

STUDIES OF THE FUNCTION OF THE AMYGDALOID COMPLEX IN *MACACA MULATTA**

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Abstract—Two groups of experiments are described. The first tested the ability of amygdalec-
tomized monkeys to perform behavior sequences. Impairment was limited to those sequences
which were not externally prescribed; i.e. amygdalectomized monkeys appear unable to make
choices within the context of some internally produced set. The second group of studies
tested directly the ability to develop sets. Amygdalectomized Ss failed to form discrimination
reversal learning set, an impairment produced by the split brain procedure in the amygdalec-
tomized hemisphere only. The conclusion reached is that the amygdala is important to choice
behavior dependent on the development of sets and that this formation of sets is unlikely to be
a "motor" phenomenon as typically conceived.

INTRODUCTION

THE EFFECT of temporal lobectomy on behavior [1] is by now well known. A complex of
changes, usually referred to as the Kluever-Bucy syndrome [2] results. Neurobehavioral
analysis has shown that the visual manifestations of this syndrome follow from interference
with the functions of temporal isocortex, while the changes in motivational-emotional
behavior can be ascribed to the "limbic" formations lying on the medial aspects of the lobe
[3]. The amygdala, especially, serve as foci or funnels for functions basic to motivation-
emotion [4] and so have received a great deal of attention from experimenters.

For the most part, the explanations given for the taming, the loss of fear, the alterations
in conditioned avoidance behavior which follow amygdalectomy have invoked the close
anatomical connection between the amygdaloid nucleus and hypothalamus. These ex-
planations gained force from the role of hypothalamic mechanisms in viscerio-autonomic
functions and the Jamesian view of emotions as viscerally based phenomena.

This explanation of the functions of the amygdala does not readily account, however,
for the results of experiments reported by SCHWARTZBAUM and PRIBRAM [5] showing lesions
of the amygdaloid complex to radically alter behavior in a transposition task. Having
been trained on brightness discrimination, normal monkeys responded to the relative
brightness of two novel cues while amygdalectomized monkeys responded to their novelty
only. Subsequent studies [6-8], have confirmed that amygdalectomy changes a rhesus
monkey's responsiveness to novelty.

A response to novelty must be made within a context of the familiar. It would seem
that the ability to develop and maintain a stable "familiar" behavioral set would be even
more important when the stimulus conditions and the required response to them become

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more complex. Simple discriminative choices which are not interfered with by amygdalotomy apparently do not sufficiently tax this ability to maintain set—probably because a stereotyped response is required in a simple repetitive situation. On the other hand, the difficulty might well be manifest where choice is not wholly given by the stimulus array facing the subject [9]. In such tasks “context” becomes more important; any particular required response of a sequence depends not only on the stimuli present but on the consequences of prior behavior. The present experiments were therefore undertaken to test monkeys on problems demanding sequential behavior and to probe further the importance of the amygdaloid complex to the utilization of prior experience.

BEHAVIORAL SEQUENCES

The first set of experiments were designed to investigate whether the amygdaloid complex is involved in sequential or iterative learning and, more specifically, whether there is a selective effect of amygdalotomy upon two types of sequential tasks. One type, in which the order of choice is prescribed by the experimenter, is called an “externally ordered” sequence. The other (the “internally ordered” task), requires the making of the second choice in the light of a first choice which is left to the discretion of the subject.

Method

Six immature bilaterally amygdalotomized rhesus monkeys and four “sham operated” controls were prepared for the first part of the experiment (externally ordered sequential discrimination), and a second set of three bilaterally amygdalotomized and three unoperated control monkeys were used in the second part of the experiment (internally ordered sequential discrimination). A computer controlled Discrimination Apparatus for Discrete Trial Analysis (DADTA) was used in all training [10]. The externally ordered sequential visual discrimination task involved the display of the letters, H and M, randomly over the sixteen panels of the apparatus. Each trial consisted of two presentations in which the stimuli were positioned exactly the same. Between each trial there was a *ten* second pause when the houselights were dimmed; between each presentation there was a *one* second pause when the houselights were blinked. If, on the first and second presentations, an “H” then an “M” were pressed, the animal was rewarded with a peanut. If an “H” was pressed on the first presentation and an “H” again on the second, the animal received no reward. If an “M” was pressed, there was no second presentation and no reward. Fifty trials per day were given until a criterion of 40 out of 50 correct was reached.

For the internally ordered sequential visual discrimination problem the task differed from the previous one in that a reward could be obtained in either of two ways. A “4” and an “8” appeared in a random fashion across the four center panels of the sixteen display panels. Either a “4” or an “8” on first presentation followed by the other on the second, would gain the reward. Pressing either two “4’s” in succession or two “8’s” in succession was not rewarded. Criterion performance was 40 out of 50 correct.

