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SOME FEATURES OF THE DORSOLATERAL FRONTAL AND INFEROTEMPORAL SYNDROMES IN MONKEYS

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Abstract. Our frontal- and temporal-lobe experiments to date support the following conclusions. Anterior temporal or inferotemporal lesions affect object learning set retention, and older work dealing with this task has indicated that temporal ablations, at the very least, retard initial acquisition of the set. Inferotemporal monkeys may lose object sets and yet have no deficits in either the learning or short-term retention of single visual habits. Their well-known impairments in visual pattern learning are products of background-cue learning which become most marked in test situations which bias their responses to these cues. Their pattern-learning deficit is an accentuation of a normal characteristic of the monkey, and implies no profound qualitative alteration of the way that they perceive stimuli.

Our work that has dealt with frontal preparations indicates that Jacobsen's effect can be produced either by proactive interference or by difficulties in attending. The latter are probably compensable if lesions are produced in very early infancy, but data from experiments with cats has suggested that perseverative interferences are not. Perseverative tendencies can be suppressed with practice in discrimination learning situations, but the tendencies can then be fully reinstated by relatively minor distractions. Frontal-lobe lesions have almost no effects upon object learning set formation, nor do they have important effects upon a monkey's short-term retention of a habit.

The problems with which we are concerned in this report were first posed some 20 years ago by the outcomes of a study carried out with rhesus monkeys by Harlow et al. (1952). The animals had previously served as subjects for quite a number of investigations, some of which were first described by Harlow (1949) in his classic paper on learning-set formation. The earliest had dealt with the effects of extensive unilateral cerebral ablations which were aimed at the destruction of as much of the frontal and parietotemporal "associative" cortex as could be approached with techniques then in use. By the time of the Harlow et al. (1952) study, these so-called "semi-hemi" preparations had also been operated either for removal of the contralateral dorsolateral intrinsic isocortex anterior to the arcuate culcus or for removal of the contralateral parietotemporal area.

The surgeon's intentions and the final reconstructions were dissident in several respects. However, the lesions were sufficiently well placed to permit the behavioral experiments to show that delayed response deficits and visual learning deficits are reasonably specific to ablations of the frontal and the posterior sectors of the cortex. This crude conclusion has since been refined by the outcomes of numerous inquiries in which, I would judge, the majority of workers assembled here have had an active part.

Our own work has centered on the nature of the difference between delayed response and learning problems, and particularly, the kinds of learning problems which were failed by the semi-hemi-posterior monkeys. Of these, the most instructive were object learning problems presented in a two–trial paradigm: a training trial arranged with a pair of novel objects, and then a single test trial with those objects.

Two-trial object learning measures different processes from those which underlie the acquisition of object discrimination learning by monkeys that have not been trained in learning sets. One simple proof of this is found in the fact that monkeys with temporal-lobe lesions are generally reported to have only mild deficits when tested with "easy" object problems. However, intrinsic isocortical ablations of the tissue anterior to the vein of Labbe produces, as was shown by an experiment described in part by Meyer (1958) and in part by Akert et al. (1961), a profound impairment of retention of a previously established object learning set and, at best, slow relearning of the set. Thus, as is summarized in Fig. 1, performances on second trials of six-trial object problems reveal no evidence of object-set retention following ablations of this kind. In at least some animals, the set is re-established by further postoperative practice, and is also learnable to some degree by monkeys which are not trained prior to operation.

Trial-two performances, but not performances on later trials of object learning problems, reflect the probabilities that monkeys are using concepts in solutions of these problems. As we have shown in studies of the problem of relationship between sets and habits, improvements over later trials reflect the same processes as those which are involved in the entire course of learning of such problems by set-naive monkeys (Meyer 1971).

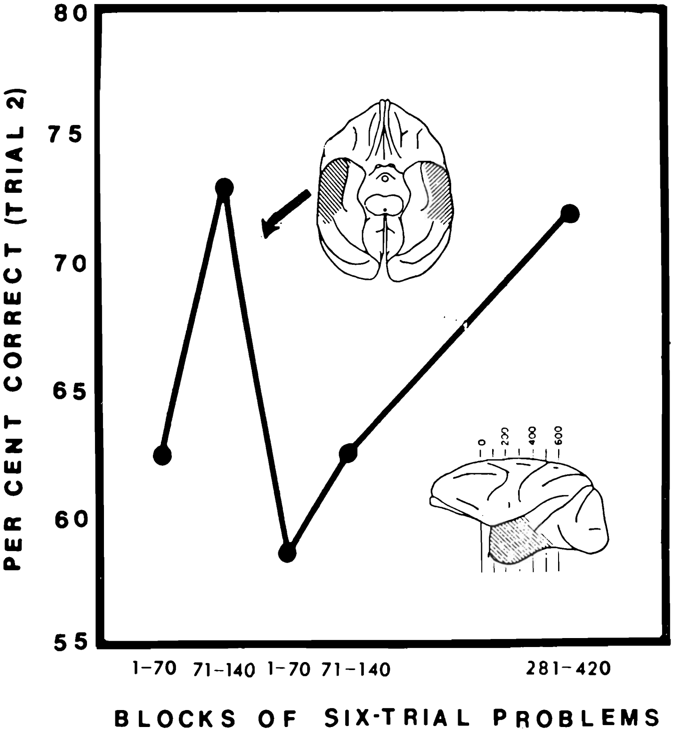

Fig. 1. Effects of anterior temporal decortication upon retention of an object learning set. (From experiments reported by Meyer 1958, Akert et al. 1961.)

Since set-trained monkeys can approach object problems with two completely different strategies, it is possible for set-sophisticated animals to suffer impairments that cannot be detected in monkeys that are trained on single problems.

Lesions of the dorsolateral frontal isocortex do not produce important object learning set impairments. That this is the circumstance is clear from Fig. 2, which compares the performances of monkeys with lesions of the sulcus principalis or the inferotemporal cortex on a series of 392 six-trial object discrimination problems. The inferotemporal monkeys, like anterior temporal monkeys, had marked deficits on trial 2, but the trial-two scores of the frontal preparations were only of the order of about 10% below those obtained from these same animals before the operations were performed. The latter loss is stable, and is not much affected by whether the lesion is a principalis lesion or extends across the dorsolateral surface.

