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LEARNING OF VISUAL TASKS BY MONKEYS WITH EPILEPTOGENIC IMPLANTS IN TEMPORAL CORTEX[1]

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Alumina cream was implanted bilaterally in monkeys, either on anterior medial temporal cortex (AMT) or on inferotemporal cortex (IT). Normal controls and 2 epileptic groups were tested after onset of epileptic discharges. IT group was greatly impaired on the 1st 2 of 8 simultaneous visual discriminations and on 1st stimulus reversal, but overcame their deficits on succeeding discrimination and reversal problems. AMT group was only slightly poorer than normals on first discrimination and reversal tasks but showed little improvement in acquisition of succeeding problems. It is concluded that IT cortex is implicated in searching behavior on visual tasks, whereas AMT cortex (amygdaloid structures) is implicated in the solution of tasks which require utilization of previous experiences.

Behavioral consequences of focal epileptogenic cortical discharges, produced by chronic implantation of alumina cream in monkeys, have been reported in previous communications (Stamm, Knight, & Warren, 1962; Stamm & Pribram, 1960, 1961; Stamm & Warren, 1961). Monkeys which were trained after the onset of focal epileptic discharges from neocortical structures were impaired in the acquisition of specific tasks. The nature of the impairment corresponded to that obtained after ablation of the corresponding cortical areas. On retention tests for tasks that had been learned before alumina cream implantation only slight behavioral impairment was observed after the onset of epileptic discharges. However, more extensive and persistent behavioral deficits were obtained with epileptogenic foci in anterior medial temporal cortex (Stamm et al., 1962). Monkeys with implants in these structures were found retarded in the acquisition of tasks involving visual and somesthetic discriminations and delayed alternation. Moreover, retention deficits were also obtained on each of these tasks. The results of that investigation suggest that the amygdaloid system is not primarily implicated in the acquisition of a particular task, but serves in the performance of tasks which involve transfer effects from previous training. A similar formulation has been expressed by Schwartzbaum and Pribram (1960), who consider the amygdaloid structures to be implicated in generalizations of learned responses.

Although recordings with scalp and implanted electrodes have indicated restricted epileptogenic foci within the implanted cortical structures, the hypothesis should be considered that behavioral impairments are the consequence of the propagation of discharges to other cortical areas. The proximity of inferotemporal cortex to the site of medial temporal implants would particularly implicate this area in the propagation of epileptic discharges. Consequently, in the present experiment a comparison group of monkeys was used with inferotemporal epileptogenic implants.

In investigating the role of amygdaloid structures in behavior, epileptogenic implantation appears to be a suitable technique. Histological examinations of brains have revealed only minimal structural damage to the neuronal elements, so that the behavioral deficits are the consequence of physiological dysfunction of the discharging neuronal system. In experiments with the technique of cortical ablation behavioral deficits are correlated with the site of ablation. It has been suggested, however, that ablated monkeys may be able to perform adequately on some tasks in which the medial-temporal system is implicated in normal monkeys, because they are able to utilize alternate neuronal pathways. The behavioral deficit seen in ablated monkeys,

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therefore, may be relatively small in relation to the extent of structural damage. In epileptic animals the medial cortical system, although physiologically disturbed, is still implicated in mediating behavioral processes. Finally, epileptogenic foci in medial-temporal cortex have been observed frequently in clinical investigations. Thus the findings with epileptic monkeys could be of relevance to our understanding of the behavioral consequences of "temporal lobe" epilepsy.

The present experiment was designed for evaluation of transfer effects on a series of simultaneous visual discriminations and on a visual stimulus reversal task.

Method

Subjects

Three groups of four immature, experimentally naive rhesus monkeys were used.

Surgery was performed aseptically under Nembutal anesthesia. Commercial Amphojel was boiled to the consistency of a thick paste and packed in small teflon disks (9 mm. in diameter). The disks were placed under visual exposure bilaterally on the cortical surfaces of temporal lobes. In the AMT group one disk was placed on the medial surface, just posterior to the temporal pole. For IT placement two disks were placed on the posterior ventral surface, lateral to hippocampal gyrus. The dura was closed by sutures over the disks, and overlying muscle and skin were sutured in layers.

EEG Recordings

For recordings of scalp EEGs the *S* was placed supinely in a wooden restraining box and electrodes (wound clips) were attached to the scalp bilaterally over frontal, anterior temporal, posterior temporal, and occipital cortex, and vertex. Novocaine was injected into temporal muscles in order to reduce muscle potentials in the recordings. The *S* was placed in a quiet, electrically shielded room, and recordings were obtained with a six-channel Offner dynograph. Drugs were not administered. Serial EEG recordings of each *S* were taken before and during the course of the testing program.

