC rats, but this was not significant.

There were no striking nor significant effects of single ablations on activity as measured in sated animals. There were of course, increases in levels of activity measured after 24 hours of food deprivation, but these increases, like the basal measures, did not differentiate the groups. There were trends for the MS and MA to be more active than the LS, the LA, and the OC animals when deprived, the MS group dropping back when sated, while the increase in activity caused by deprivation was greatest in the LS and MS groups.

There were no important main effects of single lesions as measured by cutaneous localization. The animals were much better at making specific localization responses to stimulation of the
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**A. EMOTIONAL REACTIVITY.**

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**B. PERCENT AD LIB BODY WEIGHT WHEN SATIE.**

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**C. WATER INTAKE (ML) PER GRAM OF FOOD.**

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**D. WATER INTAKE (ML) WITHOUT FOOD.**

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**F. ACTIVITY WHEN DEPRIVED.**

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**G. PERCENT SPECIFIC LOCALIZATIONS ON DAYS 1, 3, 6. (FORELIMB AND SHOULDER).**

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**H. PERCENT SPECIFIC LOCALIZATIONS ON DAYS 1, 3, 6. (HINDLIMB AND BACK).**

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Table 1. Results for all groups on the following measures:
(A) emotional reactivity rating; (B) body weight; (C) and (D) water intake; (E) and (F) activity; (G) and (H) somatosensory localization.
front parts of their body. The responses to stimulation of the
hind-quarters were nonspecific localizations, usually escape re-
sponses in a direction away from the probe, or turning of the head
toward the side of the stimulation, both indicating that not only
was the animal aware of the stimulus but was also able to make a
motor response to it. There was essentially no change in the pat-
tern of responding to the cutaneous stimulation during the 21 day
recovery period.

The interactive effects of the ablations are to be considered
next. Emotional reactivity was enhanced by the combination of an
LS or an LA lesion with their medial counterparts (F = 4.43,
df = 2/21, p < .05 for MA interaction groups; F = 3.77, df = 2/21,
p < .05 for the LS interaction groups; F = 9.16, df = 2/21, p < .01
for the MS interaction groups). The effect is modest when an LS
lesion is combined with an MA lesion (LSMA > MA, p < .05) but is
quite dramatic when an LA lesion is combined with either septal
lesion, yielding a full-blown rage response (MSLA > MS, p < .01;
LSLA > LS, p < .05).

The only significant interactive effect with respect to body
weight was that LSMA animals were significantly heavier than either
of the other LS groups (LS, p < .05; LSLA, p < .01), and both of
the other MA groups (MA, non-significant; MSMA, p < .05), under
both conditions of food availability (F = 3.52, df = 2/21, p < .05
for food days; F = 8.33, df = 2/21, p < .01 for non-food days).
Both the MA and the LS single lesion groups tended to eat more and
weigh more, and the effect of combining the lesions seemed to be an additive one.

None of the interactions were significant with respect to water intake without food. In general, however, the increase in water intake by the LS animals was depressed by combination of an LS lesion with an LA lesion whereas the combination of an LS lesion with an MA lesion did not affect this measure. The slight increase in water intake with an MA lesion was not sustained when it was combined with a septal lesion. Thus, MA combination groups exhibited behaviors more similar to rats with the septal lesions than to the MA animals. Water intake with food presented a slightly different picture. The slight increase in drinking by rats with LS lesions was significantly suppressed by combining an LS lesion with either an LA (p < .05) or an MA (p < .05) lesion (F = 4.37, df = 2/21, p < .01). The water consumption with food by the LA rats was not altered when the LA lesion was combined with an LS lesion, but water intake was significantly increased when the LA lesion was combined with an MS lesion. The MSLA rats were actually hyperdipsic, taking in approximately 20% more water per gram of food as compared to the other LA groups. This was supported by an over-all analysis (F = 4.01, df = 2/21, p < .05) and individual comparisons (p < .05 for the MSLA-LA comparison; p < .05 for the MSLA-LSLA comparison).