Frontal monkeys nonetheless are greatly impaired if the objects used in object learning tasks are employed as supplemental cues in test

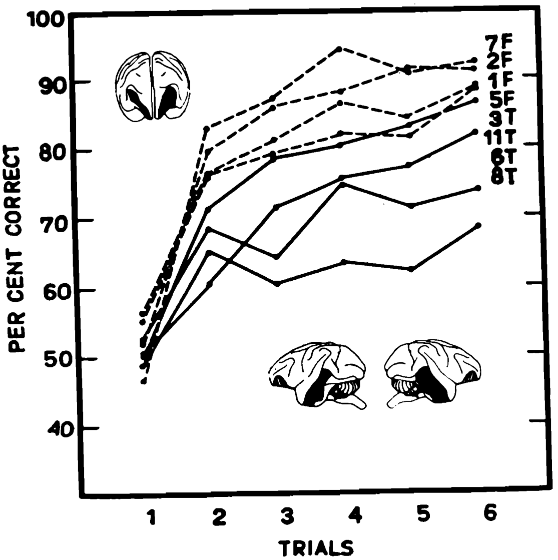

Fig. 2. Effects of inferotemporal and principalis lesions upon retention of an object learning set. (From unpublished experiments of L. E. Bettinger, R. A. Anderson, D. A. Yutzey, D. A. Dalby and D. R. Meyer.)

situations which otherwise are classical, direct method, spatial, delayed response test situations. The fact that frontal monkeys retain object sets, but fail the latter cue-augmented problems, implies and has for years that the principal sources of delayed response impairments are related in some way to the pre-delay features of this task. Thus the delay and post-delay features of two-trial object problems and cue-augmented spatial delayed response problems are of such a nature that, if these features make a difference, then the difference is in favor of performance of the cue-augmented delayed response task. Thus, on half the test trials, the positions of the objects are reversed in the two-trial object learning situation, while in the cue-augmented delayed response test, the positions of the cues and the reward are fixed. The intertrial interval of two-trial object problems is also of the order of 5 to 10 sec, or longer than the typical delay that is enforced in the object-cue-augmented delayed response tests. But the frontal preparation is able to perform in the two-trial object learning situation, and typically is not when it is tested in the cue-augmented delayed response test situation.

Our earliest analysis of pre-delay factors (Meyer et al. 1951) suggested that the frontal monkey fails delayed response tests because of what would now be called impairments of selective attending. We concluded, on the basis of our own observations and Malmo's (1942) results from indirect delayed response tasks that frontal preparations are particularly deficient in attending if the test situation is in flux at the time that the cue-reward contingencies are being presented. In other words, we thought that the experimenter's actions in trying to get the frontal monkey to observe the placement of the food reward into a foodwell of the test tray of a WGTA was a major factor in the animal's failure to perform. We still think that this is why experiments involving indirect delayed response procedures have generally resulted in the frontal monkey's being better at delaying than it is when it is tested with tasks that involve direct methods.

We believed, on this basis, that a further understanding of the sources of Jacobsen's effect could best be obtained with apparatus which would make it possible to study the differences between the delayed response problem and the two-trial object learning problem in a parametric manner. What we envisioned was an automatic system such that an observing response by the monkey would program presentations of cues and rewards at precisely controlled time intervals within the period before the delay. We wished, for example, to study the effects of inversions of times of presentations of rewards and pairs of discriminative cues, as this is one feature of delayed response procedures which differs from those involved in two-trial object learning situations. We also wished to have a stable test situation in which we could study retroaction as a factor in retention when the training conditions were such that frontal animals could learn.

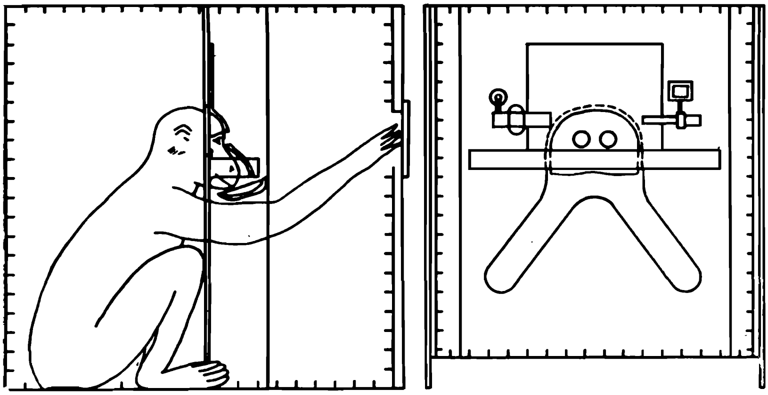

Fig. 3. Test compartment of the Mark II Ohio State Automatic Training Apparatus.

Figure 3 illustrates the general features of our automatic training apparatus. The discriminanda were rear-projected upon two screens which were placed directly opposite a mask into which the monkey could insert its head. The head-mask response, or observing response, controlled presentations of the cues, which could either appear simultaneously or separately and could both be operated upon at various time intervals in ways which were controlled by external programming devices. The system also automatically dispensed rewards for correct performances, and recorded responses in such a form that the data could be processed by a computer without any further preparation.

The lessons that we learned from our attempts to build such systems have been detailed by Meyer et al. (1965). In brief, we found that such systems are worthless for learning set experiments with monkeys, and hence that their only value is for studies concerned with stimulus-specific learning. In our own program, we have therefore returned to the use of the WGTA, which remains by far the most efficient training situation yet devised for work with lower primates. There is simply no substitute for objects as cues if one's interest is in concept formation, and concept formation is the sine qua non of our approach to frontal lobe problems.

However, we did employ our automatic system for one instructive frontal-lobe study. The system was in use at the time of the proposal by Rosvold and Mishkin (1961) that perseverative interferences are probably the source of many of the deficits exhibited by frontal preparations. We had noticed that a slight time difference in the presentation of a pair of color cues to monkeys had produced a roughly two-to-one preference for the first color cue. We were thus in a position to manipulate the preferences of monkeys for otherwise-neutral stimuli, and indeed to reverse a previously established preference for a given color cue.

These facts led us to design an experiment reported by Meyer et al. (1965) in which frontal animals and normal animals were trained on a series of red-green color discriminations and reversals of these discriminations. As Fig. 4 shows, we observed that frontal monkeys (with extensive prearcuate dorsolateral ablations) were the equals of normal animals provided that the reinforced color in a problem was the stimulus that came on first. However, if the reinforced color came on second, and therefore was the unpreferred color of the pair, the problem was difficult for frontal preparations, as predicted by the Rosvold–Mishkin theory.

We found that this difference grew smaller as a function of repeated presentations of the problems, but also, as is shown in Fig. 5, that a stimulus manipulation that had almost no effect upon the normal animals restored the perseverative effect in frontal subjects. This manipulation was a brief reversal of positions of the positive and negative cues just prior to the time that the monkey was permitted to respond. We took the reinstatement to mean that the decline of the effect of perseverative interference in the earlier series was not simply due to a process of passive recovery. Instead, it appeared that the tendencies remained, but

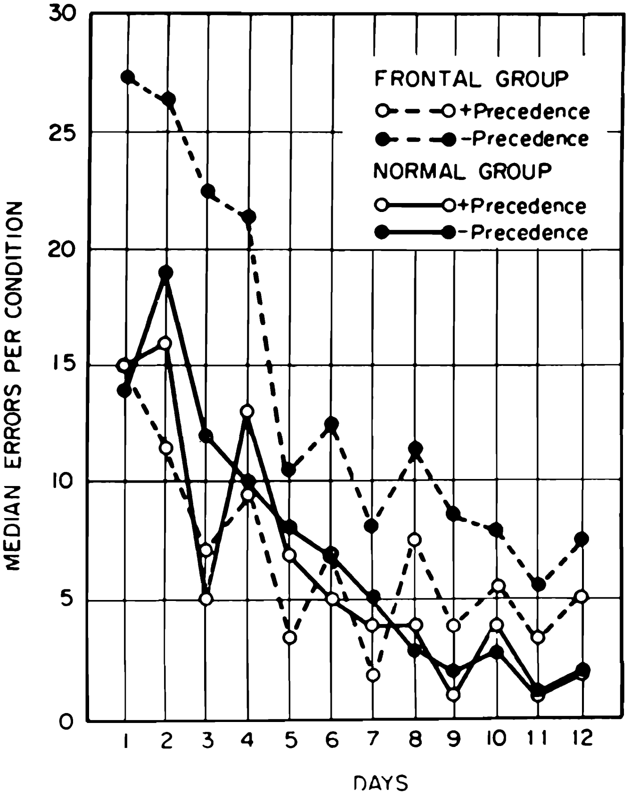

Fig. 4. Effects of cue preferences induced by time differences in cue presentations upon the acquisition of color habits by normal and frontal monkeys. (From Meyer et al. 1965.)

were undergoing active suppression by a process which could then be disinhibited by a small change in the training situation.

