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# DECISIONAL ANALYSIS OF THE EFFECTS OF LIMBIC LESIONS ON LEARNING IN MONKEYS

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In a 1969 study, K. H. Pribram, R. J. Douglas, and B. J. Pribram came to the hypothesis that behavior during discrimination learning and reversal is under control of two competing variables: the patterned cues to be discriminated and the noncontingent schedule of reinforcement. The current study using a modified decision theoretic procedure shows that in fact these two variables are operative and that noncontingent reinforcement produces a strong position bias against discriminating. This bias is quantitatively more easily overcome by normal subjects than by monkeys with hippocampal-amygdala lesions though the strategy and tactics used are the same for both groups. Thus, hippocampus and amygdala are shown to influence attention through mechanisms that regulate motivational bias.

Recently, Pribram, Douglas, and Pribram (1969) reported that monkeys with both hippocampus and amygdala bilaterally removed (hip-am ablations) showed a peculiar deficit in the original learning and reversal of a pattern-discrimination task. During the acquisition phase of the experiment, the experimental subjects, when compared to their controls, showed a prolonged period of chance performance before they began to respond differentially to the rewarded cue. Once discrimination commenced they reached criterion normally. During reversal training the hip-am ablated monkeys extinguished their responses to the previously rewarded cue as readily as did the intact subjects. But, as in acquisition, the experimental subjects performed at chance for a long period before responding to the reversed contingencies. Again, once discrimination commenced, criterion was achieved as rapidly as by the unoperated controls. Thus, the major difference between the performance of the experimental and intact monkeys during both original and reversal learning was a long period of chance performance.

Pribram et al. (1969) suggested that this period of chance performance results from the fact that monkeys with hip-am ablations were unable to keep their attention fixed on the relevant stimulus dimension long enough during periods of relatively random reinforcement such as occur at the beginning of original learning and after the extinction phase of reversal training. Instead, they give up attending (observing) though they continue responding, which apparently comes under the control of a noncontingent reinforcement schedule (50% variable ratio).

The present experiment, using the same subjects, was undertaken to replicate and to extend the earlier study. The aim was to gather more data which could be subjected to a variety of analytic procedures that would test the suggested hypothesis. Especially important, a modified response-operator-characteristic technique derived from signal-detection theory was instituted in an attempt to determine whether the attentional deficit of the hip-am monkeys is due to a change in selective capacity (discriminating the stimulus pattern from noise) or to a change in the motivational bias that alters the response to that stimulus pattern.

## METHOD

### Subjects and Lesions

The subjects were eight adolescent rhesus monkeys individually housed with free access to water. After behavioral testing they were fed once per day with Purina monkey pellets and fruit of sufficient quantity to maintain normal growth and reliable responding for the duration of their daily test sessions. Four monkeys had been subjected to

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bilateral removal of the amygdala and hippocampus through direct visual identification and constituted the experimental hip-am group (Figure 1). Details of the surgical procedure have been reported elsewhere (Douglas & Pribram, 1966). The remaining four monkeys were unoperated and served as an intact normal control group. However, one unoperated monkey died shortly after the initiation of these experiments, thus reducing the control group to three subjects. This placed considerable strain on the statistical procedures that were used to determine the reliability of the results obtained. The deceased control monkey was not replaced, however, since both the hip-am and
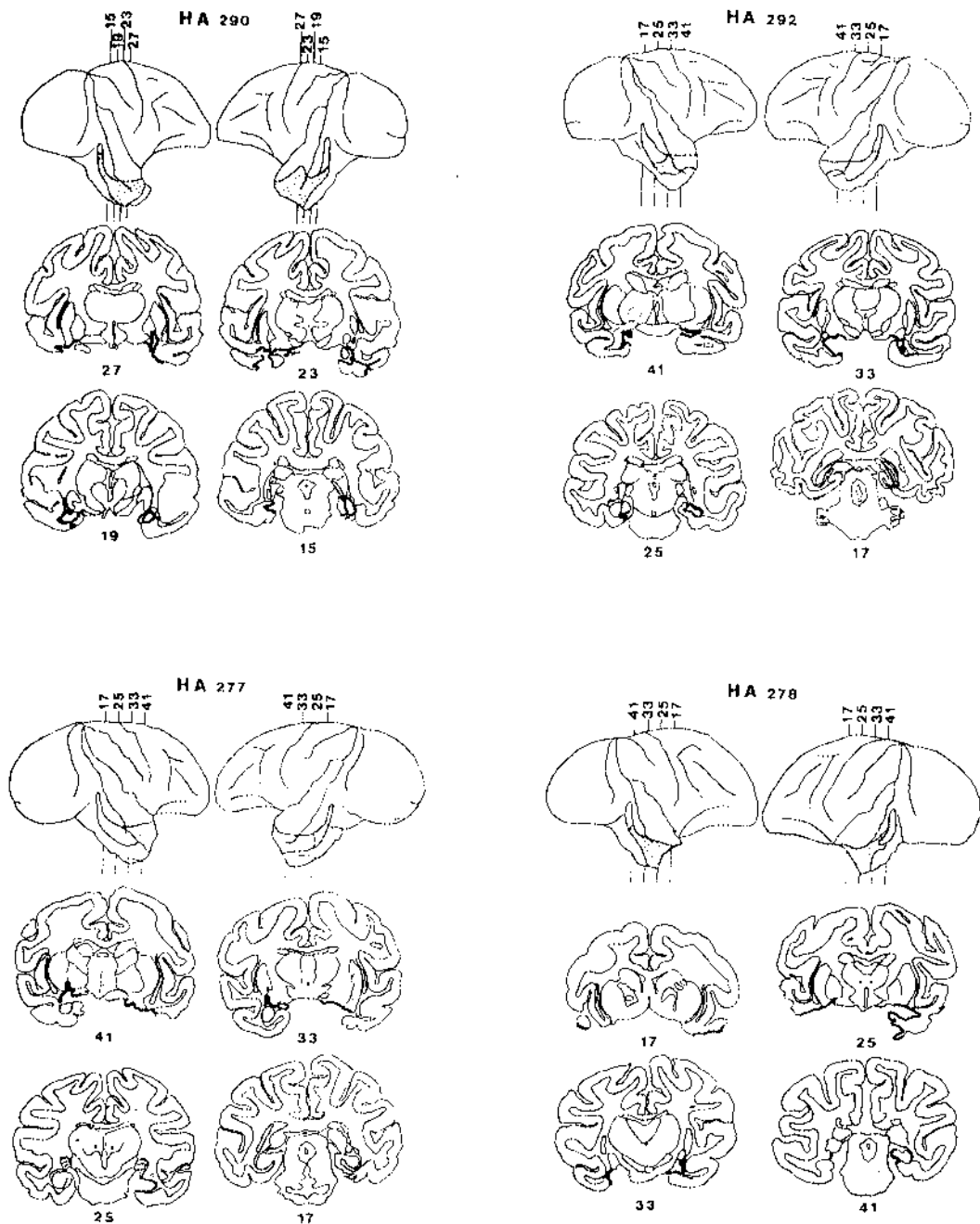


FIG. 1. Reconstruction of hip-am lesions. (Strippling indicates spared hippocampus; crosshatch, the lesion. On cross section, lesion border is indicated by heavy black.)

intact monkeys were those used in the earlier study (Pribram et al., 1969); and thus, it was very difficult to provide a new subject with identical experience.

