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ALTERNATION IN NORMAL AND FRONTAL MONKEYS AS A FUNCTION OF RESPONSE AND OUTCOME OF THE PREVIOUS TRIAL[1]

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Normal monkeys can learn to perform well on the delayed-alternation task; monkeys with bilateral lesions of the lateral frontal cortex cannot (Jacobsen & Nissen, 1937). In this experiment, attention is drawn to two characteristics of the usual delayed-alternation test, and each of those is varied, in order to determine whether they affect the behavior of monkeys and to facilitate analysis of trial-by-trial influences upon alternation behavior.

Alternation is usually presented with the rerun correction technique: When *S* makes an error, the next trial is presented with the reward unmoved, so that on this trial *S* can "correct" by going to the side which was baited on its unrewarded trial. An obvious variation of this is to run the series as a strict noncorrection procedure; when *S* makes an error, the reward is nevertheless moved (alternated), so that *S* must go again to the side which was previously unbaited in order to be correct.

Alternation is usually presented as a contingent procedure, in the sense that the information available to *S* on each trial depends to some extent upon the response that *S* has made. Thus, the response (of opening a box, displacing a foodwell cover, etc.) customarily lets *S* see whether or not there is a reward in the box or foodwell responded to, but does not inform *S* whether or not the *response not made* would have been rewarded. The obvious variation here is to arrange the apparatus so that response to either side opens both sides (and thus information is not contingent on the response made), although *S* can only *get* the reward if it is on the side responded to.

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METHOD

Subjects

Eight rhesus monkeys served as *Ss*; four of these animals had received cortical ablations approximately 15 mo. previous to this testing. They had all been used by J. S. Stamm preoperatively and postoperatively in an experiment on social behavior in a food-reward situation, and in an experiment involving pressing a bar for food reward on a DRL schedule. They had had no previous training on an alternation task.

Lesions

The monkeys in the experimental group had received one-stage bilateral resections of an anterofrontal cortical area corresponding approximately to von Bonin and Bailey's (1947) areas FD; the general surgical and histological procedures have been previously described (Pribram, Mishkin, Rosvold, & Kaplan, 1952). Copies of the reconstructions of the lesions may be obtained from the author; they are quite similar to others which are already available (Mishkin & Pribram, 1955).

Apparatus

Within a Wisconsin General Testing Apparatus, *S* was presented with a special testing board, consisting of a black horizontal surface upon which were mounted two black plastic boxes separated by a transparent Plexiglas barrier. The boxes, which served as covers for shallow foodwells, were hinged at the back and weighted. An aluminum clip could be attached to connect the boxes so that if the front of either box were slightly raised, both would fly open. For those trials on which it was desired that response to a given box would cause only that box to open, "half-clips" were attached to each of the boxes, giving an appearance quite similar to, although probably discriminable from, the single-clip situation.

Procedure

Preliminary training was confined to 2 days. On the first day, *Ss* learned to open transparent boxes of the same design as those used in the experiment proper but mounted on a different board. On the second day, the regular testing board and opaque boxes were employed. On all but the last trial *S* was permitted to open each of the two boxes in turn and to get rewards placed under each. On the last trial the clip was used, so only one opening response was required.

The *Ss* received 40 scored trials a day for 20 days.

TABLE 1

Mean Number of Response Alternations in 200 Trials under Each Procedure

Procedure	Normals	Frontals
Correction-Contingent	113.00	80.25
Correction-Noncontingent	104.50	80.50
Noncorrection-Contingent	106.00	79.50
Noncorrection-Noncontingent	105.00	76.50

Each testing day consisted of four series of 10 trials each, conducted under a different one of the four procedures described below. On a given day each of the four normal animals was assigned to a different order of procedures, such that each procedure was first for one normal *S*, second for another, etc.; furthermore, for each *S*, within any block of 4 days, each procedure was first on one day, second on another day, etc. Each operated animal received the same sequence of testing as one of the normal *S*s.

A single peanut served as the reward throughout the experiment. For the correction-contingent series of trials, the reward was always placed on the side other than the one *S* had last responded to, and the two half-clips were used; for correction-noncontingent, the single clip was used. In the noncorrection-contingent procedure, the reward was always placed under the box that had not been baited on the previous trial, and the half-clips were used. For noncorrection-noncontingent, the single clip again was employed. The intertrial interval was approximately 5 sec.

Each series of trials was preceded by an unscored free trial. For a free trial, the reward was placed where it would have been if the *previous* series of trials were being continued, but the box (or boxes if the new series was to be noncontingent) was open. For the first scored trial of a series, then, the reward was placed on the other side.

Results

In Table 1 are shown, for each group, the mean number of response alternations made under each of the procedures. Only a few of the scores go much above 100 (50%), but the effect of lesion upon tendency to alternate is borne out. An analysis of variance of the data broken down into five blocks of trials disclosed no source of variation significant at the .05 level except the effect of lesion and the effect of blocks. In other words, there is no evidence that either of the two experimental variations affected directly the overall tendency to alternate in either the normal or the operated animals, although the two groups differed and all *S*s increased their rates of alternation during the course of the experiment.

