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LIMBIC LESIONS AND ERROR REDUCTION[1]

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Three monkeys with hippocampal lesions, four with ablations of the amygdala, and four sham-operated *Ss* were trained on a series of visual discrimination problems in which there was always one rewarded stimulus while the number of unrewarded cues varied between one, two, and four. Animals with amygdaloid lesions did not reliably differ from the sham operates on any test and no differences between any of the three groups approached reliability when only one negative cue was used. On tests involving multiple negative cues, however, the group with hippocampal lesions required significantly more sessions to reach criterion than did either of the other two groups.

According to the model of limbic function proposed by Douglas and Pribram (1966) the hippocampus is postulated to play an important role in the elimination of responses which lead to nonreinforcement. The mechanism is thought to involve efferent control of response-initiating stimuli rather than a direct inhibition of muscles or responses. This process, termed gating, is postulated to play a part in such decremental behavior as habituation, extinction, reversal, and possibly passive avoidance, as well as in the elimination of errors. There is now abundant evidence that hippocampectomized animals are impaired on all of these types of behavior but the last (see review by Douglas, 1967). This is ironic, since the system has been termed the error evaluation system. The main reason for the lack of direct proof of a deficit in error avoidance after hippocampal lesions is that under most circumstances it is impossible to distinguish in the record between repetition of correct responses and the cessation of incorrect ones.

The present authors reasoned that perhaps a deficit in error elimination might be detectable if a series of problems was used in which the relative importance of error reduction was systematically changed. This was accomplished through the training of three groups of *Ss* on four visual discrimination problems, according to a technique developed by Pribram (1960), with the number of rewarded stimuli kept constant at one on all problems while the number of negative cues varied between one, two, and four. In addition to the experimental group of three monkeys with bilateral hippocampal lesions, a control group of four sham-operated *Ss* was used, as well as a group of four monkeys with amygdaloid lesions. The latter group was included because, according to the model mentioned earlier, amygdalectomy should not interfere with error reduction processes. Previous experiments had shown that hippocampal removal results in little or no deficit in problems with one positive and one negative cue (Kimble & Pribram, 1963). Therefore, it was expected that the present hippocampectomized *Ss* would be normal in learning speed when one negative cue was used, but they would have a progressive deficit, compared with normal *Ss*, as negative cues were increased.

METHOD

Subjects

Subjects were 11 rhesus monkeys of an age and size corresponding to late adolescence or early adulthood. Bilateral removal of the hippocampus had been performed in three *Ss*, bilateral lesions of the amygdala were accomplished on four *Ss*, and

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the remaining four were sham-operated *Ss*. Subjects were individually housed with free access to water and were maintained on a diet consisting of seven monkey pellets, roughly half of their usual ration. All feeding took place after completion of daily testing.

Surgery and Histology

The surgical preparation of *Ss* consisted of the following procedure. To perform the bilateral amygdalectomy a linear incision was made extending from the zygoma upward and parallel to the supraorbital ridge. The zygoma was removed and the temporal muscle split. The skull was opened by means of a burr hole, enlarged to expose the floors of the orbital and temporal fossae. The dura was opened in a cruciate manner. The temporal lobe was elevated by gentle packing in such a fashion that the middle cerebral artery could be followed down to the circle of Willis and the entire periamygdaloid region visualized. A 19-gauge blunt needle-stock sucker was inserted into the amygdala and the entire amygdaloid complex gradually removed. The medial extent of the lesion was signaled by brainstem and optic tract; the posterior extent by the temporal horn of the ventricle and the hippocampus. Bleeding was controlled by gentle packing with cottonoid patties; the wound was thoroughly rinsed with saline and the dura was closed with individual silk sutures. Muscle, subcutaneous tissues, and skin were closed in layers.

In order to remove the hippocampus, the cranial opening was similar to that above, except the incision was arched posteriorly over the ear. After the inferior temporal gyrus was exposed, the brain was gently elevated from the temporal fossa by packing with patties to expose the hippocampal gyrus. A small "window" was made in the gyrus and the hippocampus was exposed, identified, and removed by aspiration.

Sham operations were performed in the identical fashion except that no cerebral tissue was removed. Instead brain was retracted for several minutes and then allowed to settle back into place.