Although these effects were very large effects indeed, we were still not convinced that this impairment could account for delayed response deficits as well as it accounted for other frontal symptoms. The problem, as we saw it, was that object-cue-augmented classical direct delayed response tasks are substantially more difficult for frontal preparations than are two–trial object learning tasks. We therefore continued to believe that frontal subjects are impaired in the former situation because of their failure to selectively attend to the tester's pre-delay demonstrations. We thought that such a deficit was also implied by the fact that perseverative tendencies don't make the go–no-go form of the delayed response problem insolvable for frontals (Pribram 1955). Our view was that the go–no-go training procedure aids selective pre-delay attending, and that this was the principal difference between it and the classical delayed response procedure.

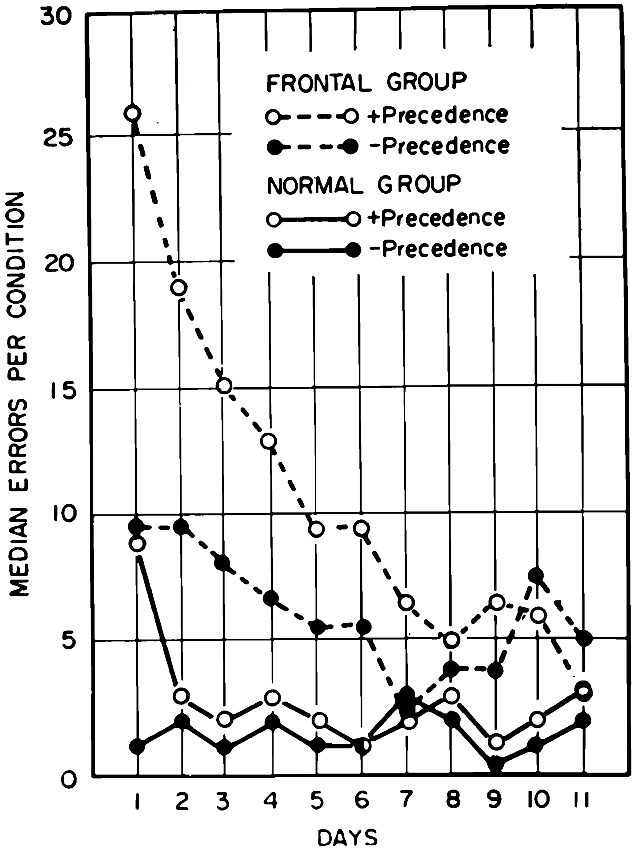

Fig. 5. Effects of cue changes upon compensated perseverative tendencies induced in frontal monkeys by cue preferences. (From Meyer et al. 1965.)

Our next step was therefore to develop a procedure for studying the differences between the object-cue-augmented delayed response task and the two-trial object learning task insofar as these can be conveniently assessed through the use of the WGTA. As Finan (1942) had observed, pre-delay reinforcement facilitates delayed responding by the frontal monkey, but the problem then becomes akin to two-trial object learning in that a reward given prior to the delay is a feature of object learning methods. In classical delayed response procedures, food rewards are shown to, but are withheld from the subjects, and this by itself could be a factor in the frontal animal's delayed response impairment. Accordingly, we wanted to withhold food rewards during trial setting prior to a delay, but we also wanted to employ food rewards in a manner which would guarantee selective pre-delay attending to cue-reward relations.

We solved this problem by constructing a modified formboard for the WGTA. As Fig. 6 shows, this formboard or test tray had a thin metal lid upon which objects could be placed. Three holes were cut into this lid to correspond to three small underlying foodwells, but a gap was left between the lid and the foodwells so that transparent plastic lids could be inserted and hence employed as clear foodwell covers. Therefore, when these covers were in place and the monkey displaced an overlying cue object, it could see into the foodwell underneath that object but could not obtain a food reward from it.

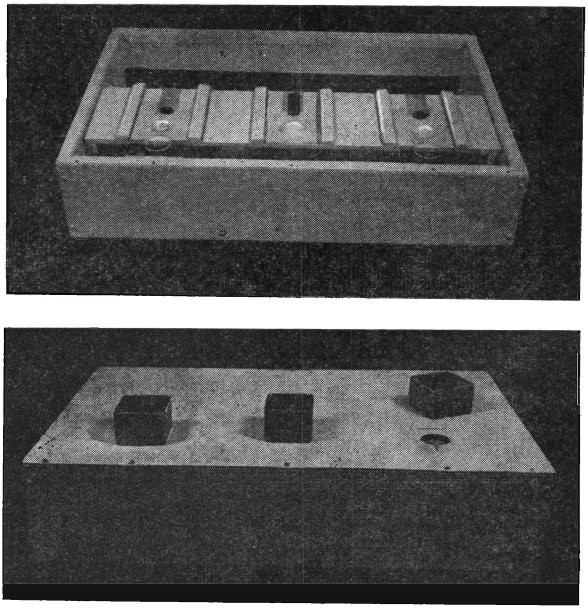

Fig. 6. Interior features of the Blake et al. (1966) apparatus, and appearance of the test tray as arranged for the first experiment.

We used this test tray in an experiment reported by Blake et al. (1966). We built it to accomodate three objects because of our interest in the finding of Konorski and Ławicka (1964) that frontally-ablated animals may fail an indirect delayed response test and yet, if permitted a subsequent correction, show some evidence of retention. This result prompted us to look, initially, at performances of normal and dorsolateral frontal monkeys in three-trial task situations. These were all cue-augmented spatial problems, with a red cube, a green cube, and a blue cube which remained in the same positions on the formboard serving as the manipulanda. On first trials, the baited foodwell was sometimes uncovered and sometimes covered, but it could always be seen into as soon as the monkey displaced the overlying colored cube. On second trials, the test trials, the animals were given a choice between the three colored cubes, and when their choices were incorrect, they were given third or correctional trials on which they were permitted to choose between the two remaining cubes.

As we anticipated, normal animals were not challenged by these kinds of problems. However, frontal monkeys with prearcuate dorso-lateral lesions were unable to perform beyond chance levels on either the test trials or on the correctional trials. This was so regardless of whether the rewards were obtained or were withheld, although visible, on training trials. Hence, it appeared that interferences between successive examples of the problems were so strong that it simply didn't matter whether the frontal subjects attended to the cues or not or whether they were given pre-delay reinforcements when responding to the cues or not.

