D-29,170

Reprinted from THE JOURNAL OF COMPARATIVE AND PHYSIOLOGICAL PSYCHOLOGY
Vol. 49, No. 1, February, 1956 *Printed in U.S.A.*

ANALYSIS OF THE EFFECTS OF FRONTAL LESIONS IN MONKEY: III. OBJECT ALTERNATION

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Results from the earlier studies in this series (4, 5) demonstrated that animals with anterolateral frontal lesions may achieve remarkably high levels of performance on certain variations of delayed alternation and delayed response. In one particularly effective variation of delayed response, a single, centered cup was used: the animals were trained to approach the cup to obtain food if Object A had been presented as the predelay cue, and to avoid the cup (i.e., the cup was empty) if Object B had been presented. On this task the learning scores of frontal operates equaled those of controls. Subsequent analysis, using other variations, suggested that the substitution of "object" cues for the "place" cues employed in traditional delayed response had contributed more to the successful performance of the frontal operates than had substitution of an "approach-avoid" response choice for the traditional "approach left–approach right" response choice. The results led to the conclusion that frontal operates' impairment on classical delayed-response–type problems is a function, not only of the delay, but also of some variable related to the predelay cue.

The purpose of the present study was to determine whether the important modification in those tasks solved by the frontal animals could have been the change from spatial (place) to nonspatial (object) stimuli. The procedure used was to compare frontal operates and their controls on a nonspatial, object alternation. Successful performance by the frontal operates would support the conception that the spatial aspect of traditional predelay cues is critical for "frontal-lobe deficit." Conversely, failure by the frontal operates to alternate between objects would suggest that impairment on delayed-response type problems results when qualitatively different pairs of predelay stimuli are used. The frontal operates' successful delayed-response performance in the earlier experiments would then have to be accounted for in terms other than the change from spatial to nonspatial cues.

[1] We wish to thank Margaret Varley, Lawrence Weiskrantz, and William Wilson for their help in preparing this manuscript, and Lila Rupp and Ann Kowalski for their technical assistance.

EXPERIMENT 1

Method

Subjects. The *S*s for Experiment 1 were eight rhesus monkeys, four with bilateral anterofrontal resections (LF-2, 3, 5, 11) and four with bilateral inferotemporal resections (IT-4, 15, 26, 37). (Anatomical data on the two operate groups are contained in References 4 and 7, respectively.) All eight animals had had comparable past experience as described in the earlier papers of this series (4, 5, 7). The data for the present experiment were obtained in the period between 10 months and 12 months after surgery.

Procedure. All eight animals were given 50 trials a day for a total of 1,000 trials on a nonspatial, object alternation. The two cues, a tobacco tin and an ash tray, were the same as those used in the earlier experiments. The two dissimilar objects were presented 15 in. apart in a random left-right order. Correct response (rewarded with food concealed in a food well below the object) consisted of choosing that object which had not been rewarded on the previous trial, irrespective of the object's position. Delayed self-correction was allowed. Following this procedure the four frontal operates were given 50 trials a day for 1,000 trials on the classical spatial alternation task (left-right alternation to two identical objects), again with delayed self correction for errors.

Daily sessions on each task began with a free trial, i.e., both food wells were baited. Beginning with the next trial, the first scored trial, the object (or place in spatial alternation) *not* chosen on the free trial was baited; on the second scored trial, the alternate object (or place in spatial alternation) was baited; and so on through the 50 alternations. In both tests, trials and corrections were separated by the interposition of an opaque screen for 5 sec.

Results

Figure 1 shows the performance curves of the two operate groups on object alternation, together with the performance curve of the anterofrontal group on spatial alternation. Inspection of the figure shows that, on object