Procedure

Training was started 12 weeks after the implantation of alumina cream, at which time epileptic spike discharges were recorded in all experimental *S*s. The experimental and control *S*s were trained in a Wisconsin General Testing Apparatus. During preliminary training *S*s learned to jump into the testing cage, to pick peanuts from a single foodwell located in the testing compartment in front of the center of the cage, and to displace a gray wooden block that had been placed over the foodwell.

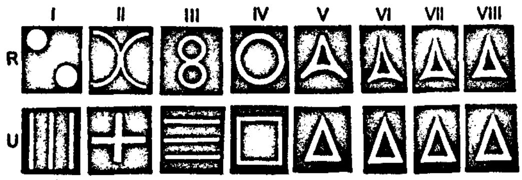

Fig. 1. Eight pairs of patterns used for visual discriminations—upper row (R), rewarded; lower row (U), unrewarded patterns.

Successive discriminations. Fifty trials were given daily, generally 6 days per week. On each trial the monkey faced two vertical Lucite plaques, mounted on wooden blocks, which were placed over foodwells, with 12 in. between centers. Each plaque was 3½ in. wide and 5 in. high and contained a white pattern against a dull black background. The total areas of all white patterns were approximately the same. A half kernel peanut was placed in the foodwell underneath the correct pattern. The rewarded patterns were placed at the left or right position on successive trials according to a chance sequence.

The *S*s were trained on the sequence of the eight discriminations shown in Figure 1. An *S* was tested on a discrimination until it met the criterion of 45 correct responses in one session. On the following day it started with the next problem. As seen in Figure 1, the rewarded patterns consisted of circles or curved lines, the negative stimuli of straight line figures. On Discriminations V through VIII the negative patterns were isosceles triangles, and the positive patterns were distorted triangular figures with curved sides.

Stimulus reversals. After completion of the series of successive discriminations, each *S* was retrained on Discrimination IV until it attained the criterion of 90 correct responses in 10 successive blocks of 10 trials each. On the following day (Reversal 1) responses to the square were rewarded and training was continued until this criterion was again met. On the next day (Reversal 2) the circle became again the rewarded cue until the criterion of 45 correct responses in 5 blocks of 10 trials each was met. This procedure was continued through the fifth reversal. For the succeeding stimulus reversals the criterion of 27 correct responses in 3 blocks of 10 trials was selected for each discrimination. Reversals always started on the day after a criterion had been attained. A maximum of 50 trials was given daily. The *S*s, with one exception, were tested for at least 19 reversals, while some *S*s were given 31 reversals.

Because of infectious illness, two normal *S*s and one *S* with IT implants were dropped from this experiment. One additional *S*, which had first been trained on successive visual discriminations, was added to the normal group.

The Mann-Whitney *U* test was used for statistical evaluations of differences in response scores between groups of *S*s.

Results

Seizure Signs

Paroxysmal spike discharges were seen in the EEGs of all *S*s with epileptogenic implants in recordings taken 9–11 weeks after implantation. In *S*s with IT implants the recordings were similar to those described previously (Stamm & Pribram, 1961), with focal spike discharges recorded from posterior temporal electrode placement. Behavioral seizure signs were rarely observed in this group of *S*s.

In *S*s with implants in AMT cortex focal paroxysmal spike discharges were recorded from anterior temporal electrode placements in recordings like those described in a previous experiment (Stamm, et al., 1962). In most *S*s a dominant discharging focus was seen in one hemisphere, and in a few *S*s a secondary focus in contralateral hemisphere was recorded. Concomitant with the onset of EEG discharges in *S*s with AMT implants, behavioral seizure signs were observed, which included a sequence of head turning, staring, facial twitching, mastication, and salivation. During some seizure episodes only the early signs of this sequence were seen, whereas occasionally seizures continued to generalized motor convulsions. Seizure episodes were observed in all AMT *S*s throughout the period of experiment. Anticonvulsive medication was not administered.

For each *S*, except one, the serial EEG recordings and expressions of behavioral seizures remained essentially constant throughout the experimental period. The early EEGs for *S* No. 634, with IT implants, revealed some epileptic spiking from anterior temporal cortex, in addition to the primary focus from posterior temporal lobe. On succeeding recordings the anterior temporal discharges became more pronounced, so that during the period of reversal testing marked seizure activity was seen from both anterior and posterior temporal electrode placements.