In the second experiment, the same groups of subjects were tested with the same apparatus. The paradigm employed was delayed matching from sample. As shown in Fig. 7, each trial began with the presentation of a sample object above the center foodwell. On half the delay trials, a reward could be obtained as soon as the monkey displaced the sample object. On the other trials, a reward was visible, but not immediately obtainable. The same object, itself a novel object, was then paired with

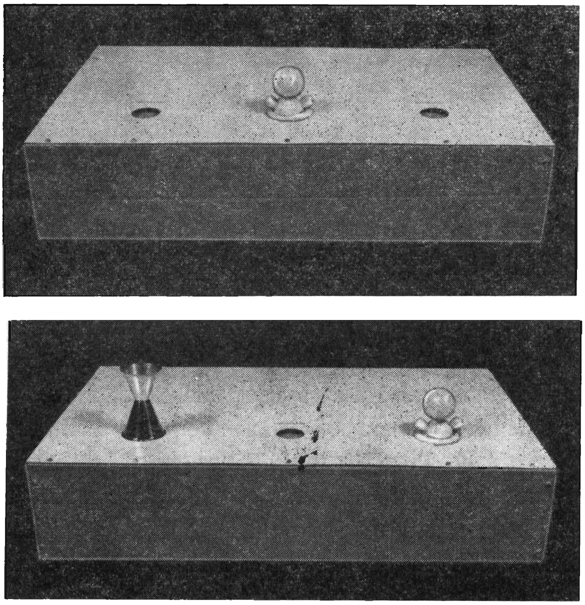

Fig. 7. Appearance of the Blake et al. (1966) apparatus during presentations of a matching stimulus and during test trials in all varieties of two-choice tasks.

another novel object, and the animal was finally permitted to choose between the two objects after a delay of 5 sec. The results of this study were that normals and frontals performed well under both conditions, which suggested that the outcomes of the first experiment had not been produced by a frustrative effect of showing but withholding rewards.

In the main experiment, we trained the animals on two-trial, two-choice object learning problems in which, on the first trial, the animal displaced the objects and obtained a food reward, and on quasi- or implicit-discrimination problems which differed from the object learning problems in that, on the first trial, the animal displaced the objects and could see, but could not obtain a food reward placed beneath the object whose selection on the next trial would be reinforced with that reward. The monkeys were also tested daily on a series of object-cue-augmented delayed response problems. Figure 8 shows the procedure in this problem,

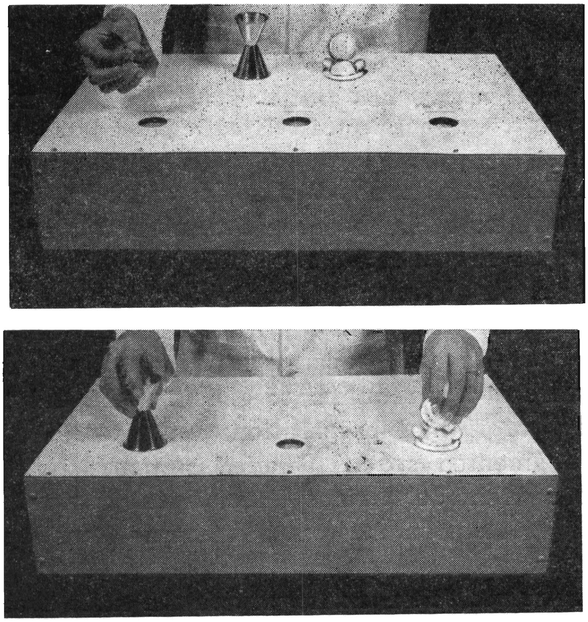

Fig. 8. Appearance of the Blake et al. (1966) apparatus during pre-delay presentations of contingencies in object-cue-augmented delayed response tasks.

and serves to make clear that on the test trials the appearance of the test tray was the same regardless of the way that pre-delay information was presented to the subject.

As Fig. 9 shows, all but two of six frontal monkeys failed the delayed response task. One of these subjects was subsequently found to have an inadequate lesion; the other, which had an initial deficit, eventually was

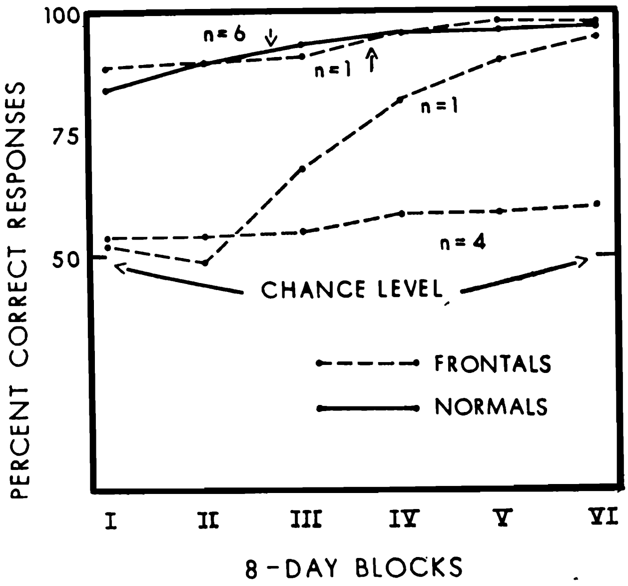

Fig. 9. Performance of normal and frontal monkeys on the Blake et al. (1966) object-cue-augmented delayed response tasks.

able to perform. The six normal subjects did well from the beginning and hence, with the one exception noted, the results of this study confirmed an old finding of the Meyer et al. (1951) study.

As Fig. 10 demonstrates, all animals did well on two-trial object learning problems, and this again confirms a result which was obtained from the semi-hemi-frontal preparations. These data also show that a pre-delay reward is not required to generate the difference between the performances of frontal preparations on two-trial object learning tasks and cue-augmented spatial delayed response tasks. Withholding the reward had a slight deleterious effect upon obtained performances, but this was no greater for the group of frontal monkeys than it was for the group of normal monkeys.

Finally, we retrained these monkeys with the same procedures as had been employed in the first study. Our thoughts were that intraserial interferences had produced the initial deficits and, since we found in the experiment conducted by Meyer et al. (1965) that such impairments are partially compensible, that some improvement might be expected. We found that the frontal monkeys still had deficits, but that all performed better than before, and concluded that delayed response impairments can, in fact, be produced by perseverative interferences alone when the animals are tested in situations which maximize such interferences.

Our over-all conclusion thus was best expressible in a play on the language of logic: perseverative tendencies can sometimes be sufficient, but are not necessary for the demonstration of the classical delayed response impairment. In test situations which maximize proaction, it may not matter whether dorsolateral frontal monkeys attend to the pre-delay contingencies or not. In test situations which minimize proaction, frontal monkeys still may have a deficit provided that pre-delay attending to the cue-reward contingencies is not guaranteed by the procedure. Either of these limitations of the frontal monkey appears to us to be severe enough to generate delayed-response deficits as measured in most delayed-response situations.