Surgery was performed according to a procedure outlined in PRIBRAM and BAGSHAW [3]. Reconstructions of the lesions for the first group of amygdalotomized animals is contained in BAGSHAW and BENZIES [7]. The reconstruction of lesions for the second group is presented in Fig. 1.

Results

The results of tests on the *externally* ordered sequential problem, (Table 1), show that both normal and amygdalotomized animals are *able* to learn the externally ordered task. There is a suggestion that the amygdalotomized animals perform the externally ordered sequence somewhat better than their controls. By contrast, the results obtained on the *internally* ordered sequence, (Table 1), show that the amygdalotomized animals were *unable* to learn the internally ordered task and had essentially extinguished responding in the situation after 2000 trials. The normal group learned in a median of 1850 trials.

It is noteworthy that neither the amygdalotomized animals nor the normal group preference for either method of obtaining a reward (i.e. 4, 8 or 8, 4).

BILATERALLY AMYGDALECTOMIZED ANIMALS

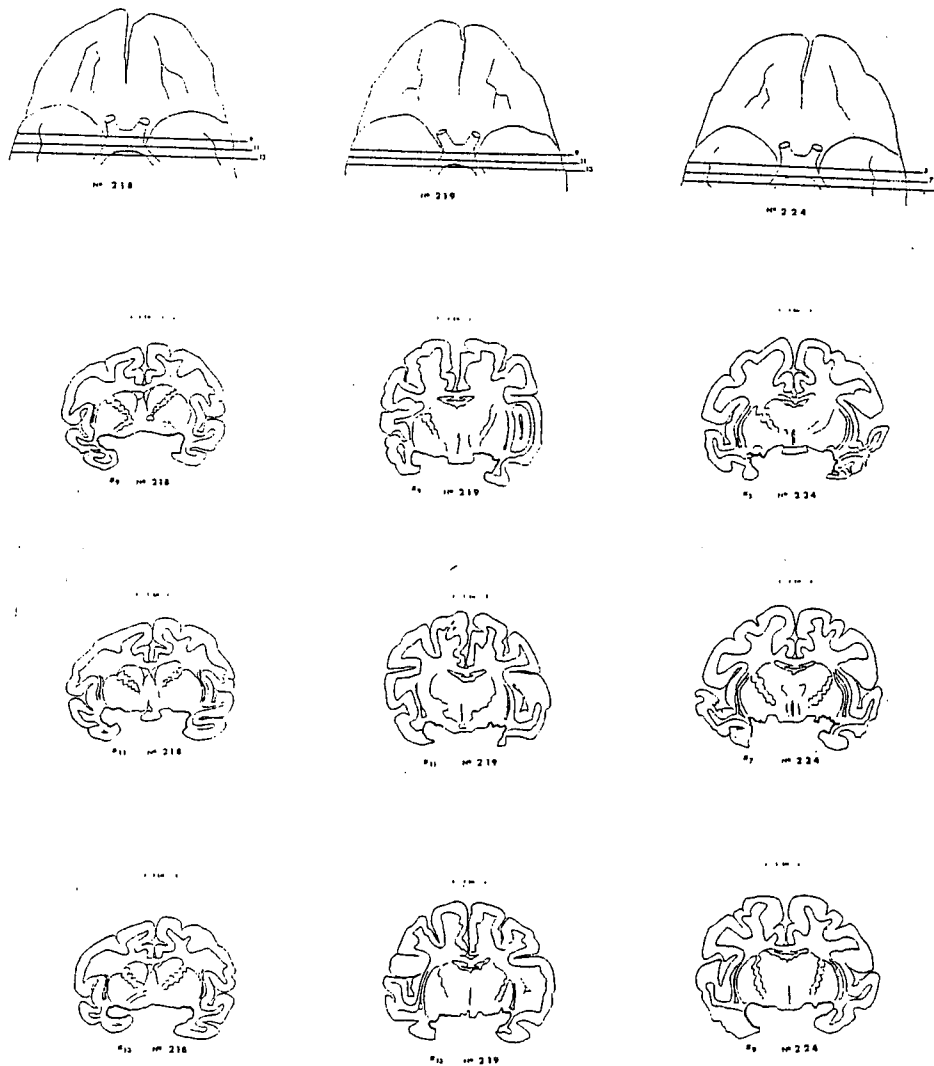


FIG. 1. Histology—Bilaterally amygdalectomized monkeys.