TABLE 1
Successive Visual Discriminations

Group	Trials to Criterion on Discrimination							
	I	II	III	IV	V	VI	VII	VIII
Norm.	185	75	0	0	0	0	0	60
AMT	340	190	40	15	180	85	25	120
IT	550	360	45	15	65	0	0	200

Discrimination Learning

Table I presents the scores of median number of trials to criterion (exclusive of criterion trials) required by each group on each discrimination. On the first discrimination the normal *S*s required 140–200 trials, whereas the AMT epileptics needed 290–350 trials to criterion ($p = .014$). On this discrimination the IT *S*s (300–980 trials to criterion) were also deficient when compared to normals, and three of these epileptic *S*s required more training than did any of the AMT *S*s. Although both epileptic groups were retarded in acquisition on this task when compared to normals, the learning curves, as illustrated in Figure 2, indicate marked differences in learning rates between the epileptic groups. The IT *S*s responded at chance level much longer than did the other groups, but their learning curve then increased at approximately the same rate as the curve for the normal group, whereas the AMT *S*s were retarded primarily after their learning curve had risen above chance level.

The succeeding discriminations were learned more rapidly than Discrimination I by all three groups, as seen by the scores in Table I. On Discrimination IV criterion performance was attained during the first 50 trials by all normal *S*s and by two *S*s in each of the epileptic groups.

On Discrimination V the AMT *S*s showed an appreciable learning deficit, since they required 130–490 trials to criterion, compared to zero to 90 trials by the IT group ($p = .014$). Three normal *S*s responded at the criterion during the first 50 trials, while the fourth required 40 additional trials. On this discrimination all *S*s responded above 60% correct during the first 50 trials (median for AMT group 72% correct). The AMT *S*s therefore were most markedly re-

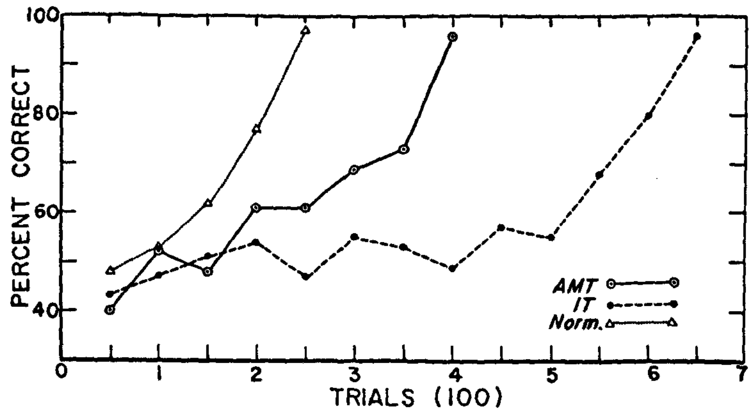

FIG. 2. Learning curves on Discrimination I for groups of monkeys with anterior medial or inferotemporal epileptogenic implants and normal controls. (The ordinate indicates median scores of percentage of correct responses in successive blocks of 50 trials.)

tarded after their learning scores had risen above chance level.

On Discriminations VI and VII, which were of increasing difficulty, learning deficits by the AMT group persisted, whereas the IT *S*s learned these discriminations as rapidly as did the normals (Table 1). On each of these problems the normal group obtained medians of three errors. The rapid learning by the IT group is indicated by its median score of only one error on Discrimination VII. On the final discrimination (VIII), which was designed for maximum difficulty, the normal group obtained a median of 9 errors during the first 50 trials, compared to 17 errors for each of the epileptic groups.

Stimulus Reversals

Figure 3 represents the group median scores of trials to criterion on the successive stimulus reversals, (Stimulus Pair IV, Figure 1) with the square as the rewarded pattern. The groups of monkeys consisted of 4 AMT *S*s, 2 IT *S*s, and 3 normals. One IT monkey, No. 634, which was not included in these tests, was exceptionally slow in learning the first five reversals and upon failure on the sixth reversal after 1,000 trials, was dropped from the experiment. On the earlier discrimination tasks this *S* performed as well as the other IT monkeys. The curves for reversals with the circle as rewarded cue (even-numbered reversals) are similar to those in Figure 3, except that the scores for the AMT and normal groups are somewhat higher for the first three reversals to the circle.