The interactive effects of the lesions on activity as measured after deprivation proved to be non-significant, but they correlated well with the significant interactions under satiation conditions.
The general increases in activity observed with MA lesions were depressed by combination of MA lesions with either septal lesion (F = 5.28, df = 2/21, p < .05 for food days only; individual comparisons, p < .05). The near-normal LA rats were similar to rats that had combined MS and LA lesions, but both of these preparations were more active than the LSLA combination group (F = 4.85, df = 2/21, p < .05; individual comparisons, p < .05). The increase in levels of activity measured after deprivation was greatest for the LS group. This sensitivity to motivational level was reduced by combinations of an LS lesion with either amygdaloid lesion (F = 8.36, df = 2/21, p < .01). The LSMA lesions were the most effective in reducing the amount of change between food and non-food days, producing a drop of 24% compared to LS scores (p < .05), while the LSLA animals exhibited a 14% drop in the change compared to LS animals (non-significant). It is of interest to note that the activity of the LSMA rats changed the least amount with deprivation, and that it was this group that exhibited the heightened weight levels.

None of the interactions were significant with respect to somatosensory localization. There was a trend for the LS combination groups to localize specifically on the front parts of their bodies slightly better than their single lesion counterparts, whereas the reverse was true of the MS combination groups.
Discussion

The data with respect to emotional behavior obtained in this study confirm some prior findings but are somewhat divergent from others. No alterations in emotionality with medial septal lesions were reported by Clody and Carlton (1969), McGowan, Hankins, and Garcia (1972), or Poplawsky and Johnson (1973), and the present outcomes support these conclusions. However, the present LS group was found to be slightly hyperreactive while Poplawsky and Johnson found that lateral septal lesions caused a large increase in reactivity, as did McGowan, et al. (1972). In amygdaloid animals, effects upon this measure appear to be produced by LA lesions in that MA lesions were without consequence, and the increase found after basolateral damage were comparable to those that have been previously observed after total bilateral amygdalectomy (Kleiner, Meyer and Meyer, 1967; Jonason, Enloe, Contrucci, and Meyer, 1973).

Simultaneous lesions of the septum and amygdala have been shown to produce highly reactive animals (Kleiner, et al., 1967; Jonason, et al., 1973). In the present study, combination-lesion groups with LA lesions exhibited a hyperreactivity of the same degree. In contrast, however, the MA combination groups did not exhibit prominent Brady-Nauta syndromes but, instead, appeared to be non-reactive or reactive as a function of their septal lesions.
Stark and Henderson (1972) have related the hyperreactivity observed after large septal lesions to decreases in brain Ach. Girgis (1972) has reported large concentrations of acetylcholinesterase in the basolateral but not corticomedial amygdala which suggests that the changes in emotional behaviors observed in this study after LA lesions may be due to the effects of the latter operation upon a cholinergic mechanism. With large septal lesions there is a decrease in the total amount of acetylcholine in the brain (Sorenson and Harvey, 1971) and when levels are returned toward baseline with injection of an acetylcholinesterase inhibitor, physostigmine, hyperreactivity is attenuated (Stark and Henderson, 1972). Presumably, then, combinations of subtotal lesions of the septum with LA lesions would deplete acetylcholine levels to a greater extent than any of these lesions alone.

The overall lack of main effects in food intake support previous findings. No important changes in food intake have been observed following medial septal lesions (Kelsey and Grossman, 1969), lateral amygdaloid lesions (Rolls and Rolls, 1973; Pellegrino, 1968; Anand and Brobeck, 1952), or medial amygdaloid lesions (Sclafani, Belluzzi, and Grossman, 1970; Pellegrino, 1968). That there are no differences respective to this measure correlates nicely with the fact that there were also no effects of such lesions upon prandial drinking. Singh and Meyer (1968) reported no change in the water/food consumption ratios following total septal lesions, and the present outcomes for small septal lesions came as no particular
surprise. There was one significant interaction between the MS and LA lesions such that rats with both of these lesions drank approximately 20% more than either of the single lesions alone.