## Apparatus

All testing was done with the DADTA III system described in detail elsewhere (Pribram, 1969). The animal-testing unit consisted of an enclosure with one of the sides a $4 \times 4$ matrix of 16 translucent panels with a food cup below. The discriminanda were lighted numerals projected from the back of each panel. Stimulus pattern and position were controlled by a PDP-8 computer which also recorded and collated response parameters such as stimulus choice, the position of the panel pressed, the latency of the response and whether or not the response was correct and rewarded.

## Procedure

All subjects received the following training regimen: pretraining, pattern discrimination, two successive reversals using a strict criterion, and five subsequent successive reversals to a lax criterion.

Since the monkeys had already been trained on pattern-discrimination and reversal paradigms, it was not necessary to put them through an extensive shaping and pretraining program. However, the long interval between the end of Pribram et al.'s (1969) study and the beginning of the present experiment made it expedient to rehearse the shaping procedure. On the first day (50 trials) 4 of the 16 panels pseudorandomly displayed the numeral "1," the other 12 panels remaining blank. On the four subsequent 50-trial blocks, only two instead of four panels displayed the 1. During these five pretraining sessions, the depression of an *unlit* panel was recorded, but did not affect the display or advance the program to the next trial. A press of a panel displaying a 1 produced the delivery of a 190-mg. Noyes banana pellet, the initiation of a constant 5-sec. intertrial interval, followed by a new stimulus display. The five pretraining sessions were sufficient to ensure that all monkeys were responding consistently with short response latencies.

For pattern-discrimination training the numerals "3" and "8" were simultaneously displayed; the other 14 panels remained blank. Unlike pretraining, however, the stimuli did not appear randomly over all panels. Rather, the display was restricted to the panels of the left and right columns of the DADTA matrix with the middle two panel columns always blank. During a trial the 3 and 8 numerals were displayed randomly on one of the four panels of either the left or right column, the remaining numeral, on one of the four panels of the opposite column. Thus, stimulus position was determined randomly on each trial with the constraint that only one of the stimuli appeared in each of the two end columns and that each stimulus appeared in each column on 50% of the daily 50-trial sessions.

The daily 50-trial blocks were continued until the subjects pressed the 3 panel 90% on 3 successive days. This strict criterion was chosen to assure that all vestiges of position bias were eliminated before the monkeys were considered to have learned the pattern-discrimination task.

The first and second discrimination reversals began on the day following the attainment of criterion and involved similar procedures. (For the first reversal the 8 was rewarded; during the second reversal, the 3.)

The subsequent five reversals were identical to the first two reversals except that a more lax criterion was adopted. The monkeys were advanced to the next reversal after only one 50-trial session in which they responded 90% to the reinforced stimulus.

## RESULTS

### Pretraining

All monkeys retained aspects of their previous experience. When introduced into the apparatus during the first pretraining session they immediately began to press panels with lit-panel depressions predominating. In fact, very few blank-panel presses occurred during any of the five pretraining sessions. Unlike original shaping, there were no reliable differences in the number of blank-panel presses between the experimental and intact monkeys ($Mdn = 4$, $Mdn = 6$, respectively) during pretraining.

### Analysis by Trials and Errors

The results of the discrimination problem are summarized in the first column of Table 1. As in original acquisition the lesion produced a significant learning deficit, the hip-am monkeys requiring over four times as many trials as the intact subjects to reach the lax criterion. The difference proved to be statistically reliable ($p < .03$) according to a Mann-Whitney $U$ test. Unlike original acquisition, however, we found that rate of blank-panel presses was not different for the two groups. No monkey exceeded a rate of more than one blank press per day over the acquisition session. Once monkeys reached the lax criterion during pattern-discrimination acquisition, they went on to reach the strict criterion after two successive sessions. The only exception was one hip-am subject that required 1,400 addition trials to reach the

TABLE 1

Mean Number of Trials to Criterion and Mean Reversal
Ratios for the Hip-Am and Intact Groups

| Group | Acquisition | | Reversal | | | | | | | | |
| | Lax | Strict | 1 | | 2 | | 3 | 4 | 5 | 6 | 7 |
| | | | Lax | Strict | Lax | Strict | Lax | Lax | Lax | Lax | Lax |
| Mean no. of trials to criterion | | | | | | | | | | | |
| Hip-am | 675 | 1100 | 1588 | 2138 | 1113 | 1438 | 875 | 575 | 563 | 450 | 513 |
| Intact | 150 | 250 | 250 | 350 | 200 | 300 | 183 | 183 | 183 | 200 | 167 |
| Mean reversal ratios | | | | | | | | | | | |
| Hip-am | — | — | — | 2.6 | — | 1.8 | 1.3 | .8 | .9 | .7 | .7 |
| Intact | — | — | — | 1.4 | — | 1.2 | .7 | .7 | .7 | .8 | .7 |

Note. Reversal ratios were calculated by expressing the number of trials required to reach the strict criterion for the first two reversals and the lax criterion for the five remaining reversals, as a ratio of the number of trials to reach the strict criterion during acquisition.

strict criterion after having reached the lax criterion.

Table 1 also summarizes the results of the seven successive reversals. It can be seen that the hip-am subjects required significantly more trials to reach the lax criterion than the intact monkeys over all the reversals ($p < .03$; Mann-Whitney $U$ test). Moreover, in the first two reversals, the hip-am subjects showed a marked difficulty in reaching the strict criterion even after the lax criterion was acquired. Whereas all the intact monkeys required only the minimum 100 trials to reach the strict criterion after the lax, only one hip-am in the first and a different experimental monkey in the second reversal were able to accomplish this. This difference was reliable at the .06 level according to a Mann-Whitney $U$ test.

It is possible that the significant differences in the reversal performance of the experimental and intact monkeys could be attributed to their initial differential abilities to acquire the pattern-discrimination task. Thus, the animal's reversal performance was adjusted to take account of their ability to perform the pattern discrimination by expressing trials to criterion on successive reversals as a ratio of the number of trials to reach the strict criterion during acquisition. The results of this analysis are also summarized in Table 1. It can be seen

that higher ratios than those shown by the intact monkeys were again found for the hip-am subjects during the initial two reversals. However, the ratio differences between normal and experimental monkeys rapidly decrease during the initial two reversals, with a slower rate of decrease apparent during the later reversals. There was only a single overlap in group ratios during the first reversal, but over half the hip-am animals showed lower ratios than the intact subjects by the seventh reversal. Overall group differences reached the .06 level of significance according to a Mann-Whitney $U$ test.