Following the termination of the experiment the animals were sacrificed and their brains perfused with saline and 10% formalin. The brains were frozen and cut at 50-μ intervals and stained with thionin according to the technique detailed by Sharer and Pribram (1962). The reconstructions of the brains of amygdalectomized *Ss* have already been presented (Bagshaw & Benzies, 1968). The reconstructions of the three brains of hippocampectomized *Ss* appear in Figure 1.

Apparatus

The subjects were trained in a modified version of the DADTA machine described in Pribram, Gardner, Pressman, and Bagshaw (1963). The apparatus consists of a small enclosure which effectively seals *S* off from the external environment and the experimenter. A 4 × 4 array of 16 depressable panels is imbedded in one of the walls, with a food cup located at bottom center. A one-way glass for subject viewing makes up most of another wall. The panels are constructed of clear plastic, and various stimuli can be projected onto them from projectors located to the rear. The stimuli appear as white patterns on a black background. Stimulus location is varied in a pseudo random manner so that the same stimulus rarely appears at the same location (panel) twice in a row, and will appear at all possible locations over a large number of trials. Control of stimulus presentation, recording of responses, and delivery of rewards (190-mg. Noyes banana pellets) is automatically governed by a specially programmed PDP-8 computer.

Procedure

Subjects were trained consecutively on four problems in which one stimulus was rewarded while either one, two, or four stimuli were unrewarded. The exact stimuli are difficult to describe verbally, and will be referred to in terms of the numbers accompanying the pictures in Figure 2. On all tests the stimuli were simultaneously projected onto the panels and *S* rewarded with one banana pellet if the positive stimulus was responded to (pressed). A press of any stimulus resulted in the disappearance of all stimuli for 5 sec., after which they were again presented, but at different locations. Daily sessions of 50 trials each were used and training continued on each problem until 45 correct responses had been made in a single session. The next problem then began on the following day.

On the first test the positive stimulus was "1" and the negative "2." The rewarded stimulus on the second test was "3" and the unrewarded were "4" and "5." On the third test "6" was rewarded while "7," "8," "9," and "10" were not. On the final test the positive stimulus was "11" and the negative "12." Learning was evaluated in terms of sessions to criterion including the session in which 45 or more correct responses were made.

Results

One Negative Cue

The first and last tests of the series involved one positive and one negative cue. Mean sessions to criterion for the three groups on the first problem were: sham operates, 4.0; amygdala lesions, 3.0; and hippocampal lesions, 3.67. On the last problem the means were: sham operates, 2.0; amygdala lesions, 1.25; and hippocampal lesions, 1.3. None of the intergroup differences even approached sta-