Discussion

The data obtained from the experiments involving amygdalotomy in monkeys reported here extend the suggestion that both frontal and limbic lesioned animals have difficulty with internally ordered but not externally ordered sequences. PINTO-HAMUY and LINCK [11] reported that lesions of the dorsolateral frontal cortex interfere with tasks monitored internally but not with those programmed by an external source. KIMBLE and PRIBRAM [12] document that monkeys with hippocampal lesions were impaired only on a task demanding self-ordering.

Table 1. Sequential tasks trials to criterion

	Externally ordered sequence					Internally ordered sequence					
					Mdn					Mdn	
Normal group	991	1452	2043	2087		1498	1850	1781	1900	1850	
Amygdalectomized group	526	805	837	1033	1448	1741	935	>2000	>2000	>2000	>2000

The indication that amygdalectomized animals are somewhat superior in learning ability on the externally ordered task, is probably due to an inability to transfer the prior training they had received. Their superiority can be considered, therefore, as a "superiority by default."

With the externally ordered task each choice is dictated by the problem conditions. The internally ordered task, on the other hand, requires a decision to be made to perform within the context of what has been decided upon in the past, i.e. on the first presentation; *and this decision is not dictated by the problem conditions*. To learn the internally ordered sequence, therefore, the animal must make both "conjunctive" (1st response) and "exclusive OR" (subsequent response) choices. Since the two groups do not differ in their preferences for either the 4, 8 or 8, 4 sequence, this would indicate that a *conjunctive* "OR" change is made by both groups. The results of the externally ordered sequential task show that amygdalectomized subjects can make the *exclusive* "OR" choice as well. Thus, the deficit shown by the amygdalectomized subjects on the internally ordered task indicates an inability to couple these two relationships: i.e. to make it possible for a second response to be performed within the context of a choice of first response. The question then might be asked: how does amygdectomy affect the ability to couple present responses to the context of past choices. The experiments to follow attempt to answer this question by using a discrimination-reversal learning set situation.

DISCRIMINATION REVERSAL LEARNING SET

Early investigations of the function of the amygdaloid complex have focused on its role as a monitor of responses. This emphasis is based either on the belief that in a general sense every brain structure affects the organism's behavior or on the belief that the amygdaloid complex is positioned on the post-decisional "output-side" of the brain. This latter view stems from the fact that many classical neuroanatomy texts include the amygdaloid complex as a part of the basal ganglia.

There is some merit to this view. It certainly is the case that there exists a functional connection of some kind between the amygdala and the caudate nuclei [13]; and the amygdaloid nucleus and the putamen lie next to each other. However, the caudate nucleus itself would appear to be involved in visual information processing [14] thus calling into question the conception that the basal ganglia are concerned exclusively with motor functions.

The results of the experiments reported above also call into question the view that the amygdaloid complex is primarily a "motor" structure in the usual sense of the conception. One way in which contexts of past responses are established is through the acquisition of learning "sets". The method of HARLOW [15] has usually been used to test for learning set. This method introduces a new problem before any criterion of performance has been reached

i.e. a set number of trials is given per problem. From the present interest this paradigm must be changed, however, and a criterion must be attained in order that the opportunity be presented for a stable "context" to be achieved.

SCHWARTZBAUM and POULOS [16] have shown that amygdalectomized rhesus monkeys are "seriously impaired" on reversal learning to a criterion of 85% correct responses using the WGTA. The number of trials to criterion is not stated. Only the failure to exceed chance levels within the first 20 trials of the last eight reversals is reported. It is unclear whether this slow start was followed by later rapid recovery within each set. As each session consisted of 20 trials, this seems hardly a lengthy enough period upon which to base conclusions concerning the ultimate formation of a learning set or the ability to learn in an abstract sense. Thus the technique of establishing reversal learning set was once more brought to bear in the current endeavour.

The study of DOWNER [17] also places the function of the amygdala somewhat closer to the input rather than the output side of the brain. Downer used a split-brain unilateral amygdalectomized preparation and reported "taming" only in the amygdalectomized hemisphere. Only two monkeys had been studied at the time of the initial communication, (one with unilateral temporal pole removal and the other with unilateral amygdalectomy), and no subsequent report has been made. Further, no quantitative techniques of behavioral assessment were used.

The following experiment tests the effect of amygdalectomy on behavior in such a manner that an estimate could be reached concerning whether its influence was primarily on input or output mechanisms. To this end a unilateral removal of the amygdaloid nucleus in a brain split by sectioning the optic chiasm, anterior commissure and corpus callosum was undertaken. Thus, the performance of the normal hemisphere could be pitted against that of the amygdalectomized hemisphere.