To demonstrate whether the acquisition and reversal data of the present study were comparable to those of Pribram et al. (1969), we used the same method of analysis as they did, i.e., the method of successive criteria. This analysis (as shown in Figure 2) assessed the number of trials required by hip-am and intact monkeys to approach the strict criterion in successive 10% increments in performance. This figure indicates that, below the 50% level of performance during acquisition and reversal, both experimental and intact monkeys improved at comparable rates. The major differences in performance between hip-am and intact monkeys thus became apparent only after the 50% level of performance had been
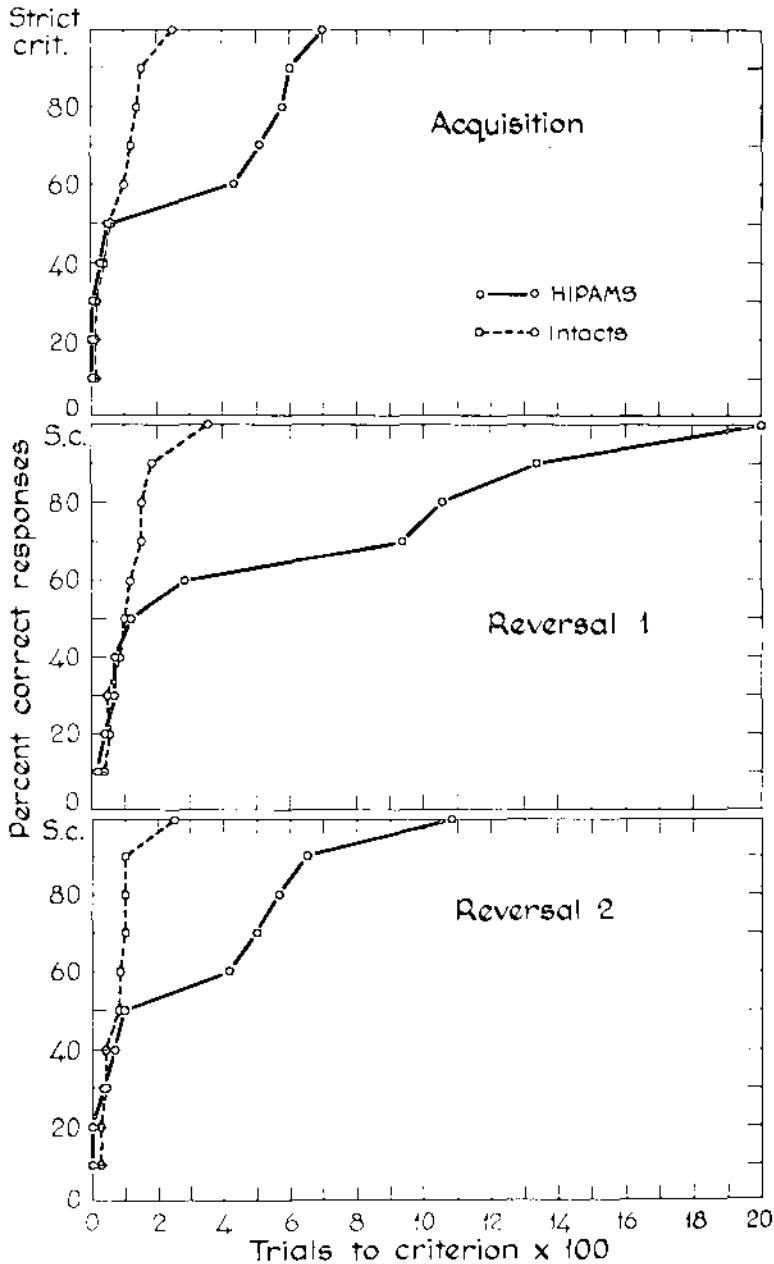
Fig. 2. Number of trials required for 10% increments in performance and the acquisition of the strict criterion after the lax criterion had been achieved during pattern-discrimination learning and the first two reversals.

achieved. During acquisition the hip-am monkeys required more trials to shift from the 50% to 60% level of performance than the intact monkeys. This difference is illustrated by a decrease in the slope of the curve generated by the experimental monkeys compared to the slope of the intact keys

monkeys' curve between the 50% and 60% levels of performance. After the experimental subjects achieved the 60% level of performance, their rate of improvement again became comparable to the control animals until the strict criterion had been acquired. During the first reversal, however, rate of

improvement by the hip-am group was slower than that of the intact $Ss$ at all points beyond the 50% level of performance as indicated by a decreased curve slope which is maintained up to the acquisition of the strict criterion. By the second reversal, however, the hip-am and intact curves showed striking parallels to the curve generated by the experimental and intact subjects during pattern-discrimination learning. As in acquisition, the intact and hip-am curves separate at the 50% level of performance with the experimental monkeys showing major difficulties reaching the 60% level of performance but no difficulty in achieving the lax criterion. Unlike acquisition, however, the experimental monkeys also showed deficits in reaching the strict criterion after the lax criterion had been acquired.

*Analysis by Latency of Responses*

Table 2 shows median response latencies and mean number of nonreinforced responses for the first 50 trials of the second and seventh reversal divided into five 10-trial blocks. It can be seen that, at the beginning of each reversal, all subjects rapidly reduce the mean number of nonreinforced responses so that by the last trial blocks both experimental and intact monkeys' responses to the pattern reinforced on the previous reversal do not deviate significantly from chance levels. There is some indication that the hip-am subjects produce more nonreinforced responses than the unoperated controls during the last trial block of both the second and seventh reversal; however, this difference is not statistically reliable.

Supplemental to the analysis by trials and errors, Table 2 shows salient differences in response latencies between the experimental and intact animals. In effect, these confirm the data obtained when analysis is made by trials and errors. Here, however, response latencies by the experimental monkeys do not differ significantly from those produced by the unoperated controls during the first trial block. It is only over the course of the first 50 trials of the second reversal that the hip-am group show a gradual increase in response latencies and that the intacts show a gradual decrease. The difference is maintained through the seventh reversal. Thus, during the last trial block of the second reversal the intact controls had decreased their response latencies over their initial values, whereas three of the hip-am subjects took longer on the average to make choices during the last trial block than they did during the first. During the seventh reversal all the intact animals took less time to respond during the last trial block than during the first. All hip-am monkeys, however, increased their mean response latencies by the last trial block. This difference in response-latency change between the first and last trial block reached the .06 and .05 level of significance for the second and seventh reversal, respectively. It can also be seen in the last trial block of the second and seventh reversal that the mean response latencies of the hip-am group are larger than those of the intact controls. This difference is significant at the .06 level according to a Mann-Whitney test.

Table 3 compares the change of the median latencies of responses made after pre-

TABLE 2

MEAN RESPONSE LATENCIES AND MEAN NUMBER OF INCORRECT RESPONSES

| Reversal and group | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| *Mds* response latency | | | | | |
| 2 | | | | | |
| Hip-am | 2.409 | 3.411 | 2.428 | 3.051 | 3.186 |
| Intact | 2.011 | 2.257 | 2.460 | 2.427 | 1.940 |
| 7 | | | | | |
| Hip-am | 1.903 | 1.648 | 2.273 | 2.308 | 3.579 |
| Intact | 2.675 | 2.476 | 2.893 | 2.262 | 2.551 |
| *M*. no. of incorrect responses | | | | | |
| 2 | | | | | |
| Hip-am | 9 | 6.5 | 6 | 6.5 | 6.8 |
| Intact | 9.7 | 8.0 | 7.7 | 5.7 | 4.3 |
| 7 | | | | | |
| Hip-am | 6.3 | 5.0 | 4.0 | 5.5 | 1.3 |
| Intact | 6.0 | 4.3 | 3.7 | 2.3 | 2.7 |

*Note.* All data apply to the first 50 trials (in 5-10 trial blocks).

viously rewarded or previously nonrewarded trials during the course of the second reversal. To assure that latency of responding during similar phases of the reversal were compared for all monkeys, the trials were organized into five Vincentized blocks of trials. Thus, for different monkeys, blocks of trials might be comprised of different numbers of trials but accounted for equal proportions of trials required to reach the strict criterion. It can be seen in Table 3 that during the first Vincentized block of trials the hip-am monkeys showed longer response latencies than the intact monkeys regardless of whether the previous trial had been rewarded or not rewarded ($p < .06$; Mann-Whitney $U$ test). In addition, an interesting interaction was observed. The hip-am group response latencies after a rewarded trial were longer than those following nonreward; the opposite relation between previous trial choice and response latency holds true for the intact monkeys ($p < .05$; Fisher Exact test). It can also be seen in Table 3 that the substantial group difference in response latencies apparent during the first Vincentized trial block was reduced progressively during the remaining trials of the reversal.