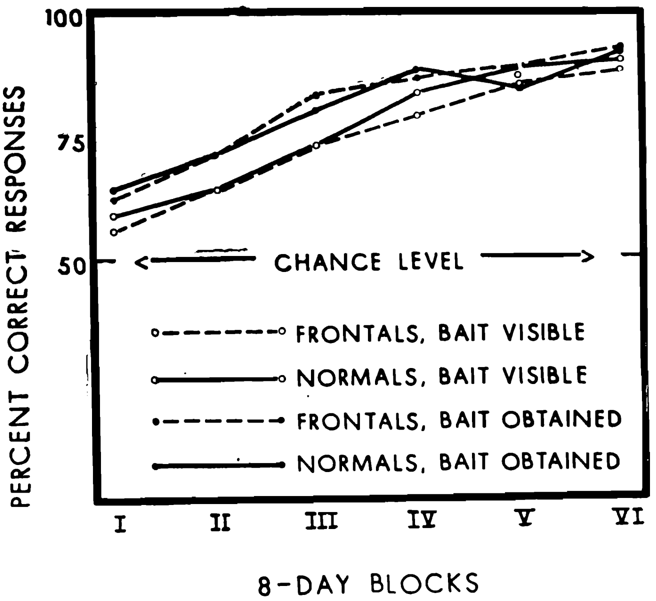

Fig. 10. Performances of normal and frontal monkeys on the Blake et al. (1966) object learning problems and implicit (bait visible but not obtained) object learning problems.

Our experiences with cats also seem to be consistent with this pluralistic view of frontal losses. Our group has had a long-standing interest in the problem of recovery of central neural functions, and hence in the relationship of age at operation to deficits produced by brain lesions. As is now well known from the experiments with monkeys performed by Akert et al. (1960), perinatal frontal extirpations in this species do not produce the Jacobsen effect. This work prompted my student, Thompson (1968), to see if this relationship applies to the indirect delayed response phenomena observed in cats by Lawicka and Konorski (1961). His choice of the indirect over the direct approach was principally determined by the failure of Warren et al. (1962) to find a consistent classical delayed response deficit in cat frontal-lobe preparations.

Thompson's apparatus, shown in Fig. 11, was a very large triangular field with a start box in the middle. The three response compartments were located at the apices. The correct compartment on any given trial was signalled by the sounding of a buzzer, and the cat was released from the start box immediately after the buzzer was sounded. If its choice was incorrect, it could return through the start box and choose between the other two compartments, and hence the situation was analyzable by the techniques developed by Lawicka and Konorski for their own three-box indirect delayed response test.

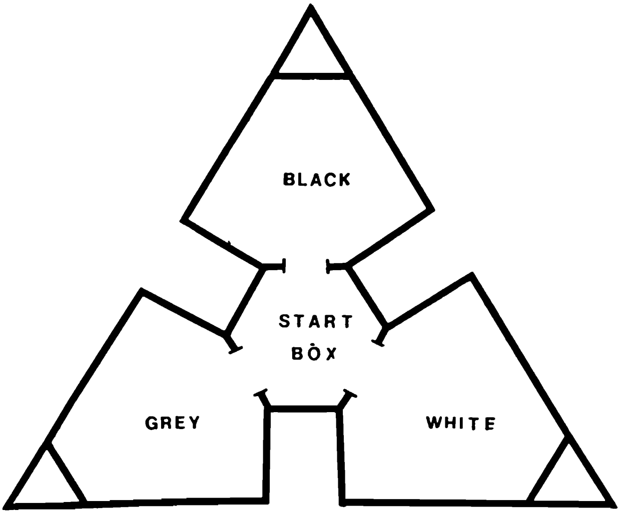

Fig. 11. Effective floor plan of the Thompson apparatus for indirect delayed response testing of cats. The stimulus sources (buzzers) were contained in the small, triangular food boxes at the ends of the choice compartments.

Thomposn was able to confirm, with frontal cats, the great majority of their results. However, more importantly, he found that such effects as increases in perseverative tendencies and changes in preference-omission errors were also observed in kittens subjected to frontal operations in the second week of life or as six-week juveniles and then tested in adulthood. This suggests either a large species difference in the age-at-operation/recovery relation which is not supported by the outcomes obtained from other studies (e.g., Benjamin and Thompson 1959, Sharlock et al. 1963, Wetzel et al. 1965), or that the compensation found by Akert et al. (1960) is for one but not all frontal deficits. To us, the latter viewpoint seems more reasonable, and we suspect that the compensable function in rhesus monkeys is the function of selective attending.

While Thompson, as we noted, confirmed the major findings of the study by Ławicka and Konorski, he was unable to detect retention on correctional trials after first-choice errors in his training situation. He concluded on this basis, and also on the basis of the findings of Blake et al. (1966), that second-choice correctional behavior is not a strong phenomenon in frontal preparations. However, in subsequent experiment with monkeys, we have found some support for the conclusion that frontal preparations may succeed on second trials after having failed on first trials.

The animals employed for this study had had extensive object learning set training prior to being prepared as inferotemporal or as sulcus principalis subjects. The tests were three-choice delayed response problems presented with Blake et al. (1966) formboard which were either arranged with groups of novel objects or with familiar objects at the cues. Following a first "trial" which was carried out with classical direct-method presentations of the cue-reward contingencies, the animals were given a second, or test trial and then a third, correctional trial if they failed to choose correctly on the second trial.

All four frontal subjects were severely impaired when recurrent objects were employed in conjunction with classical direct method delayed response procedures. They were worse in every instance than matched inferotemporals except in one pairing out of the four in which the inferotemporal animal had failed to learn the problems prior to operation. Further, when the frontal monkeys failed on test trials of problems of this kind, which maximized interference, they gave no evidence of being able to choose correctly on correctional trials.

The problems were easier, as was expected, when novel objects were employed as cues, and the deficits observed in the frontal preparations were much more modest than they were when the lesions extend across the dorsolateral surface. In this situation, after test-trial failures, their correction scores were 70±2⁰/₀ as contrasted with correction scores of 48±2⁰/₀, or chance, when problems were arranged with three recurrent or familiar objects. Thus, we can agree that a failure to delay does not always mean no retention, ant that opportunities to make corrections will sometimes show that an animal has learned but simply is unable to perform. We would stress that second-trial correctional behavior, when observed, is observed when the lesions are small or the training situation is one in which performances on first trials tend to be somewhat higher than they are in classical delay situations.

In another experiment conducted with these subjects, we were interested, primarily at least, in the role of the anterior inferotemporal cortex in the learning and retention of habits. These monkeys were the animals whose learning-set data have been summarized in Fig. 2. The inferotemporal subjects, as we mentioned earlier, had deficits in object set retention, but they also had deficits in visual habit learning. and these are not the same deficits.

Our approach to the visual habit learning deficit was via a training paradigm in which single visual discrimination habits, and reversals of these habits, were learned by the monkeys after zero, one, two or three interpolations of practice with six-trial novel object discrimination learning problems. The stimuli employed for habit training were a cut-out red circle and a cut-out green triangle which were each mounted on wedges whose surfaces were tilted upward toward the monkey. The wedges were, in turn, mounted on bases which slipped into U-shaped guards attached to the test tray in front of each foodwell so that the animal could not conveniently displace the wedges without manipulating the objects displayed upon their faces.