Method

The three immature amygdalectomized rhesus monkeys and three normal animals previously tested on the internally ordered sequence were used in this experiment. Also, three naive immature rhesus monkeys were used as "split-brain" animals to provide six hemispheres, one intact and one amygdalectomized in each animal. Controls for the split-brain animals were provided by the three bilaterally amygdalectomized animals and the three normal animals. Thus, three normal animals and three normal hemispheres were pitted against three amygdalectomized animals and three amygdalectomized hemispheres.

The surgery for the split-brain animals was performed in two stages. First the split in the corpus callosum, anterior commissure and optic chiasm was achieved in all three monkeys. After sufficient recovery from this surgery, the left hemisphere was amygdalectomized according to a procedure described in the earlier experiment reported here.

The split brain operation was conducted as follows: after trephine holes had been bored in the skull in a ring around the cranium, by the use of a Gigli saw a vertex skull flap was turned inferiorly on the left side. After dural incision, gentle minimum pressure kept the hemispheres sufficiently apart for the incision of the anterior corpus callosum and optic chiasm under direct vision. The chiasm was incised with a small corneal knife, care being taken to spare small blood vessels of the hypothalamic region as well as the more important Circle of Willis. Then the posterior part of the corpus callosum was cut. The dura was closed with interrupted silk sutures. Reconstructions of the lesion are shown in Figure 2.

The reversal training ("3" vs. "6") was given to the experimental animals and hemispheres at the rate of 50 trials a day in the DADTA. The stimuli displayed on the 16 panels of the apparatus were one "3" and one "6". The positioning of the stimuli varied randomly over the 16 panels on every trial. Half the animals commenced training with the "3" reinforced; half the animals with the "6" reinforced. After a criterion of ten consecutive correct responses was reached, the reward condition was reversed. This procedure was continued until fifteen reversals had been accomplished.

Not only were counts made of the number of trials to criterion of ten consecutive correct responses, but counts were made also of the number of trials to 2, 3, 4 . . . 9 consecutively correct responses. These levels are not criteria in the sense that their attainment initiated a reversal—no change was made in the situation, but will hereafter be referred to as "criteria".

SPLIT-BRAIN UNILATERAL
AMYDALECTOMIES

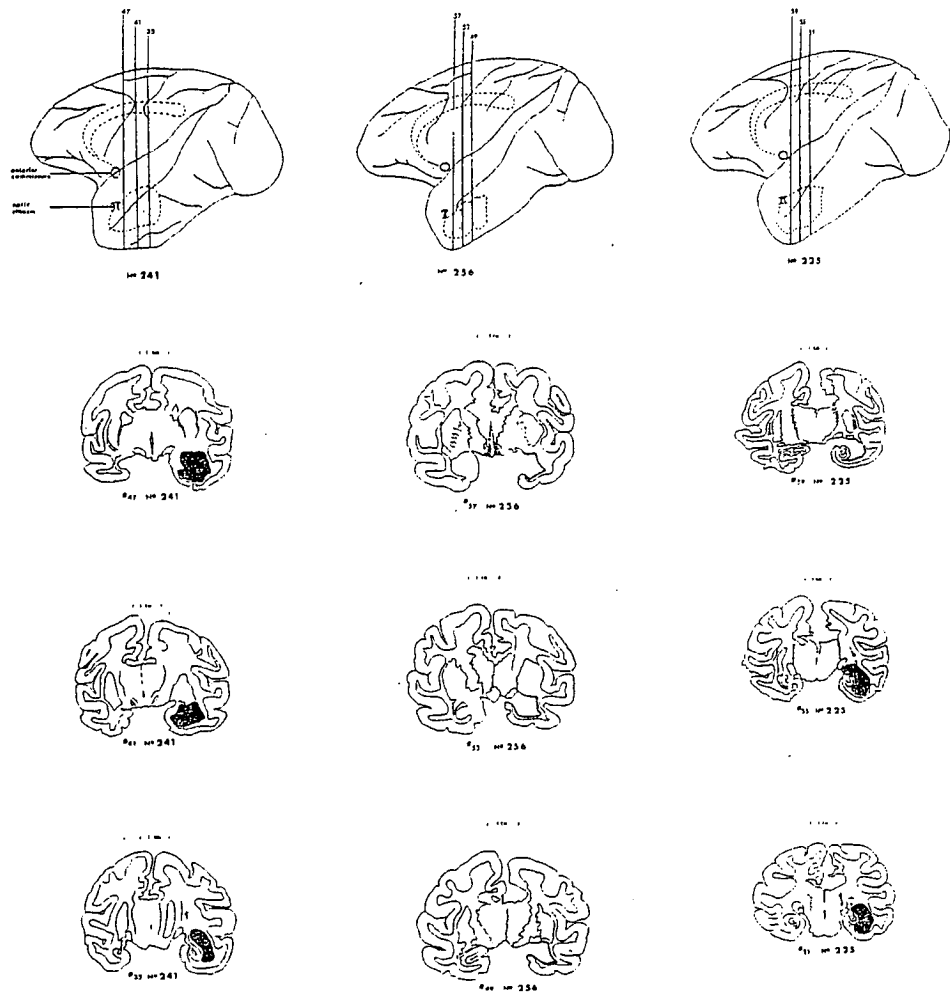


FIG. 2. Histology—Split-brain unilateral amydalectomized monkeys.