## Analysis by Signal-Detection Technique

A modified signal-detection procedure allowed us to partial out the part of the subjects' performance based on the detection of stimulus pattern from that due to position bias and is shown in Figures 3–9. Since we restricted the presentation of the reinforced and nonreinforced cues to the extreme left and right columns of panels of the DADTA we made only four stimulus/position contingencies available for the monkeys' potential responses; i.e., the monkeys could press the reinforced or nonreinforced cue in either the left or right column of the stimulus array. Within a given block of trials the number of occurrences of each stimulus/position contingency was set according to a predetermined schedule. Thus, the number of responses to either cue presented in either column could be expressed as a relative frequency of the number of times each of the stimulus/position contingencies actually oc-

TABLE 3

Hip-Am and Intact Median Response Latencies (in Sec.) after Rewarded and Nonrewarded Responses for Five Vincentized Blocks of Trials Required to Achieve the Strict Criterion during the Second Reversal

| Condition and group | Trial block | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| After rewarded | | | | | |
| Hip-am | 4.210 | 5.674 | 2.554 | 2.314 | 2.095 |
| Intact | 1.893 | 1.913 | 2.483 | 2.185 | 1.469 |
| After nonrewarded | | | | | |
| Hip-am | 3.309 | 2.884 | 2.449 | 2.537 | 1.780 |
| Intact | 2.488 | 2.120 | 2.485 | 2.359 | 2.171 |

curred within the block of trials. However, the magnitudes of these four relative frequencies were not independent. Rather, by calculating the probability of the subjects' responding to the reinforced and nonreinforced cue in one column we simultaneously determined the probability of responses to the reinforced and nonreinforced cues presented in the other column. Therefore, we merely calculated the relative frequency of responses to the reinforced and nonreinforced cue presented in one column which was sufficient to summarize the animals' detection of pattern and position bias. Animals that responded predominantly on the basis of position preference produced high relative frequencies of responding to both the reinforced and nonreinforced cues presented in the preferred column of panels. Moreover, it became apparent that the monkeys detected the difference between patterns when they produced high relative frequencies of responding to either the reinforced or nonreinforced cue presented in this position. The value of the relative frequencies of responses to both cues presented in one column were then used to define the locus of a point within an appropriately constructed square to represent graphically an individual subject's performance over a block of test trials. Figures 3–9 furnish examples of this procedure. The ordinate of the square represents the relative frequen-
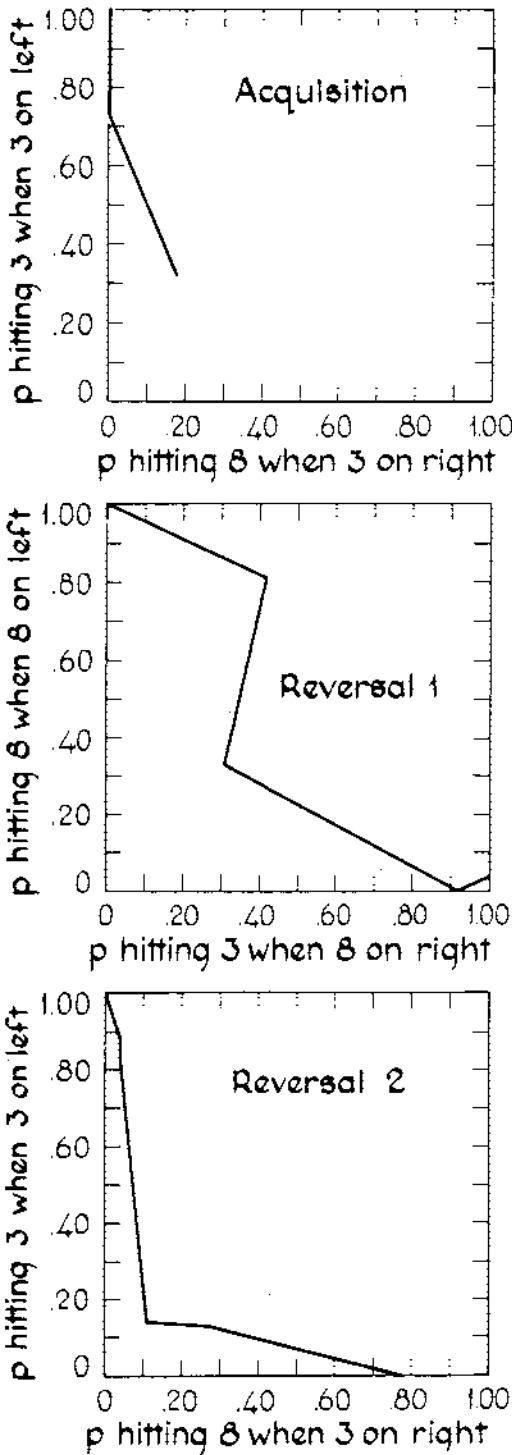
cies of the monkeys' responses to the reinforced cue; the abscissa of the square represents the relative frequencies of responding to the nonreinforced cue in the same column. Those points which approach the upper-left and lower-right corners of the square represent good detection; points in the upper left indicate that responses were controlled by the reinforced pattern and occurred in the latter stages of pattern discrimination and reversal learning; points near the lower right indicated that the subjects' responses were controlled by the nonreinforced pattern and occurred during the initial stages of reversal training. That monkeys responded more on the basis of position bias than stimulus pattern was indicated by points located at either the lower-left or upper-right corners of the square.

Figures 3–9 summarize the results of such an analysis for an individual monkey's performance during pattern-discrimination acquisition and the first two reversals, each of these phases being broken into 50-trial blocks. Responses to the reinforced (the 3 during initial discrimination and the second reversal; the 8 during the first reversal) and nonreinforced cues presented in one column were expressed as relative frequencies of all occasions. These cues appeared in this column for each block of 50 trials. Thus two parameters were available to assess each animal's performance during acquisition and reversal: the number of points in the square representing the number of trials required by the monkeys to reach criterion and the position of each point in the square indicating in what manner individual subjects' performances move through the square in achieving criterion.