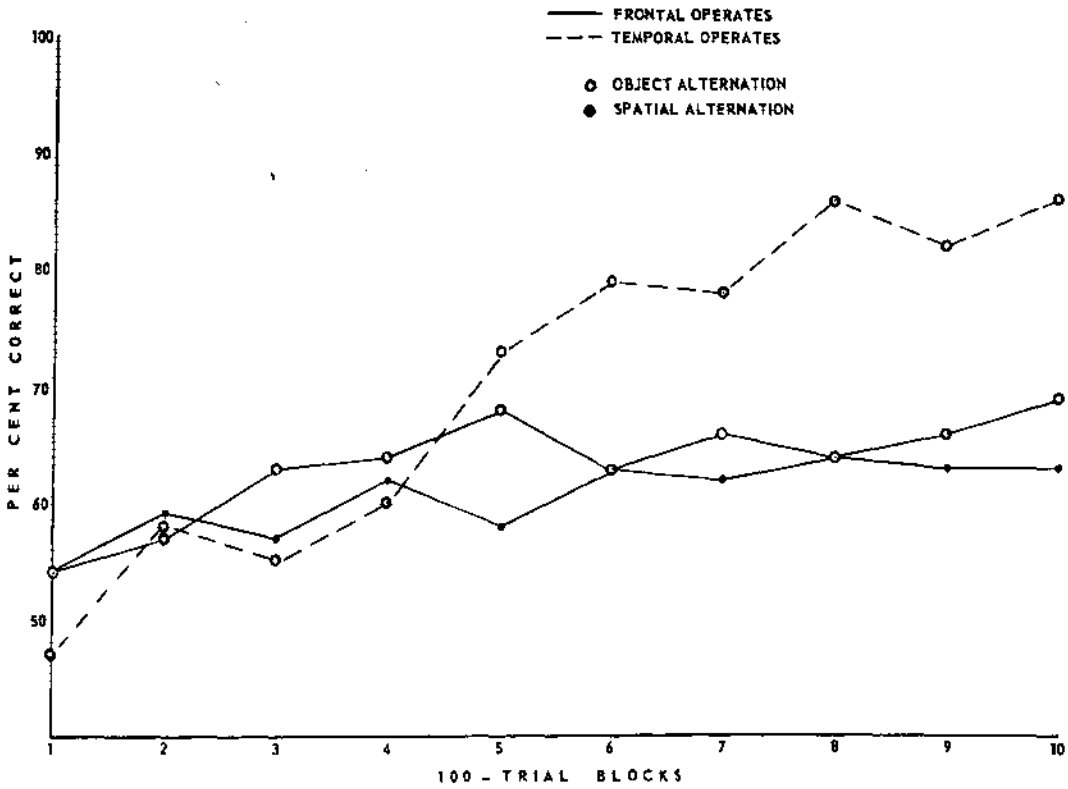

FIG. 1. Average performance, scored in blocks of 100 trials, for four anterofrontal and four inferotemporal operates in Experiment I.

alternation, the inferotemporal operates reached an average performance level above 80 per cent after 700 trials. The performance of the anterofrontal operates, in contrast, remained below the 70 per cent level on both spatial and object alternation throughout the entire training period; there is no significant difference between the frontal operates' scores on these two tasks. The object alternation scores of the two operate groups were subjected to an analysis of variance. The analysis yielded an F of 11.57 for the interaction of operate groups with trial blocks ($p = .05$, $df = 9$ and 54). Subsequent t tests run on each of the 100-trial blocks showed that the difference between the performance of anterofrontal and inferotemporal animals is significant beyond the .05 level, (t's varying from 2.18 to 2.86, $df = 54$) for four of the last five blocks.

EXPERIMENT II

Although the differences between the two operate groups in Experiment I attained significance, an analysis of the individual animals' scores showed that one of the four frontal operates, LF-3, actually achieved a performance level on object alternation equal to that of the controls. This operate also attained the highest performance of the frontal group on spatial alternation, suggesting that intensive training throughout the first postoperative year had *in this one animal* produced substantial recovery from the effects of the anterofrontal resection (1). Because of this deviant animal, it was considered advisable to perform a second experiment as a check on the reliability of the initial results.

Method

Subjects. The "deviant" anterofrontal operate, LF-3, and two of the inferotemporal operates, IT-4 and IT-15, were given additional lesions complementary to those they had received originally (now LF/IT-3, IT/LF-4 and IT/LF-15). In addition, a previously unoperated animal, the only one of four naive nonoperates to achieve a stable performance level on object alternation above 80 per cent, was also given an anterofrontal lesion (LF-36). This animal was used as a control for the other