To test the split-brain monkeys on this task an occlusive contact lens was fitted to the appropriate eye just before each session. Once fitted the lens caused no irritation. One normal hemisphere and two amydalectomized hemispheres were utilized initially. Testing was continued until the normal hemispheres had completed ten reversals. At this point, the amydalectomized hemisphere of the animal previously using its normal hemisphere and the normal hemispheres of the animals previously using their amydalectomized hemispheres, were trained until the number of trials taken by the initially trained normal hemisphere was achieved.

Results

The bilaterally amydalectomized subjects and the amydalectomized hemispheres fell behind the control group and normal hemispheres at all the consecutive correct response ("criterion") levels after the 8th reversal (Figure 3 displays graphs for 7, 8, 9 and 10 "criteria"), (U test, $p < 0.01$). There is no significant difference between the normal and the

amygdalectomized groups up until the 8th reversal, which is marked by a straight line in the graphs. However, some of the amygdalectomized hemispheres showed an even greater retardation which was manifest even during the initial phases of reversal training (see below).

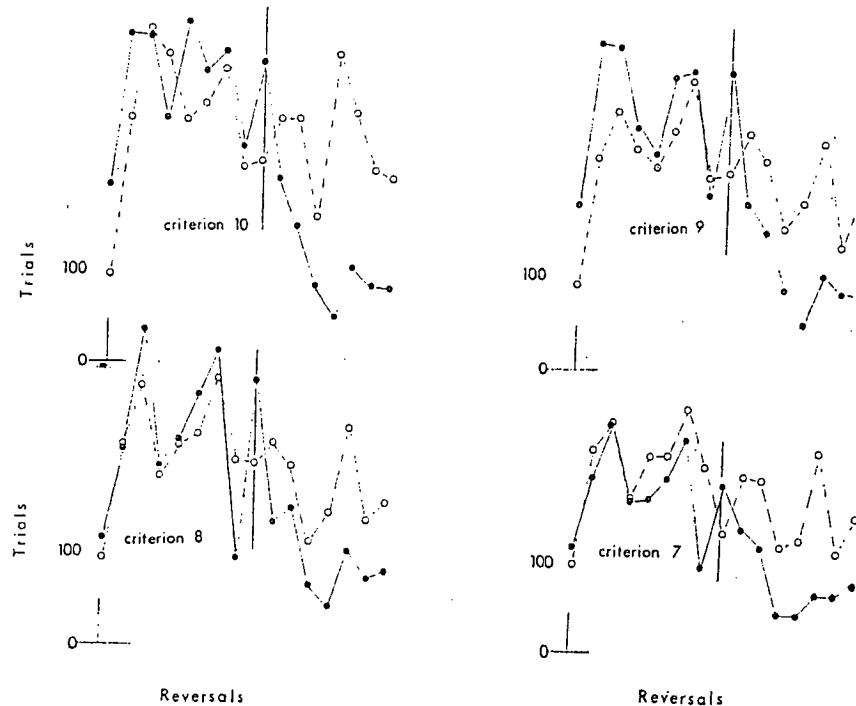


FIG. 3. Number of trials across the training task and 15 reversals to the various criterion levels. Straight line indicates normal group; hatched line indicates amygdalectomized group. Straight vertical line indicates 8th reversal.

Figure 4 shows percentage saving scores over the fifteen reversals for "criteria" of 5-10. The amygdalectomized group fail to show any savings at all, whereas the normal group eventually attain performance levels superior to their initial learning. For "criteria" 10 and 9, there is no overlap anywhere in the learning curves of the two groups. In all cases, after the 8th reversal, the difference between the two groups is statistically significant using nonparametric methods.

Contrasting the deficit obtained here with amygdalectomized operates is the capability of other brain lesioned rhesus monkeys to learn a discrimination-reversal learning set.

Figure 5 was prepared from reversal data provided by Dr. K. H. PRIBRAM [18]. Of the three groups, one was unoperated, a second had anterior frontal and a third, inferior temporal lesions. All three groups of monkeys are shown to develop learning-set formation to a criterion of 10 consecutive correct responses after a peak of errors on the second reversal.