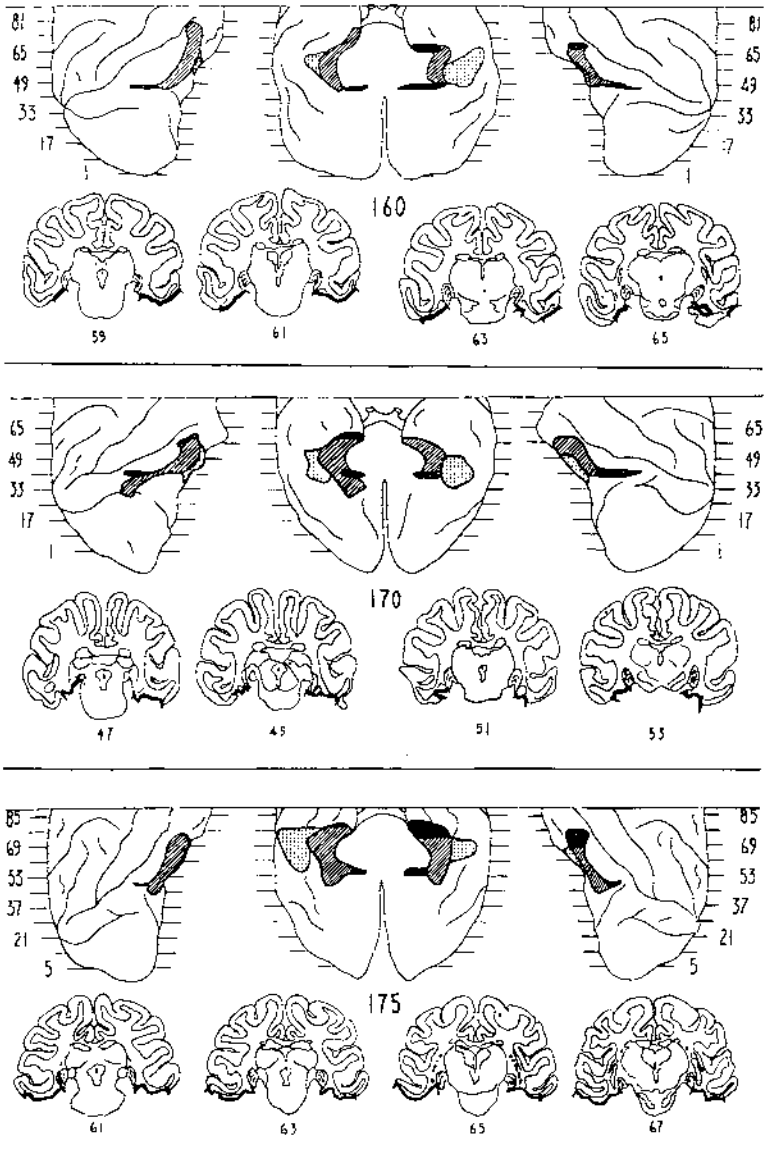

FIG. 1. Reconstructions and representative cross sections of the brains of the hippocampectomized monkeys. (Stippling indicates superficial lesions of the temporal cortex; striped area indicates the removal in the depth of the temporal lobe which includes the hippocampus; black indicates the spared remnants of the hippocampus.)

tistical significance (the largest t was .9) and overlap of scores was extensive. All *Ss* combined, however, learned the last problem in significantly fewer sessions than the first problem ($t = 4.7$, $p < .001$). Thus, there was either a marked learning set (improbable in these highly sophisticated *Ss*) or the last problem was much easier than the first for reasons unknown. In any case, some allowance must be made for this effect in the evaluation of performance on the intervening multiple-cue tests. The authors have chosen to use the mean of the two tests as an estimate of learning with one rewarded and one unrewarded cue.

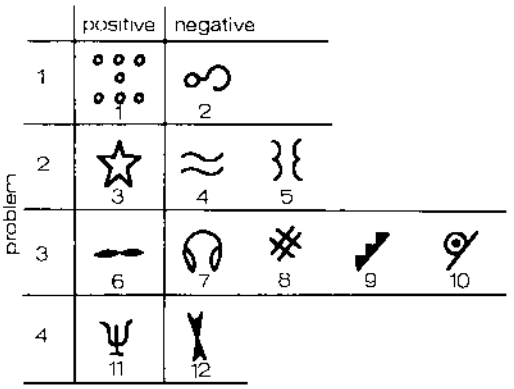

FIG. 2. Diagrams of the displays used in each problem with the identifying numeral shown in the right lower corner of each display.

Multiple Negative Cues

Mean sessions to criterion on the test involving two negative stimuli were: sham operates, 2.25; amygdala lesions, 2.5; and hippocampal lesions, 4.0. With four negative cues the means were: sham operates, 2.75; amygdala lesions, 2.75; and hippocampal lesions, 4.67. The combined mean for *Ss* with hippocampal removals on the multiple negative-cue tests was reliably higher than those of either sham-operated *Ss* ($t = 2.8$, $p < .25$, one-tailed) or the group with amygdaloid lesions ($t = 2.6$, $p < .25$, one-tailed). Differences on the two tests separately just fail to reach significance unless the two groups with presumably normal error evaluation systems are combined (their performance was indistinguishable). In that case the combined sham operates and the group with amygdaloid lesions had reliably lower means than *Ss* with hippocampal lesions on both the two negative-cue ($t = 2.7$, $p < .025$) and four negative-cue tests ($t = 2.5$, $p < .025$). Almost identical results were obtained using difference measures comparing performance on the multiple negative-cue tests with performance on the single negative-cue tests.