Inclusion of the noncorrection series permits a fruitful analysis of trial-by-trial influence upon alternation. Under the correction procedure, a correct response is equivalent to a response alternation, so that alternation following a reward cannot be separated from alternation following a previous alternation. The noncorrection procedures allow us to untie these variables and to assess separately the relationship to a succeeding alternation of a previous alternation and a previous reward.

Thus the percentages of alternation were computed separately for trials (*a*) following a trial on which *S* had alternated and been rewarded, (*b*) following a trial on which *S* had alternated and not been rewarded, (*c*) following a trial on which *S* had not alternated and had been rewarded, and (*d*) following a trial on which *S* had not alternated and had not been rewarded. (Each of these percentages of alternation was computed separately for the contingent and the noncontingent series, but no significant or suggestive differences were noted for either normal or operated *S*s; the results of these two series have been combined in the data presented in Table 2.)

It is apparent that both previous reward and previous alternation strongly affect normals; having alternated on the last trial and having not been rewarded on the last trial both lead to an increased probability of alternating on the succeeding trial, and their effects are approximately additive. Frontals

TABLE 2

Percentage of Alternation as a Function of Response and Outcome of Preceding Trial

S	Preceding Trial[a]			
	A-R	A-NR	NA-R	NA-NR
Normal				
394	53	56	40	45
396	54	53	36	49
398	49	69	27	48
384	61	83	33	72
Total	55	68	34	52
Frontal				
381	49	51	41	43
437	42	46	27	26
361	49	48	38	35
433	43	39	31	32
Total	46	46	33	33

[a] A, alternated; NA, did not alternate; R, was rewarded; NR was not rewarded.

are affected by their previous behavior, alternating more if they have just alternated, but are unaffected by the presence or absence of reward. An analysis of variance supports this conclusion. The effect of alternation is significant ($p < .001$) as is the effect of lesion ($p < .05$). There is a significant main effect of reward, but there is also a significant lesion × reward interaction (both p's $< .01$). The other interactions do not approach significance.

Since all alternation rates tended to increase during the course of the experiment, additional analyses were run on the four alternation rates computed for each of five blocks of 160 trials. For neither of the groups was there a significant interaction involving blocks. The differences between the groups with respect to the importance of previous response and previous outcome are constant over blocks and cannot simply be ascribed to difference in overall alternation tendency.

Discussion

The fact that frontal operatees maintain their patterns of response regardless of the presence or absence of reward on a given trial lends itself to interpretation in terms of two common theories of frontal lobe function. We may emphasize the lack of influence of the position of the reward and seek to explain the results in terms of some theory of a loss in the inhibition of appetitive mechanisms. Or we may emphasize the resiliency of the alternation or perseveration tendencies established by the previous response and conclude that the frontal operatee displays a loss of response inhibition. As they are usually stated, however, each of these inhibition theories is unable to subsume all of the available data, as Rosvold and Mishkin (1961) have recently pointed out.

A view presented by Mishkin, Prockop, and Rosvold (1962), which may be considered a variety of the response inhibition theory, does incorporate many of the previous data and some of those offered here. They propose that frontal operatees in particular have difficulty in relinquishing strongly preferred responses, presumably whether guided by stimuli or by previous responses. Thus, if we consider that the responses of our *S*s fall into the classes "alternate" and "perseverate," the response to perseverate is the preferred one (chosen approximately 67% of the time) when the previous response also has been one of perseveration. Normals tend to relinquish this response if it is not rewarded, frontals do not.

When the previous response has been an alternation, however, normal *S*s show no strong preference between the two responses, and yet here, too, the lack of reward does not have, for frontals, the normal effect upon the succeeding response. This would seem to be a situation in which the Mishkin theory would predict that frontals would not be different from normals (as would be also tests of *retention* of delayed response or alternation).

We return then to the idea that frontals are not so affected as normals by the outcome of previous trials. (For a similar view, see Pribram, 1960.) Since the two groups show similar response patterns when the previous trial is rewarded, it might be suggested that the frontals are particularly unresponsive to the absence of reward. It would, however encompass more data to suggest they differ from normal animals in the distribution over time of the effect of reward. In a generally rewarding situation, such as a WGTA testing situation, the animal tends to respond as if reward were continually present. There is obviously not a complete lack of effect of the time of reward; these animals do learn discrimination problems and often respond above chance on delayed response. But when the chance of confusion between trials is maximized (e.g., by delay periods within trials, or by massing of numbers of trials) or the necessity for localizing the time of reward is maximized (e.g., discrimination reversal training, or training to nonpreferred stimulus) their deficit becomes noticeable.

Regardless of the usefulness of these various lines of speculation, it should be noted that in the experiment reported here, the frontal operatees do not appear to perseverate more than normals when they are rewarded. In terms of this finding and of the discussion above, it would be desirable to study the behavior of normal and operated monkeys in a two-choice situation with reward distributed between the two sides according to various random schedules over the entire range from 0-0 to 100-100.

Summary

Four normal and four frontal-operated monkeys were tested within an alternation situation. For different series of trials, either a correction or noncorrection procedure determined the placement of reward, and either a contingent or noncontingent procedure determined the information available after a response. Neither of these variables affected the alternation scores; normals always alternated more than frontals. Analysis of pairs of trials shows that for both groups alternation was more likely after alternation on the previous trial. While normals alternated more when they had not been rewarded on the previous trial, this factor did not appear to affect the behavior of the frontals.

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