It is apparent from Figures 3–9 that the hip-am monkeys required more trials to reach the lax criterion during pattern discrimination and both the lax criterion and the strict criterion during the first two reversals. It is also apparent that the major
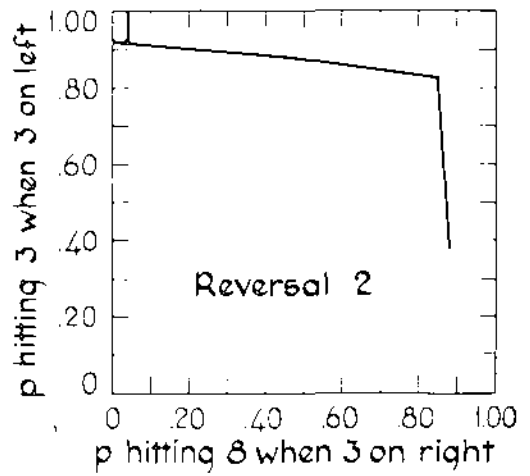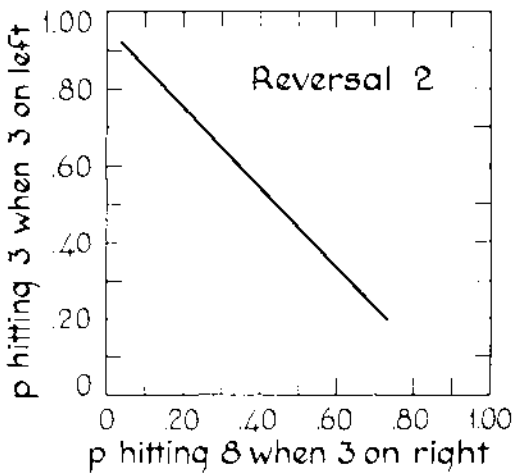
Fig. 3. Individual curves for the hip-am and intact monkeys during pattern discrimination and the first two reversals. (The curves were constructed by joining in temporal sequence points summarizing pattern-discrimination and position preference of the "lesion" and "intact" groups of monkeys for 50-trial test sessions during pattern-discrimination and reversal training. This figure shows performance of control subject 294.)
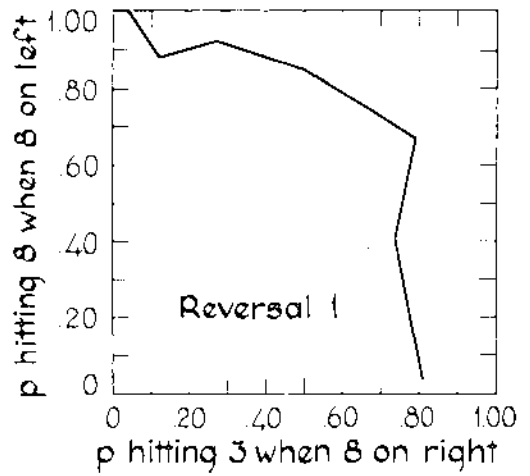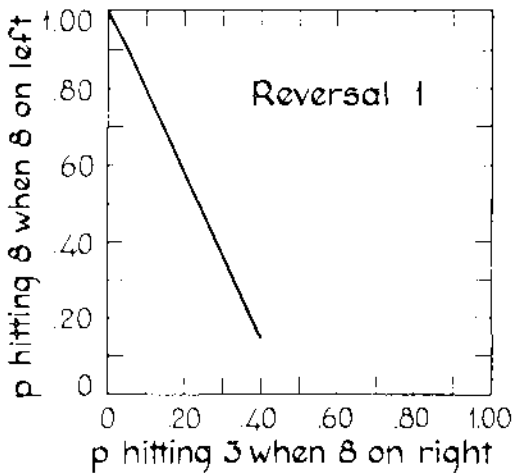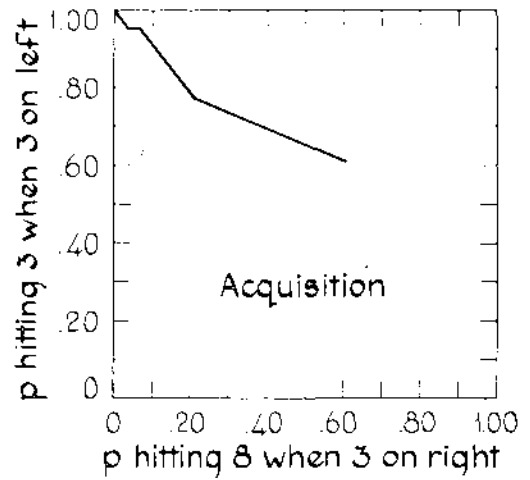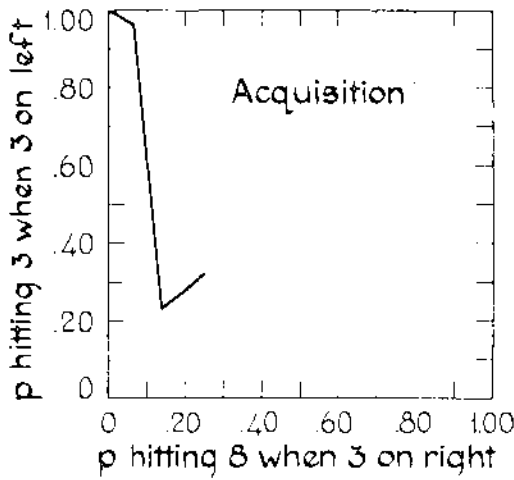
FIG. 4. Performance of control Subject 293 (see Figure 3 caption).

FIG. 5. Performance of control Subject 243 (see Figure 3 caption).

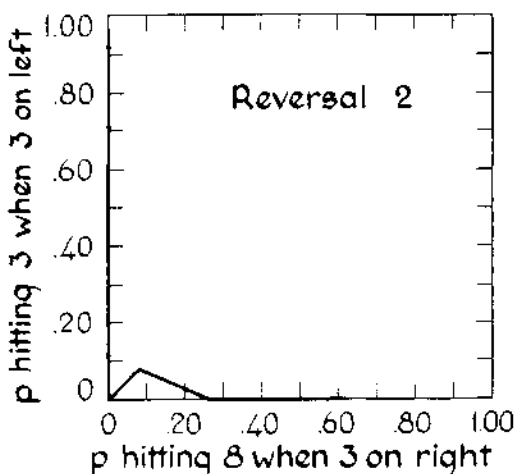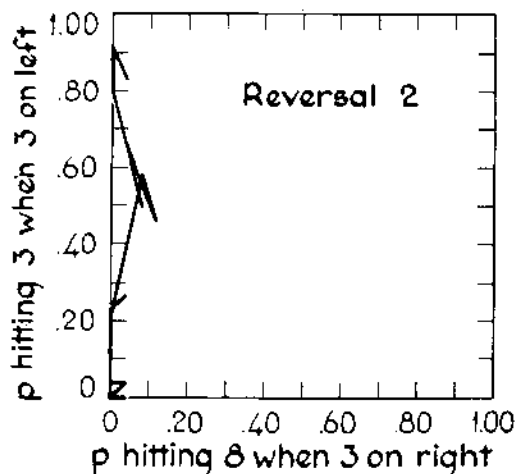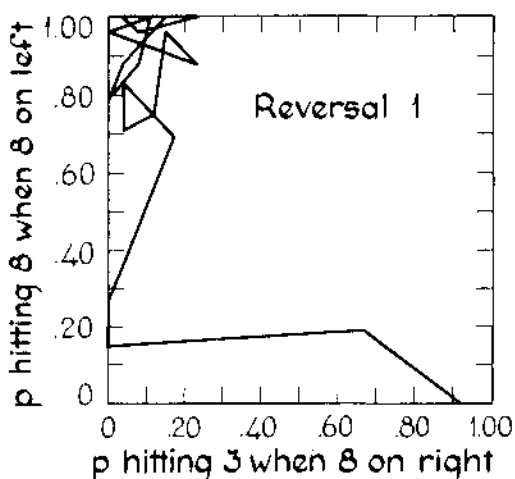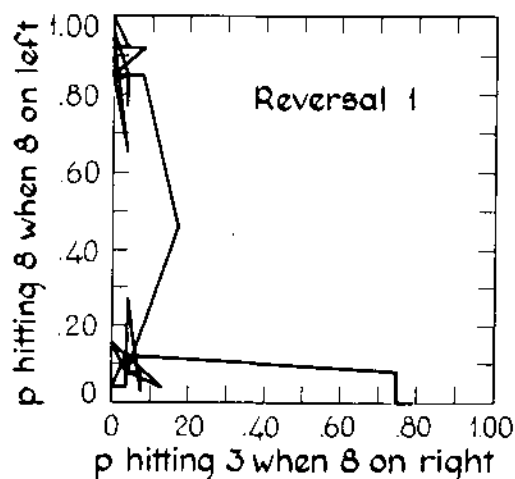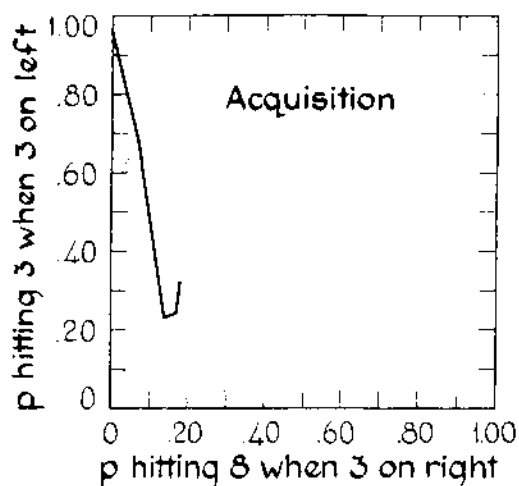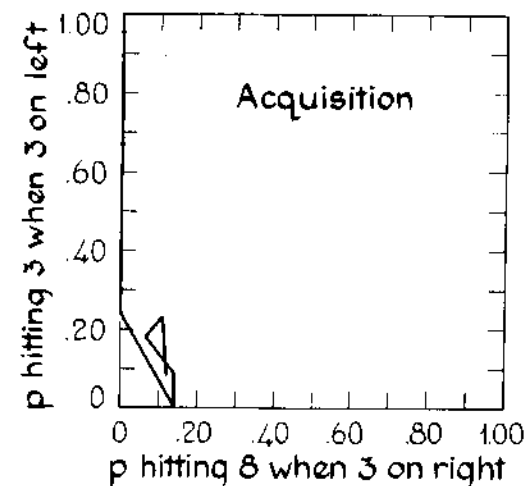FIG. 6. Performance of hip-am Subject 277 (see Figure 3 caption).