In a typical problem, the animal was trained to choose, say, the triangle until it had done so on a series of five successive trials. Then it was given practice with a series of conventional six-trial novel-object problems, and after that training, was represented with the triangle-circle discrimination problem with either the same or reversed cue-reward contingencies. Retention of this habit could thus be measured by trial-one positive or negative transfer in a series of trials which served to re-train the monkey on the habit or its reversal to the five-correct-responses-in-a-row criterion so that another series of interpolated problems could again be given. In this way, many transfer measures were obtained instead of a single transfer measure, and hence there was enough trial-one data to permit the expression of amount of habit transfer in quantitative terms.

We found that the animals, as normals, could remember the prior cue-reward contingencies until three six-trial novel-object problems had been interpolated between the last training trial and the first re-presentation trial. As Fig. 12 shows, the monkeys which were then prepared with lesions of the sulcus principalis were also able to retain the last habit for that long after surgery. This served as just one further demonstration of the fact that monkeys with delayed response impairments have little difficulty in remembering relations provided that they learn them in the first place. However, the more interesting result in this display is the poor performance of the inferotemporals, which suggests at first glance that they have memory deficits so profound as to

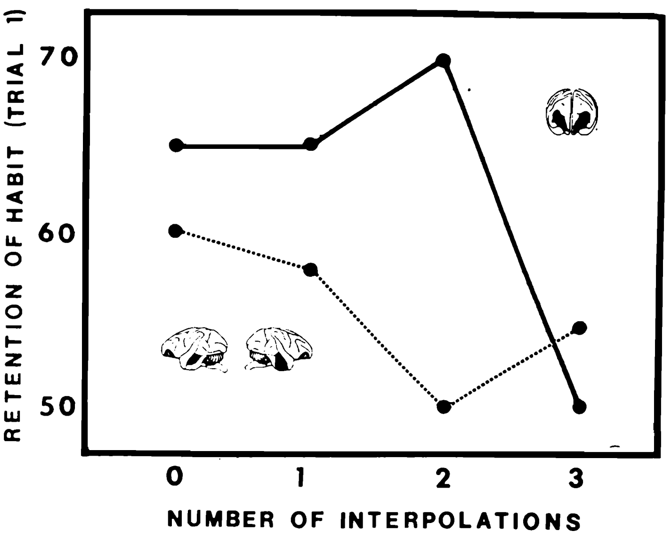

Fig. 12. Effects of interpolated practice with six-trial object learning problems upon retention of visual habits by frontal and inferotemporal monkeys. (From unpublished experiments of L. E. Bettinger, R. A. Anderson, D. A. Yutzey, D. A. Dalby and D. R. Meyer.)

be measurable even if the test is given immediately after the habit has been learned to the fixed criterion.

We have shown, nonetheless, that this impairment isn't due to a simple decay of memory traces. Its most important source is an exaggeration of the tendency we find in normal monkeys to learn habits both to pairs of differential cues and to the non-differential background of these cues when both are present in paired discriminanda. In the study just described, we manipulated backgrounds as follows. Under one condition, the backgrounds were black and remained so throughout a series of presentations of the circle-triangle problem and reversals of the problem. Under the other condition, the backgrounds changed from black to white and then back to black, and so on, each time the circle-triangle problem was re-presented to the monkeys. Importantly, however, the backgrounds were the same within problems under both conditions; that is, they were either both black or both white, and hence were not differential cues.

As Fig. 13 illustrates, changes in the background had almost no effect upon the trials required for frontal monkeys to meet the criteria of five correct responses in a row. However, under constant background conditions, the inferotemporal monkeys made many more errors than they did when the backgrounds alternated. This result supports the Butter et al. (1965) hypothesis that inferotemporal monkeys have impairments in

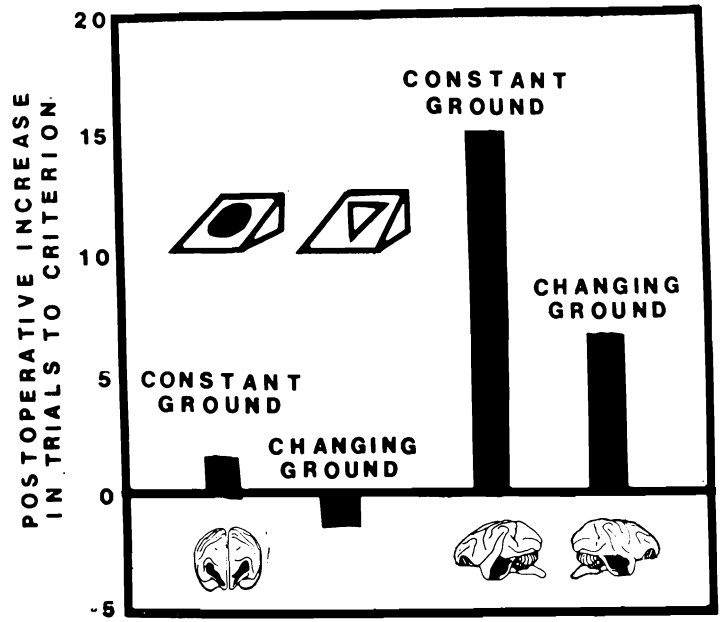

Fig. 13. Effects of alternation of the colors of the backgrounds of stimuli upon visual-habit learning rates of frontal and inferotemporal monkeys. (From unpublished experiments of L. E. Bettinger, R. A. Anderson, D. A. Yutzey, D. A. Dalby and D. R. Meyer.)

learning which of the stimuli of several in a compound are relevant to problem solution. Thus frequent changes in the backgrounds of the cues enhanced the two differential cues, and the inferotemporal monkeys then were able to learn at rats which were only modestly inflated respective to preoperative levels.

We think that these findings indicate that problems which are widely used in inferotemporal studies would be very much easier for inferotemporal monkeys if the differential cues that the animals are asked to discriminate between were displayed upon backgrounds whose properties were changed from trial to trial. The plus-square problem that is favored by M. Mishkin serves as an excellent example, and another is provided by the plus-cross problem that has been employed by W. Wilson. But we think that these problems would continue to challenge the inferotemporal animal because there is evidence suggestive of the view that such monkeys have visual sampling deficits as well.

When a plus and a square are displayed upon two cards which monkeys displace when they respond, even normal monkeys are primarily controlled by cues near the edges of the cards. This, the spatial S-R contiguity effect, has proved to be extremely powerful (Meyer et al.

1965); thus, in pattern-learning situations, cue-response separations of the order of one centimeter have been shown to affect the sampling process. The effect is the principal source, in our opinion, of differences in "saliencies" of cues (*see* Butter and Gekoski 1966, Rothblat and Wilson 1969), but its possible role in inferotemporal deficits has thus far gone undiscussed except in a recent paper of Butter and Hirtzel (1970).