Although the reversal scores for the AMT group were consistently poorer than those for normal *S*s, there was considerable overlap in scores for individual *S*s in the two groups during the first four reversals. On the fifth and the succeeding reversals no overlap in scores was found between the normal and AMT groups ($p = .028$). The normal *S*s continued to improve with training and attained the reversal criterion after a maximum of 10 trials on reversals 18–31. The two *S*s with IT implants were deficient compared to the other groups on the first four reversals, but their scores on the subsequent reversals were within the range for the normal group.

The graph for the AMT group indicates little consistent improvement in performance on successive reversals and the final scores for this group were only slightly better than scores on the first reversal. Two of the AMT *S*s showed no improvement in meeting the reversal criteria during the course of training, while two other AMT *S*s showed some improvement, although their scores fluctuated markedly on successive reversals and were always poorer than the scores for any of the normal *S*s.

Figure 4 represents curves for AMT and normal groups of the percentage of correct responses during the first 50 trials with the square as the rewarded cue (or for all trials

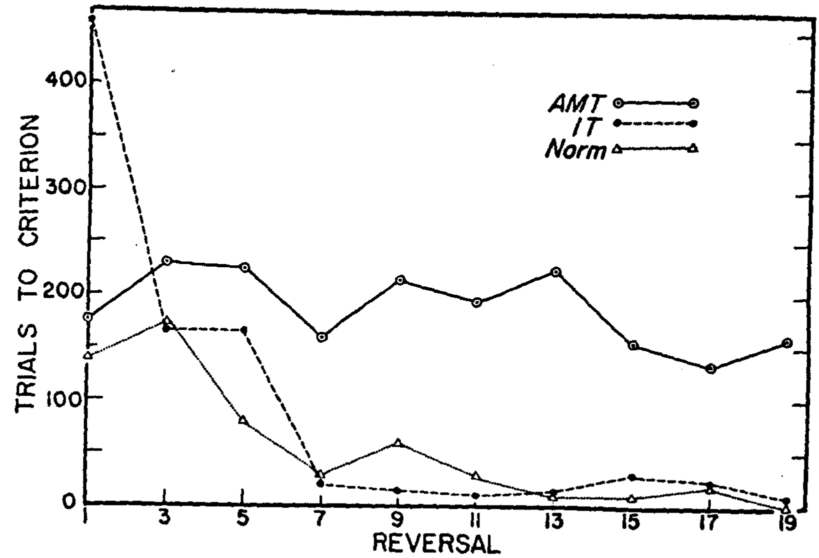

FIG. 3. Stimulus reversals. (Medians of number of trials to criterion for three groups on successive reversals (patterns IV) for square as rewarded cue.)

on each reversal when criterion was met after zero or 10 trials). The curves for both groups express high rates of perseverative responses (to the circle) during the first reversal and improvement to chance level during the following reversal tests. The curve for the normal group then continues to increase to the 90% level, whereas the curve for the AMT group remains at chance level after the eighth reversal. The scores for all normal *S*s were above those for the AMT *S*s ($p = .028$) on the ninth and all succeeding reversals. Figure 4 expresses the finding that the AMT *S*s were able to overcome the initial perseverative tendencies without difficulty.

DISCUSSION

The present results on successive visual discriminations and visual stimulus reversals express marked differences in behavior between the two epileptic groups. The *S*s with inferotemporal implants exhibited maximum impairment during the early phases of training, but were able to reduce the behavioral deficit during the course of testing. By contrast, the *S*s with medial temporal implants showed little impairment on the initial discriminations in each of the series, but their behavioral deficit became more pronounced as training continued.

The two groups of epileptic *S*s could be clearly distinguished on the basis of EEG recordings and behavioral seizure manifestations. Recordings with chronically implanted electrodes in other experiments (Stamm et al., 1962) have provided further confirmation of restricted epileptogenic foci. With AMT implantation the discharging foci were generally in anterior medial temporal cortex and the epileptic discharges propagated only occasionally to other brain structures. Cortical recordings in *S*s with inferotemporal epileptogenic implants revealed a highly restricted epileptic focus in these structures, with the exception of No. 634. Although behavioral seizures were observed in AMT *S*s, but not in the IT group, the behavioral deficit in the AMT group did not appear specifically related to seizure episodes. When the rate of incidence and severity of epileptic seizures in each *S* was related to performance data, no significant correlation could be established between measures of seizure activity and behavioral deficit. Further, No. 634 whose EEG indicated a combined IT-AMT epileptic focus during the period of reversal testing, exhibited only minimal seizure signs, although