FIG. 7. Performance of hip-am Subject 292 (see Figure 3 caption).

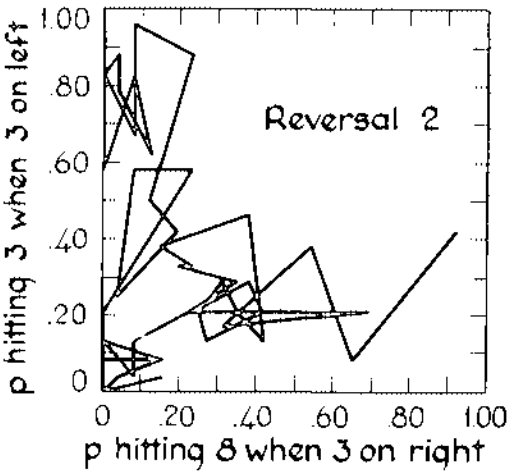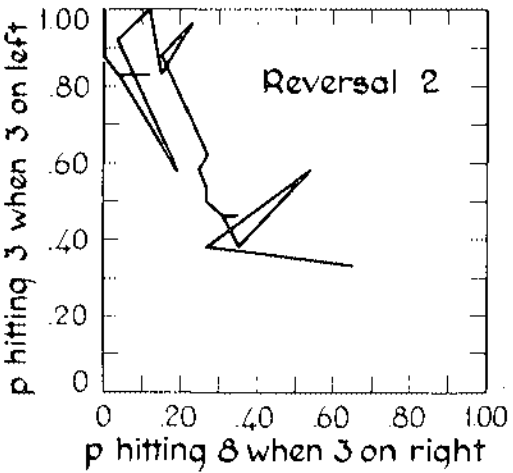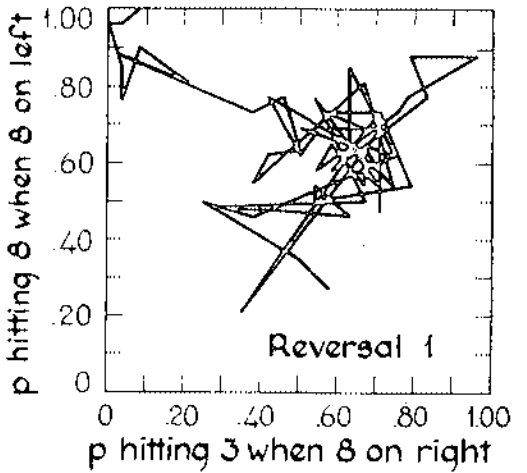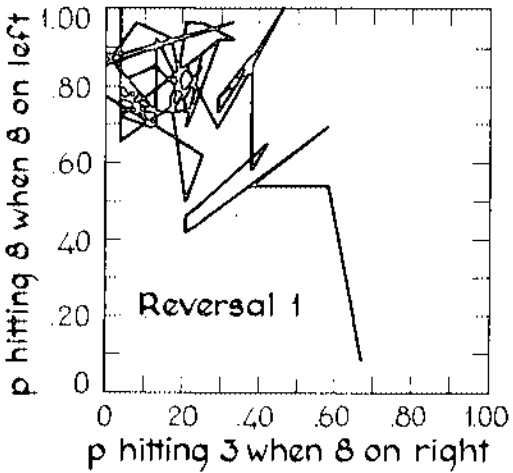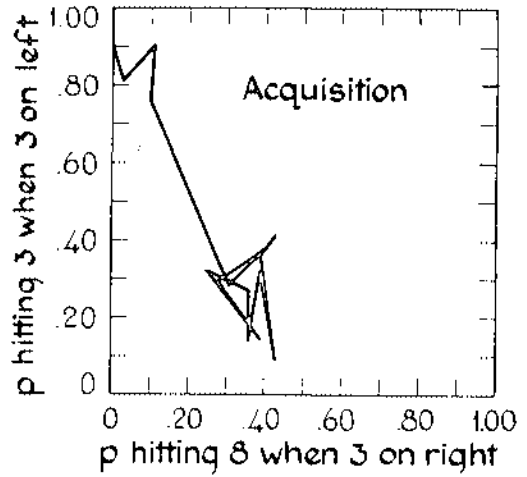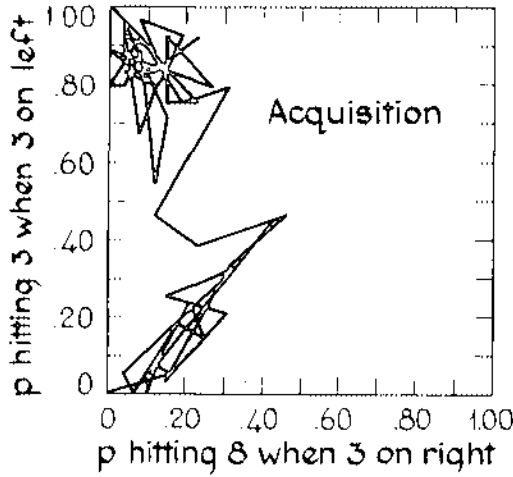FIG. 8. Performance of hip-am Subject 278 (see Figure 3 caption).