Reversal learning-set curves of trials to criterion are negatively accelerated. Figure 6 was prepared from regression analysis of the slopes of the curves obtained at the various criteria levels. The regression indices are significantly different in the two groups ($t=3.9$; $p<0.01$). The normal animals show decreasing regression indices; at the higher criterion levels, there is increasing improvement. The amygdalectomized group, on the other hand,

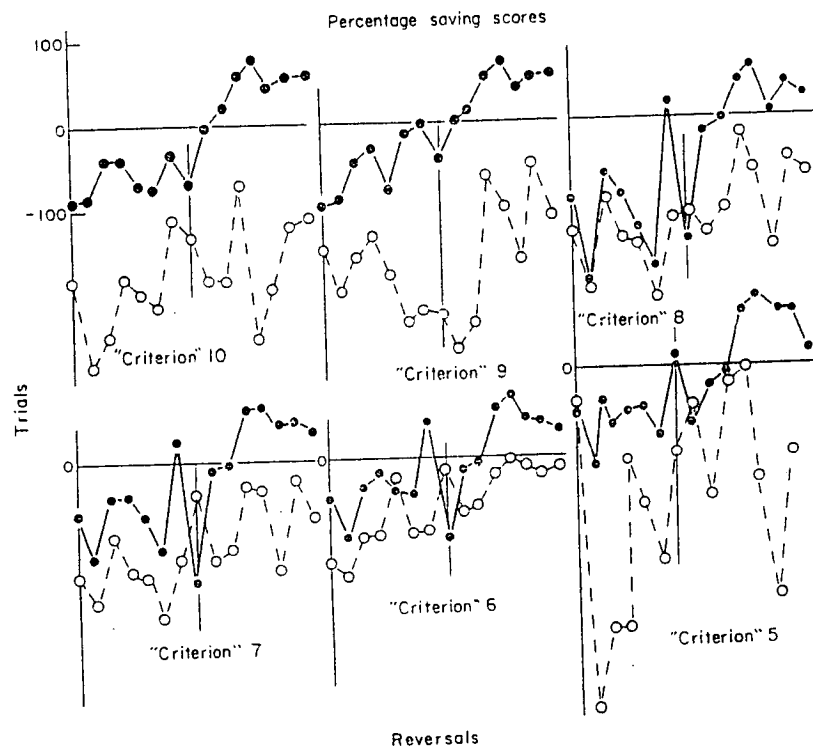


FIG. 4. Number of trials across the training task and 15 reversals to the various criterion levels using percentage saving scores. Straight line indicates normal group; hatched line indicates amygdalotomized group. Straight vertical line indicates 8th reversal.

show no change in the regression indices, which might possibly indicate that the same process of learning is operating at all levels of criteria. More "weight" is, therefore, given by the normal animals to the effect of learning at the higher criterion levels. An additional point to be made concerning Fig. 6 is that the magnitude of the slopes of the curves differ between groups.

Table 2 displays the intercepts on the y -axis obtained from regression analysis. As can be seen, in all cases there is superior performance by the normal group indicating a steeper decline in the error curve over trials.

Some additional facts about the split-brain monkeys are of interest: in 4100 trials using the normal hemisphere, one animal was able to complete a training task and ten reversals—the tenth reversal being solved in six trials. In the same number of trials another animal, utilizing its amygdalotomized hemisphere, had completed only one reversal. Using the amygdalotomized hemisphere, the first animal then extinguished to testing during the second reversal after 2400 trials, whereas using its normal hemisphere, the second animal had improved its performance to complete the training task and two reversals in this number of trials. Similar performances by the normal and amygdalotomized hemispheres of the third animal were also obtained. Total reversals and various mean scores are shown in Table 3.

It should be noted that two monkeys were initially trained with visual input to the amygdalotomized hemisphere occluded and after completion of the tenth reversal, training