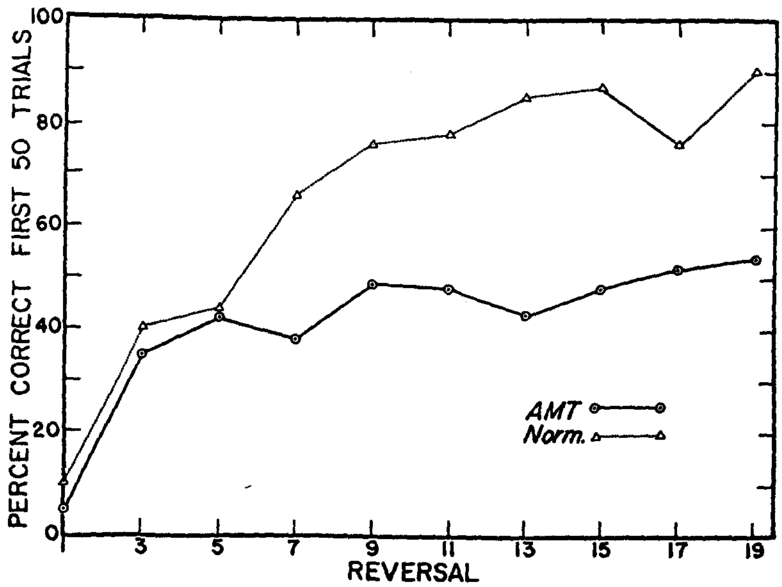

FIG. 4. Stimulus reversals. (Medians of percentage of correct responses during first 50 trials on successive reversals (patterns IV) for square as rewarded cue.)

its test performance showed maximum deficit.

The *S*s with inferotemporal epileptogenic implants were most markedly deficient in acquisition of the first visual discrimination task and again on the first stimulus reversal. These results are in agreement with previous findings with ablation techniques (Mishkin & Hall, 1955) and with methods of epileptogenic implants (Stamm & Pribram, 1961), that inferotemporal cortex is implicated in the acquisition of visual discrimination problems. According to the analyses of learning rates, the IT *S*s were particularly impaired during the early phases of the learning process, while searching for the correct solution to the task. Their high scores of correct responses on the succeeding visual discriminations and on the successive reversals indicate that these epileptic *S*s were not impaired during the later phases of testing on these tasks. The present findings thus confirm the formulation by Pribram (1960) that inferotemporal cortex is primarily implicated in the *search* for correct solutions of visual discrimination problems.

The behavioral deficits of the *S*s with medial temporal epileptogenic implants were most marked after these *S*s had had some experience on the tasks. This finding is most clearly demonstrated by the series of stimulus reversal tasks (Figure 3), where the deficits were minimal during the initial reversals but then became increasingly more pronounced, as the other groups of *S*s learned to reverse more rapidly. The analyses of learning rates on the discrimination problems also point to the difficulty the AMT *S*s had during the final phases of learning after the completion of searching behavior. The AMT *S*s, however, were able to develop learning sets under certain conditions: on the series of visual discriminations their performance improved on Discriminations II–IV and again on Discriminations VI and VII, and on the reversal tasks they were able to overcome the initial perseverative tendencies.

Thus, the behavioral impairment by the AMT *S*s is revealed most clearly on tasks which require relatively complex organizations of previously learned experiences. Similar results were obtained by Schwartzbaum and Pribram (1960) with amydalectomized monkeys on visual transposition tasks. The involvement of the amygdaloid system in perceptual functions has been demonstrated, moreover, with human epileptic *S*s having right temporal lesions who, according to Milner (1958) showed impairment in comprehension of pictorial material. Investigations and interpretations of amygdaloid functions have thus far been primarily concerned with motivational processes. Gloor, in reviewing the relevant literature, considers the amygdaloid structures to be implicated "in those motivational mechanisms which normally allow the selection of behavior appropriate to a given situation," (1960, p. 1416). This interpretation is not at variance with the present findings. Although the present experiment was concerned with visual tasks, the amygdaloid system appears also to be implicated in nonvisual problems, because monkeys with medial-temporal epileptogenic implants were found deficient in acquisition and retention of somesthetic discriminations and delayed alternation (Stamm et al., 1962). The implication of this neuronal system in perceptual proceses involving other sensory modalities and in tasks of differing response processes is a problem that needs to be examined by further experimentation.

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