FIG. 9. Performance of hip-am Subject 290 (see Figure 3 caption).

difficulties encountered by the experimental monkeys during acquisition and reversal occurred after above-chance responding to the reinforced cue had been initiated, the majority of points produced by the hip-am monkey being positioned above the chance-performance line joining the upper-right corner to the lower-left one. In general, it can be seen that the acquisition of criterion by the experimental animals was preceded by a long period of responses based on position bias, most hip-am monkeys showing a cluster of points at either the lower-left or upper-right corners of the square. Even as their performance approached criterion levels, the experimental monkeys still retained vestiges of their position bias, committing a majority of their errors when the nonreinforced cue appeared in the preferred position in the stimulus array. In marked contrast, the intact subjects showed much less position bias than the experimental monkeys. Few if any of their points appear at either the lower-left or upper-right corners of the squares.

It is noteworthy that the intact monkeys' performance was characterized by smooth and progressive increments until criterion was achieved. Rarely was a point representing a particular day's performance more distal from the upper-left corner of the square than the point summarizing the previous day's performance. However, it was not unusual for the experimental animals to show drastic and sudden decrements (or more rarely increments in performance). Thus, even after the lax criterion in reversal had been reached, hip-am monkeys went for long periods before achieving the strict criterion.

In this analysis we had divided the data from each problem into 50-trial blocks. However, performance in 50-trial blocks is not an appropriate method to define phases in the solution of pattern-discrimination and reversal problems. Intact monkeys were so efficient in the solution of some phases of the experiment that they completed them in less than 50 trials. This made it difficult to compare the fine grain of the performance strategies of the two groups. We therefore divided each subject's data into 10 blocks containing equal numbers of trials (Vincentization). Thus, trial blocks consisted of different numbers of trials for different animals but accounted for equal proportions, e.g., 10% of the trials required to complete the pattern-discrimination and reversal tasks. The median value of each of the 10 points was determined for the hip-am and intact subjects permitting the hip-am and intact monkey data to be represented by two curves, each curve composed of 10 points. These curves are shown in Figure 10. Note that the hip-am curves almost coincide with their appropriate counterparts from the intact group during acquisition and the first two reversals indicating that both groups show essentially identical strategies in the solution of these problems.

Figure 4 also indicates that 80% of the points which form the first hip-am reversal curve and 70% of the points of the second hip-am reversal curve are above the chance discrimination diagonal, indicating that for the experimental monkeys between 70% and 80% of the trials required to achieve the strict reversal criterion occur after subjects begin above-chance pattern discrimination. In marked contrast the intact monkeys required only 50% of trials to reach strict criterion in Reversal 1 and 2 after they began to discriminate above chance. A related difference between the two groups is that the intact monkeys required 50% of their reversal trials to extinguish their responses to the previously rewarded cue; the hip-am monkeys, only 20%.

## Correlation between Extent of Lesion and Behavioral Effect

As can be seen in Figure 1, all hip-am animals did not suffer an equal amount of removal of the hippocampus although amygdalectomy was total in each. Rank order of the monkeys on the basis of amount of sparing of hippocampal tissue came out to be 290 < 278 < 292 < 277, the last showing the most sparing. Rank ordering of the severity of deficit in all of the analyses matched remarkably with this ordering.

Four additional monkeys were tested on all procedures, two with amygdalectomy
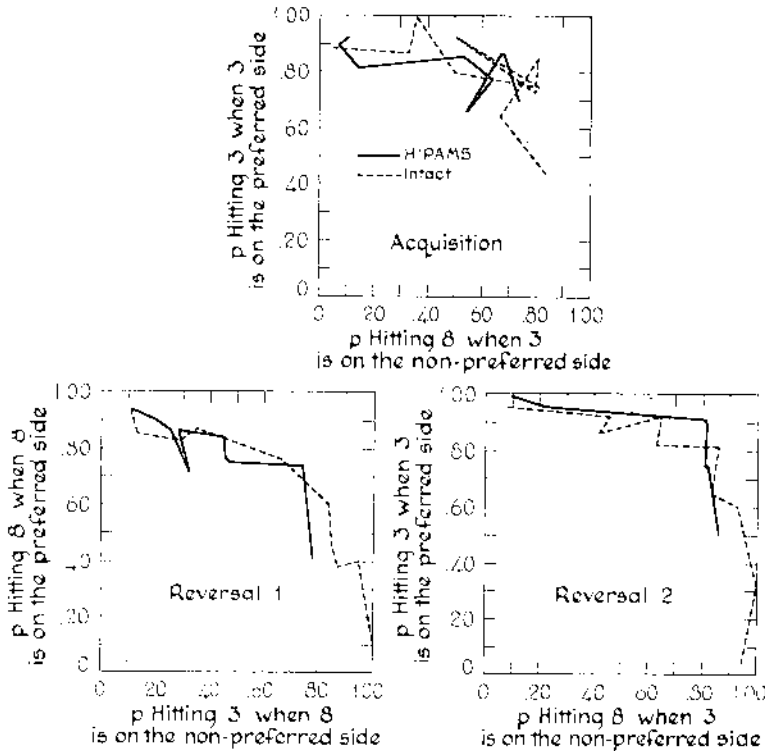
Fig. 10. Group curves (Vincentized) for the hip-am and intact monkeys during original learning and during the first two reversals constructed by joining the 10 points for each group summarizing discrimination and position-preference response. (Each point was the median value of discrimination and position-preference responses produced by individual monkeys in each group during one-tenth of the trials required to achieve the strict criterion during original learning and Reversal 1 and 2.)

and two with hippocampectomy. The amygdalectomized subjects behaved as those reported in the study by Barrett (1969). One hippocampal subject performed just as the monkeys in the current study; the other behaved more like the normal unoperated group and was found to have an incomplete removal of the hippocampus much like Monkey 277 but with somewhat more damage to the inferotemporal cortex.

## Discussion

### Analysis by Trials and Errors

In the current study the hip-am monkeys required significantly more trials than normal controls to acquire pattern-discrimination and reversal habits. However, this deficit was not equally apparent during all phases of these tasks. Rather, at the beginning of acquisition the experimental mon-

keys required more trials than the intact subjects to move from the 50% to the 60% level of performance, but achieved both the lax and strict criterion as readily as the intact controls once they reached the 60% performance level. Further, at the beginning of reversal the hip-am animals extinguished their responses to the nonreinforced cue as rapidly as the controls and thus reached a chance level of responding in about the same number of trials as the intact monkeys. After the extinction phase of reversal, however, the experimental subjects required more trials than the intact monkeys to improve their performance (as measured by successive 10% increments) and to reach the strict criterion after the lax criterion had been achieved.

These results replicate in general those reported by Pribram et al. (1969). There is one difference, however, between the two

bodies of data. In the earlier study the deficits occurred only at the chance level of performance, whereas in the current study deficits were also obtained in achieving and maintaining criterion performance after above-chance discrimination was apparent.

The differences in results between our experiment and the earlier one can be accounted for by the different procedures used in the two studies. We used the numerals 3 and 8 as discriminanda, whereas the earlier study used the numerals 2 and 4. From previous experience we know that the cues used in the current experiment are more difficult to discriminate than those used earlier. Our use of difficult discriminanda appear to have had the effect of prolonging the hip-am reversal deficit into periods of above-chance levels of responding. The curves for the first and second reversal support this supposition: By the second reversal the curve for the hip-am monkeys more closely approximates those hip-am reversal curves previously published by Pribram et al. (1969). With increased experience with the discriminanda the subjects in the present study progressively were able to overcome the difficulties presented by the less discriminable patterns.