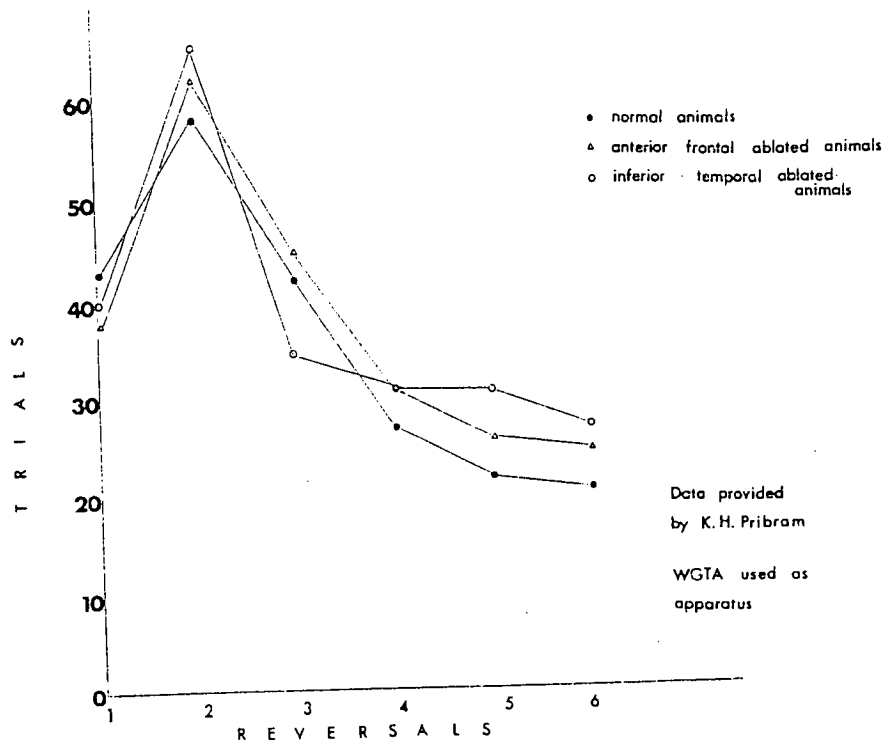


FIG. 5. Trials to criterion on reversal task with normal, anterior frontal and inferior temporal lesioned monkeys.

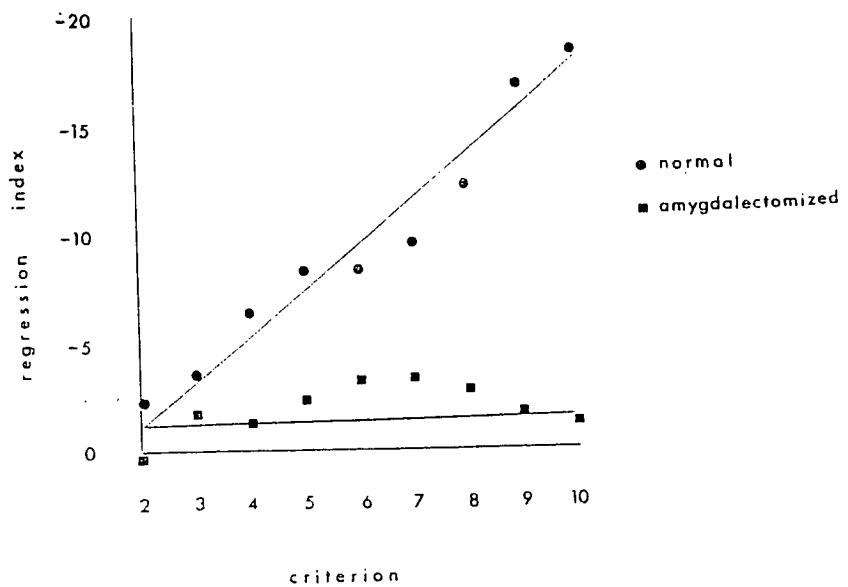


FIG. 6. Plot of points from regression analysis.

Table 2. Intercepts on y-axis from regression analysis

Criteria	Normal group intercept	Amygdallectomized group intercept
2	+35.4	+13.8
3	+64.5	+53.0
4	+120.5	+79.8
5	+167.2	+120.0
6	+187.5	+164.3
7	+218.3	+202.0
8	+268.2	+213.8
9	+341.8	+226.8
10	+367.0	+257.8

Table 3. Performance of normal vs. amygdallectomized hemispheres on reversal problems

Total No. of reversals in 6500 trials:	
Normal hemispheres	11
Amygdallectomized hemispheres	2
Mean trials per reversal:	
Normal hemispheres	259
Amygdallectomized hemispheres	835
Mean No. reversals per 1000 trials:	
Normal hemispheres	4
Amygdallectomized hemispheres	1
Mean No. errors per reversal:	
Normal hemispheres	195
Amygdallectomized hemispheres	374
Mean No. errors on first reversal:	
Normal hemispheres	134
Amygdallectomized hemispheres	357
Mean % errors of total No. trials per reversal:	
Normal hemispheres	55%
Amygdallectomized hemispheres	52%

began with visual input to the normal hemisphere occluded. The reverse procedure was adopted for the other animal. Whichever way testing took place, there is dramatic impairment when visual input is restricted to one amygdallectomized hemisphere.