The proof of this notion is not yet complete, but we do know that inferotemporal monkeys are the equals of normals in learning situations which suppress contiguity effects. In recent work with Dr. G. Hamilton, we managed to design a set of objects whose form-size differences were shown by us to be as discriminable as color differences. To do this, we emphasized near-cue differences, as near cues are virtually the only cues that monkeys attend to in formboard situations. Figure 14 illustrates this set of objects as they appeared upon the test tray; they were mounted on bases, but the base cues were rendered ineffective throught the use of U-shaped guards. The objects were painted in five different colors, and were multiply re-paired to yield problems in which the objects differed with respect to form-size, to color, or to form-size and color.

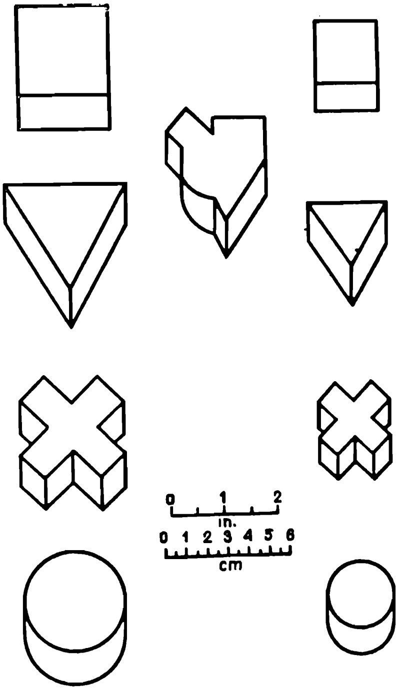

Fig. 14. Bias-free object discriminanda developed by G. Hamilton and D. R. Meyer and utilized in the G. Hamilton experiment. Color reduction was accomplished by substituting white for hues; form-size reduction was accomplished through the use of composite form-size objects. Subsequent experiments have shown that the same results are obtained when cue reduction is accomplished by substitutions of positive or negative objects.

In Hamilton's experiment, the main mainipulations consisted of additions of substractions of form-size differences or color differences after the animals had previously learned to discriminate between pairs of objects which differed in form-size, or color, or color and form-size. This paradigm was based upon a method first employed by Warren (1954) in a cue-summation study. In cue-addition problems, the monkey first learned a color or a form-size problem, and then form-size or color differences were added to the cues which were already present. In cue-subtraction, the monkey first learned a color-form-size discrimination and then, after six-trials, the color or the form-size differences between the objects were removed. Following either addition or subtraction, the animal was given six more trials, and then the initial cue conditions were restored for a further, final, six retention trials.

After a preoperative training program, Hamilton's fifteen monkeys were divided into groups of five subjects each. One group consisted of normal controls, and the other two of anterior inferotemporal and sulcus principalis preparations. The animals were then retrained, and gave the results which are summarized in Fig. 15. In general, any change whatsoever in the cues, whether of addition or subtraction, disrupted the seventh-trial performances of all groups but not the thirteenth-trial performances.

These results demonstrate that inferotemporal monkeys attend to as many cue dimensions as normal monkeys do if these dimensions can be shown to be equally discriminable dimensions. They also learn as fast as either normals or frontals and also, in the short term at least, retain the discriminations that they learn as well as either normals or frontals. Thus, when discriminative cues are made distinctive and responses to these cues are enforced, the inferotemporal animal shows none of the impairment that it has in situations which facilitate the sampling of non-differential stimuli.

These facts, together with the others we have cited, now suggest a simple explanation of an old observation that we didn't understand at the time that the data were collected. As was mentioned earlier, the subjects that were studied in the Meyer (1958) and Akert et al. (1961) experiments were monkeys with complete anterior temporal decortications. Prior to operation, four of the animals were trained with object learning set procedures, and these were the monkeys whose learning set retention data are shown in Fig. 1. Four other animals did not have learning set training before the surgery but, instead, were given practice with a green-blue discrimination problem for the same total number of trials that the set-trained animals received while learning six-trial object discrimination problems.

The 840 trials had been divided among five cases of the problem

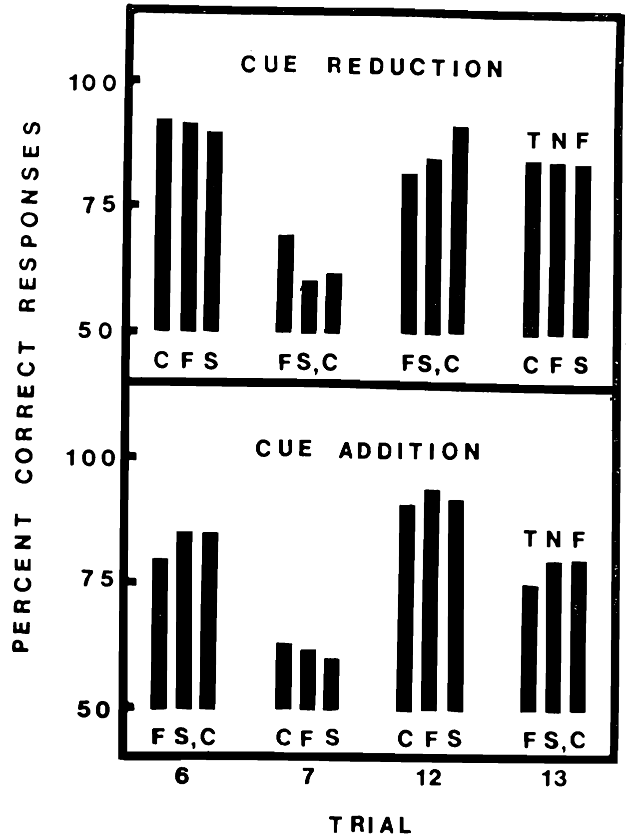

Fig. 15. Results of the main experiment of G. Hamilton. Note the similarity of rates of learning of form-size and color problems and the similarities of the effects produced by cue addition or cue subtraction upon the performances of normal, inferotemporal and principalis subjects.

which differed only in the amounts of cue presented and in the widths of common white borders surrounding the two color cues. Within pairs of stimuli, the colored areas and the widths of the borders were the same, as in the center-cue color-pattern problems examined by Warren (1953) in his program of experiments concerned with the effects of area and arrangement of cues on the rates of color-pattern discrimination learning by monkeys. Because we were not then aware of the power of the spatial contiguity effect, we displayed these patterns upon pairs of free-standing wedges which the monkeys could displace in any way that they pleased.

As Fig. 16 shows, the monkeys that had had preoperative training on the problem did very much better than the monkeys that had had preoperative training on object learning problems but not on the color-

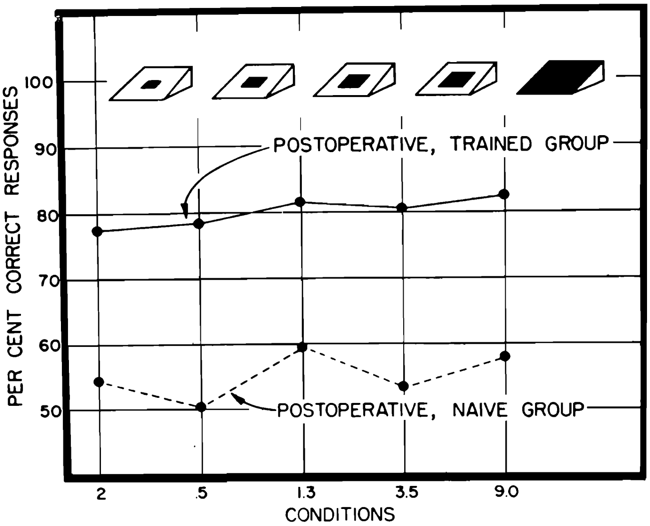

Fig. 16. Effects of anterior temporal decortications upon post-operative learning or relearning of green-blue color-pattern problems. (From Meyer 1958; brain reconstructions are reported by Akert et al. 1961.)

pattern problems. But why? We now believe that, in accordance with a theory recently developed by Stollnitz (1965), the monkeys given training on these problems while normal developed observing responses which survived the effects of anterior temporal lesions. The monkeys not given preoperative training were unable to acquire there responses because, being subject to sampling biases, they were being trained on problems which only very rarely presented the color cues to them.