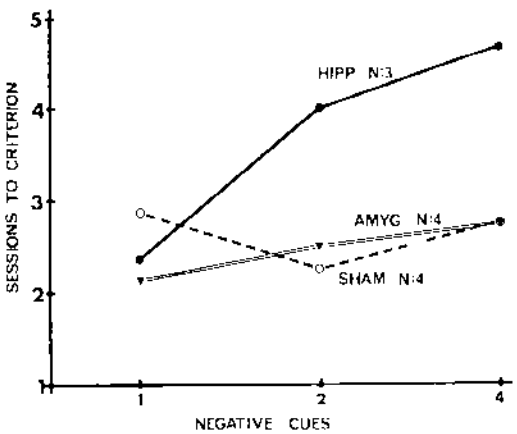

FIG. 3. Graph of the results of changing the number of negative cues in a set of discrimination problems.

Thus, as can be seen in Figure 3, all groups were virtually identical when only one negative cue was used, and sham-operated *Ss* and *Ss* with amygdaloid lesions behaved on all tests as if drawn from the same population. The only differences which even remotely approached significance were those between *Ss* with hippocampal lesions and those in the other two groups when more than one negative stim-

TABLE 1

DAYS OF SESSIONS TO CRITERION

S	One negative cue			Two negative cues	Four negative cues
	Test 1	Test 2	*M*		
Hippocampal lesions					
160	3	2	2.5	4	7
165	3	1	2.0	3	4
170	5	1	3.0	5	3
M	3.7	1.3	2.5	4.0	4.7
Sham or control group					
147	2	1	1.5	2	2
149	7	2	4.5	1	3
153	3	3	3.0	3	3
154	4	2	3.0	3	3
M	4.0	2.0	3.0	2.25	2.75
Amygdala lesions					
144	3	1	2.0	3	3
146	4	2	3.0	2	4
150	3	1	2.0	3	2
151	2	1	1.5	2	2
M	3.0	1.25	2.1	2.5	2.75

ulus was used. This evidence confirms the original hypothesis that the hippocampus is involved in the active reduction of errors while the amygdala is not. Scores for individual animals are shown in Table 1.

Discussion

It can be seen in Figure 3 that none of the groups appears to be as hampered by the additional negative stimuli as one might intuitively expect. This is especially true of the sham-operated group and the *Ss* with amygdaloid lesions to which it made little demonstrable difference whether there were one or many negative stimuli included in the problem. The *Ss* with hippocampal lesions also do not appear to be as slowed up as one might expect. Part of the reason for this is that on the four negative-cue test all stimuli were not responded to equally. Monkeys with hippocampal lesions virtually ignored Stimulus 9, pressing it only $\frac{1}{10}$ as often as the mean for the other three. In the remaining two groups this difference was not as pronounced, but Stimulus 9 was pressed only half as often as the mean for the others.

Using these figures it is possible to make a gross calculation of the degree of difficulty of each problem if performance were based on a purely positive reward-based system. In that case learning should be in large part evaluated against the probability of success by chance.[4] Learning by the group with hippocampal lesions fits such an assumption remarkably well, while that of the sham-operated and amygdalectomized groups does not appear to be at all related to the probability of chance success. This suggests that in these *Ss* some factor in addition to a purely positive or reward-based system was operative. The authors submit that this factor is the error evaluation system.

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[4] Assuming that the one negative-cue problem has a degree of difficulty of 1.0 (probability of .5), then the relative difficulty for the two and four cue tests would be 1.5 and 2.5. If the latter figure is modified in light of the data presented above, the difficulty sequence for the group with hippocampal lesions would be 1.0, 1.5, and 2.0, while it would be 1.0, 1.5, and 2.25 for the other two groups. Now if one divides the mean sessions to criterion on the multiple negative-cue tests by the mean for the single negative-cue tests, the progression for *Ss* with hippocampal lesions is 1.0, 1.6, and 1.9. This is a very good fit, indeed, to the theoretical progression above. On the other hand, no such fit is obtained for the other two groups; the progression for the group with amygdaloid lesions is 1.0, 1.2, and 1.3, while that for the sham operates is 1.0, 0.8, and 1.0.