Water intake when food was not available significantly increased after lateral septal lesions, and the increased intake was similar to that observed after total septal lesions (Harvey and Hunt, 1965; Singh and Meyer, 1968). There was also a slight but non-significant increase in consequence of MA lesions, and combinatorial lesions of LS and MA produced the same changes as those observed after LS lesions. However the effect of the LS lesion was attenuated when combined with an LA lesion, which is puzzling inasmuch as LA lesions yielded no main effects nor effects when combined with MS lesions as in group MSLA.

Body weight was not significantly affected by any of the single lesions in the present study. Clody and Carlton (1969) found that body weight is lowered after medial septal lesions, but no such differential alteration was observed in the present MS group. Basolateral lesions of the amygdala have not been shown previously to change body weight (Murphy, Wideman, and Brown, 1972; Rolls and Rolls, 1973) and the present LA data with respect to this measure are consistent with these previous findings. Also, in agreement with Sclafani, et al. (1970), MA lesions by themselves have no significant effect upon chronic body weights although, when combined with LS ablations, weights are significantly increased. This finding is interesting in light of the fact that this group did not
significantly increase their food intake, although they showed the highest mean intake of all the groups.

Baseline activity measures in the present study did not significantly differentiate the single lesion groups. The MA animals showed slight increases in general activity similar to those observed by Sclafani, et al. (1970) in open field behavior after MA lesions, and also by Schwartzbaum and Gay (1969), Corman, Meyer and Meyer (1967), and Jonason and Enloe (1971) in open field activity following total bilateral amygdalectomy. Other studies showing alterations in activity as a function of small lesions cannot be directly compared as the activity measures were not similar, e.g., increases in activity during the intertrial interval in an active avoidance learning situation (Donovick, 1968) or decreases in running wheel activity (Clody and Carlton, 1969) following damage to the medial septum.

Deprivation conditions have been shown by Anderson (1970) to increase activity following total septal lesions, in animals placed in an activity compartment which was reasonably similar to the apparatus utilized in the present study. The present LS group showed a similar sensitivity to deprivation conditions, increasing their activity more than any other group. This hypersensitivity of the LS subjects to changes in motivation was significantly attenuated when this lesion was combined with either amygdaloid lesion. Medial amygdaloid lesions had the greatest combinatorial effect in this respect, i.e., the LSMA group showed the least alteration of activity
levels due to deprivation condition of any group. The rats of the LSLA group exhibited decreased activity levels under both conditions of food availability, but the amount of change with deprivation was comparable to all but the LS and LSMA groups. Thus, the LS lesion, whether alone or in combination with an amygdaloid lesion had the most profound effect upon activity.

Ability to localize somatosensory stimuli was not significantly impaired by any of the various surgical procedures of this study. Turner (1973) has reported that rats, if subjected to total amygdalectomy, exhibit marked deficits in their ability to localize stimuli presented to the surface of the body. He found no such deficit in consequence of lesions confined to the basolateral region, nor did he find such a deficit in rats with large lesions of the septum. The findings of the present study confirm these results and shows that small lesions of the medial and lateral septum do not affect this measure, and neither do small lesions of the corticomedial amygdala. Thus, lesions of the basolateral and medial amygdala do not yield significant effects on this measure while total amygdalectomy does. It is possible that the medial lesions were not extensive enough, or as suggested by Turner (1973) the critical locus for the deficit may be the area between the amygdala and lateral hypothalamus.

In conclusion, the intrinsic divisions of the septum and amygdala into medial and lateral components seems to be valid with respect to the behavioral results of the present study. This
division in the septum is more strongly supported by the present findings than this type of division in the amygdala. It had been hoped that there would be some common organizational principle in the septum and amygdala that would be evident such that, e.g., medial lesions of both structures would produce similar or perhaps opposite alterations of the same behavioral measures. However, no simple consistent picture across measures emerged from the results of this study. Thus, it may be that a more appropriate intrinsic division of either of these limbic structures would be more adequate and would yield some commonality of function across behavioral tests.
References