Another difference between our procedures and those of the earlier study was that for the strict criterion we required our monkeys to maintain a 90% level of correct performance for 3 successive days, whereas the earlier study terminated discrimination of reversal after only 1 day of 90% correct performance. Thus, our experiment clearly demonstrated that experimental subjects, in marked contrast to the unoperated monkeys, showed deficits in maintaining criterion performance.

One of the purposes of the present study was to determine whether the reversal deficit produced by bilateral amygdalectomy and hippocampectomy is alleviated by practice with the reversal paradigm. Thus, monkeys were required to complete seven successive reversals after pattern-discrimination training. It is apparent that the experimental animals required progressively fewer trials to complete each successive reversal. The intact subjects also showed improvement albeit (since their initial performance was better) at a slower rate than the hip-am monkeys. Thus, deficits in the ability of hip-am animals to reverse independently of their ability to perform pattern discrimination was substantially alleviated by practice with the reversal paradigm. Nevertheless, the hip-am subjects still took more trials to complete the seventh reversal than did the intact monkeys.

Our results are in only partial agreement with those obtained when the amygdala alone is removed bilaterally. Barrett (1969) showed that the development of reversal learning sets is retarded by amygdalectomy. Our adoption of the lax criterion for later reversals may have mitigated against the development of the rather larger difference in learning-set performance between operated and control groups found in the earlier study. This interpretation is borne out by the sudden improvement in reversal performance by the experimental subjects on the third reversal when the lax criterion was adopted as the signal for the initiation of reversal.

## Analysis by Latency of Responses

In view of the ambiguity of interpretation allowed when analysis is restricted to trials and errors, other methods of recording and analysis were instituted in the current experiment.

The recording of response latencies was one such addition. The results showed that hip-am monkeys were slower to respond in general than their controls. More interesting, we obtained a marked difference between groups when the analysis was made in terms of whether the previous trial had been rewarded or not (correct or incorrect). Under the assumption that a longer response latency indicates some disruption of habitual response, the conclusion can be reached that nonreward is more disruptive for normal subjects while rewards interfere more with facile performance of hip-am monkeys. These results can be interpreted in the light of previous findings (Douglas & Pribram, 1966) to indicate that, in the current study, error sensitivity ascribed to hippocampal function was more severely im-

paired than registering reward ascribed to the amygdala.

### Signal-Detection Analysis

Pribram et al. (1969) suggest that the deficits in discrimination and reversal learning produced by bilateral hippocampectomy and amygdalectomy are due to two separate, but related, factors. First, the lesion reduces the frequency with which the salient dimensions (pattern) of a stimulus array is observed, thus prolonging the periods of chance performance apparent at the beginning of acquisition and after the extinction phase of reversal. Second, a VR2 (50% variable ratio) schedule of reinforcement is sufficient to maintain the experimental subjects' chance performance long after the intact monkeys have switched their attention to the salient stimulus dimension.

Clearly, any experiment which proposes to test the validity of the Pribram (1967) hypothesis, as does the present study, must develop means to specify the variables which effectively exert control over the monkeys' performance throughout all phases of discrimination and reversal learning. A modification of the analytical techniques developed by the theory of signal detection offered one such possibility. This analysis permitted us to determine the relative amount of control exerted by the dimensions of the stimuli and by the position bias on the subjects' discrimination and reversal performance. Thus, when equal size blocks of 50 trials were each represented by a point in an appropriately constructed decisional square, it was possible to observe the daily changes in responding to the stimulus pattern and position bias as the monkeys performed discrimination and reversal tasks.

In this analysis the position bias was taken as the major alternative to stimulus pattern in controlling an animal's discrimination and reversal behavior. Most subjects while acquiring discrimination and reversal showed, during at least some periods, an almost exclusive position preference. This is demonstrated in the analysis by the fact that the points representing their daily performance are positioned at either the upper-right or lower-left corners of the decisional square. The periods of maximum position bias were most apparent at the beginning of discrimination learning and after the extinction phase of reversal learning. This result, therefore, strongly supports the Pribram et al. (1969) assumption that during periods of chance performance the behavior of the monkeys comes under the control of noncontingent reinforcement. The decision-theoretic analysis allows this to be stated in terms of discrimination and bias: Monkeys tend to revert to position preferences when their behavior is not under the control of a discriminable stimulus pattern.

This analysis further indicated that monkeys did not necessarily completely overcome the position bias even after they achieved above-chance levels of responding. Rather, the fact that the subjects' performance points approach either the upper-right or the lower-left side of the square as they near criterion suggests that throughout the acquisition of discrimination and reversal the position bias vies with the stimulus pattern for control of the monkey's behavior. Thus, errors committed throughout the acquisition of these tasks occur because the appropriate stimulus dimension fails to hold the attention of the subjects. This is clearly demonstrated by the fact that selection of the incorrect pattern during periods of above-chance performance most frequently occurs at the animal's preferred position. This result also suggests why the hip-am monkeys, especially during reversal learning, show such sudden and large shifts in performance. It is difficult to account for these performance shifts by recourse to any possible reductions in the subjects' ability to discriminate between the cues. It is more likely that these large swings in performance levels occur when animals fail to attend to the stimulus dimensions, fall back on their bias, and settle for the VR2 schedule of reinforcement with the concomitant reduction in effort required.

This hypothesis suggests that the major effect produced by bilateral amygdalectomy and hippocampectomy may be to alter the intensive aspects of attention (Berlyne,

1969). If hip-am subjects expend less effort than the intact monkeys for obtaining reward they will show position preferences during a larger proportion of discrimination and reversal trials than do intact controls. Whenever there is a reduction in the incentive value accruing to the stimulus dimension—as during the chance reward periods of the reversal—the experimental monkeys resort to a period of position preference (chance levels of responding) more rapidly than do the intact controls. The resulting period of chance performance is more prolonged for the experimental animals because they show less incentive than the unoperated monkeys to attend to the stimulus dimension in order to gain access to the higher density of reinforcement potentially provided by this dimension. Even after the hip-am subjects do eventually begin to respond on the basis of the stimulus dimension, presumably because the intensity of their attentional state has been sufficiently altered, they still retain their increased tendencies to give up attending and resort to the position bias.

This hypothesis also suggests an explanation for the difficulties of the hip-am monkeys to maintain a criterion level of performance once they have already achieved the lax criterion. The same bias for position preference which caused the experimental animals to remain at a chance level of responding at the beginning of pattern-discrimination learning and at the end of the extinction period of reversal, and to retard their achieving criterion, is still apparent even after criterion has been reached. Thus, the experimental subjects, because they inconsistently attend to the stimulus dimension, have difficulties in maintaining criterion performance during 3 successive test days.

Signal-detection analyses, therefore, have clearly demonstrated that the major difference between the hip-am and the intact subjects is in the intensive rather than the selective dimension of attention—or, to put it more baldly, in the monkeys' motivation. Further, the analysis has shown that this motivational difference between the experimental and unoperated monkeys during discrimination and reversal learning is a quantitative and not a qualitative one: The Vincentized discrimination and reversal response-operator-characteristic curves show identically shaped learning curves for the two groups.

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