We next wish to look at the loci and extents of the lesions of Hamilton's monkeys. Figures 17 and 18 present conservative initial estimates of the sites of the sulcus principalis lesions and the inferotemporal lesions respectively. It is our impression that the inferotemporal placements tend to be Iwai and Mishkin's (1969) zones III and IV. Hamilton found that her inferotemporal monkeys were impaired in learning card-pattern problems presented without the use of edge guards, a result which is consistent with the learning impairments of our naive anterior temporal monkeys. The lesions are out of the focus proposed by Iwai and Mishkin for relearning a plus-square habit, and we judge from our results from the anterior temporal monkeys that Hamilton's monkeys would not have been impaired on relearning of such tasks if they had been presented prior to surgery. We offer, on these bases, the speculation that the plus-square relearning gradient reflects a posterior temporal focus for impairment of retention of observing responses.

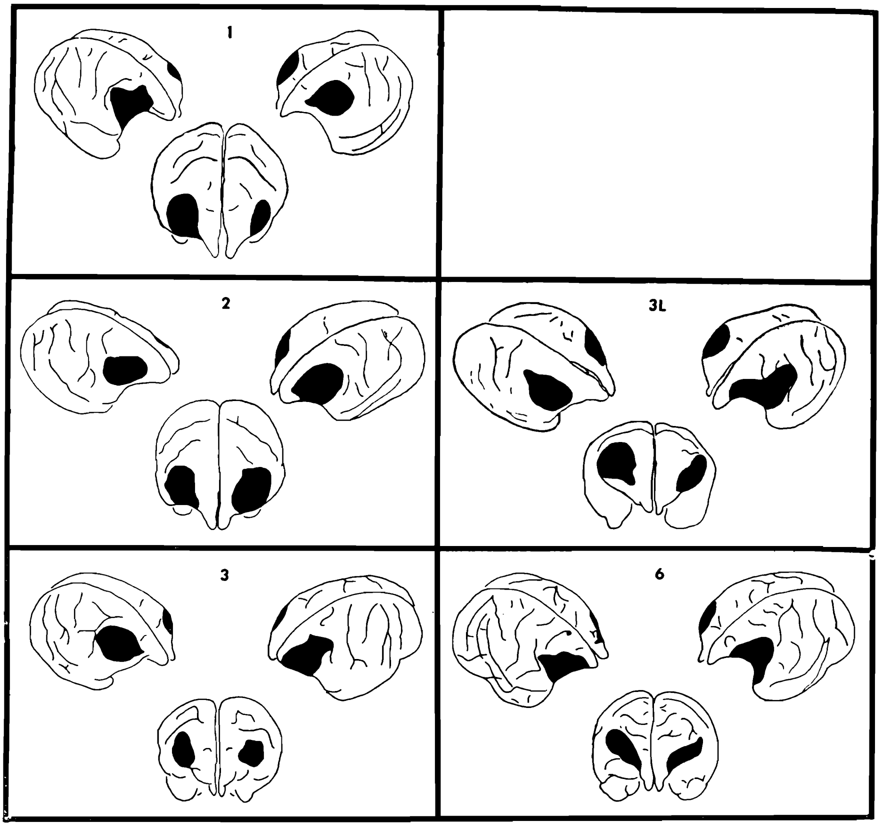

Fig. 17. Appearance of the lesions of the G. Hamilton principalis subjects. All of these animals had deficits when tested on classical delayed response problems.

Finally, the lesions of the inferotemporal subjects studied by Hamilton are in the focus that has been proposed by Iwai and Mishkin for impairments of learning of concurrent discrimination problems. Inasmuch as object learning sets are also grossly affected by lesions in this region, we are posed with the problem as to whether these two tasks are measures of the same processes. We suspect that they are, but we are not aware of any systematic studies of the question; however, we consider having it defined as a very good start for future work.

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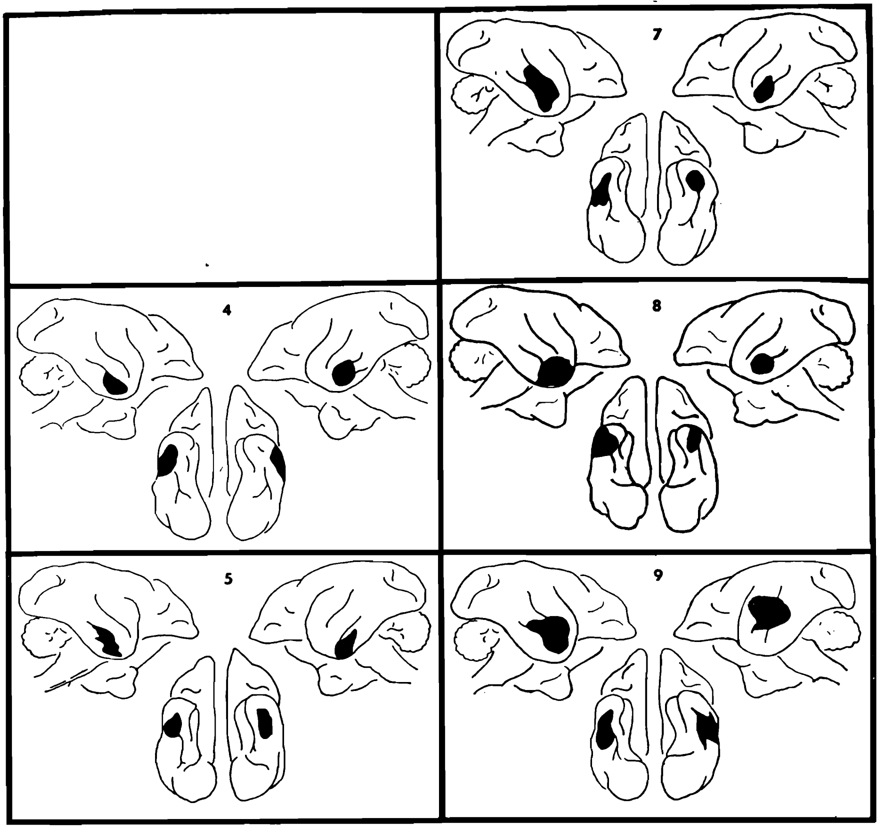

Fig. 18. Appearance of the lesions of the G. Hamilton inferotemporal subjects. All of these animals had deficits when tested on traditional visual pattern problems.

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