Gross observations of the behavior during testing support the performance scores. With visual input to the normal hemisphere occluded, all animals behaved similarly to the bilaterally amygdallectomized animal described by PRIBRAM and BAGSHAW [3], i.e. with a lack of fear coupled with a lack of aggression ("tameness"). If, however, the monkey was touched, this "tameness" was immediately replaced by the attack response of the normal

rhesus monkey. When visual input to the amygdalotomized hemisphere was blocked, the preparation appeared to behave as a normal animal. When testing in the apparatus with either hemisphere occluded, the animal would systematically search the sixteen panels for the stimuli when they appeared on the occluded side. With visual input to both hemispheres, they did not, however, appear normal. Both aggression and fear were reduced, which is in contrast to the behavior shown when the visual input to the lesioned side was blocked. The animals appeared to sample the world with both eyes and due to their more lengthy deliberations appeared somewhat vacillating with respect to the weight given either visual input. The gaze of one animal, in particular, was noticeably abnormal in that both eyes did not appear to be functioning in unison. In agreement with DOWNER's [19] finding, the preparations appeared to use the arm contralateral to the visual input more often.

Discussion

It has been shown here that both bilaterally amygdalotomized rhesus monkeys and amygdalotomized hemispheres of split-brain unilaterally amygdalotomized rhesus monkeys do not form a discrimination-reversal learning set. Normal rhesus monkeys and normal hemispheres of split-brain unilaterally amygdalotomized rhesus monkeys are able to do so.

It is known that transfer of training is impaired with amygdalotomized animals [5, 20] and our own data, (cf. the external sequence problem) support this view. The result obtained in the reversal problem indicates, in addition, that the transfer involved in the formation of learning sets—at least those used in mastering a reversal problem—is impaired by amygdalotomy. This is especially evident from the regression analysis.

The results from the split-brain unilaterally amygdalotomized preparations indicate clearly that the amygdaloid complex is concerned with the processing of input. This suggests that the difficulty amygdalotomized subjects have in performing internally ordered behavior sequences and in forming reversal learning sets is due not to interference with motor performances *per se* but to interference with some aspect of a decisional mechanism. The results of these experiments indicate that the locus of this interference lies in placing the stimulus in proper context. According to this analysis, then, the difficulty experienced by amygdalotomized monkeys occurs in making the present relevant to past experience.

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Résumé—Deux groupes d'expériences sont décrits. Le premier teste la capacité de singes amygdectomisés d'accomplir des séquences comportementales. Le trouble est limité aux séquences qui ne dépendent pas des prescriptions "extérieures", (déterminée par les conditions du problème); c'est-à-dire que les singes amygdectomisés se révèlent incapables de faire un choix dans le contexte de toute série "intérieurement" déterminée. Le second groupe d'études testait directement la capacité de développer des séries. Les singes amygdectomisés échouaient à constituer une attitude d'apprentissage de renversement de discrimination. Ce déficit n'était produit par la méthode du split-brain que sur l'hémisphère où avait été pratiquée l'amygdectomie. On aboutit à la conclusion que l'amygdale est importante dans le comportement de choix dépendant du développement des séries et que cette formation de séries a peu de chance d'être un phénomène "moteur" tel qu'il est conçu typiquement.

Zusammenfassung—Es werden 2 Gruppen von Experimenten beschrieben. Die erste Gruppe, bei der die Fähigkeit amygdalektomierter Affen, Verhaltensfolgen auszuführen, geprüft wurde, bestand aus 2 Versuchen. Bei dem einen mußten die Affen die Buchstaben H und M erkennen, die von dem Versuchsleiter immer in derselben Reihenfolge dargeboten wurden. In dem anderen Versuch wurde entweder eine 4 oder eine 8 gezeigt und der Affe mußte dann, um die Belohnung in Form einer Erdnuß zu erhalten, als zweite Ziffer die nicht dargebotene drücken. Amygdalektomierte Affen erwiesen sich als unfähig, diese zweite Aufgabe zu lösen. Bei der Reihenfolge nicht vom Versuchsleiter vorgegeben wurde, sondern die Wahl aus dem Zusammenhang her-aus getroffen werden mußte.

Die zweite Gruppe von Experimenten prüfte die direkte Fähigkeit, Verhaltensfolgen zu entwickeln. Amygdalektomierte Affen waren nicht imstande, Umkehrvorgänge bei den zu erlernenden Verhaltensfolgen zu unterscheiden (nach 10 aufeinanderfolgenden richtigen Antworten wurde die Reihenfolge der dargebotenen Ziffern 3 und 6 umgekehrt). Beim Split brain-Experiment zeigte sich die Störung nur an der amygdalektomierten Hemisphäre. Es wird daraus geschlossen, daß der Nucleus amygdalae wichtig für die Wahl des Verhaltens ist, wenn dieses davon abhängt, Handlungsfolgen zu entwickeln, und daß es unwahrscheinlich ist, daß diese Ausbildung von Handlungsfolgen ein motorisches Phänomen ist, wie man annahm.