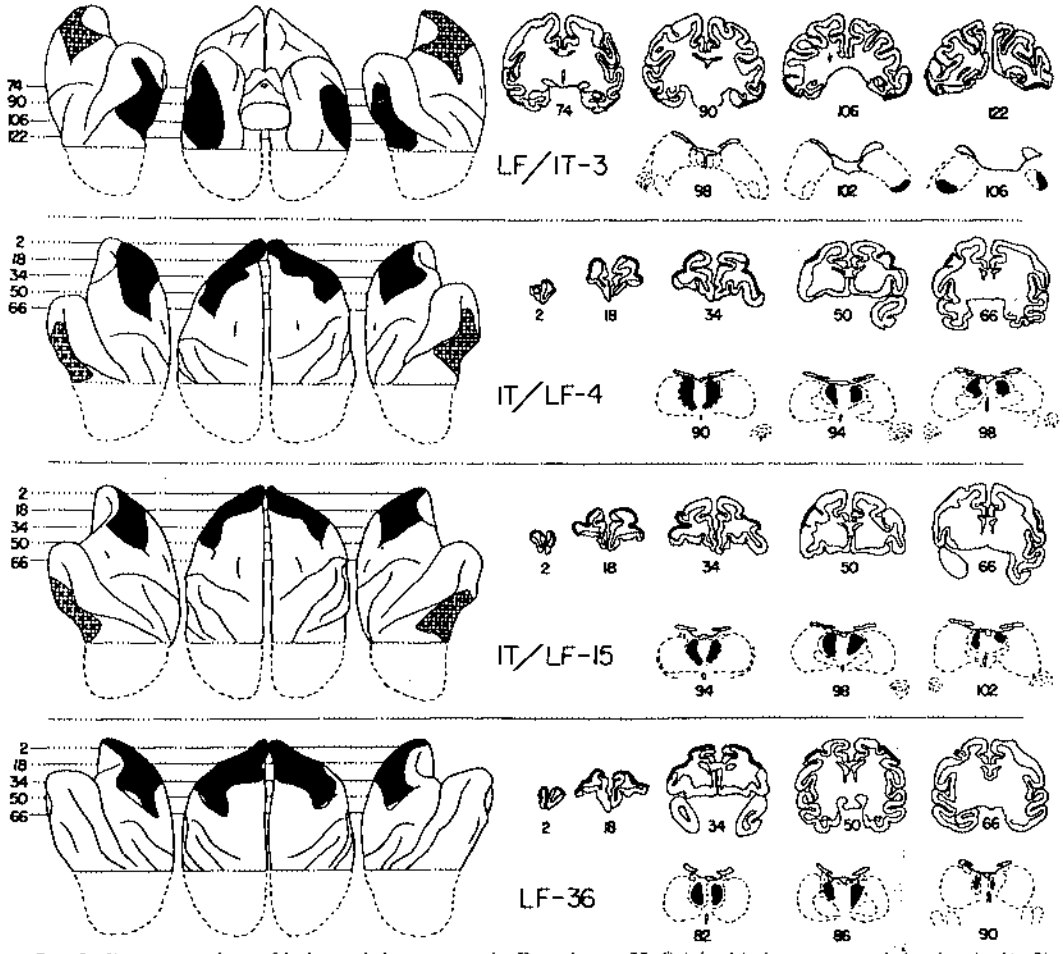

FIG. 2. Reconstructions of lesions of the operates in Experiment II. Original lesions, reported previously (4, 7), are indicated by the checkered areas; lesions made for the second experiment are shown in black. Numbered cross sections (damaged areas in black) and sections through the thalamus (retrograde degeneration in black) relate to the more recent lesions.

anterofrontal operates of the second experiment, since an impairment in these latter animals might be ascribable to the combination of lesions, or to the order in which the combined operations were performed. The failure of the unoperated animals to perform the object alternation probably reflects their relative lack of test experience. The operated animals, as was mentioned above, had previously served in a long series of postoperative experiments.

The *S*s of this second experiment, then, consisted of four animals performing above 80 per cent on object alternation: Two with prior inferotemporal resections and one without prior surgery, were subjected to anterofrontal removals; the fourth animal, a prior anterofrontal operate, received an inferotemporal resection. Reconstructions of lesions and representative cross sections through the lesions and through the thalamus, of the *S*s as used in this experiment, are shown in Figure 2.

Procedure. The procedure used in Experiment I was repeated in detail. All animals received 1,000 trials of object alternation, followed by 1,000 trials of spatial alternation.

Results

The results of the second experiment appear in Figure 3. Inferotemporal resection did not interfere with the performance of LF/IT-3 on object alternation; indeed, with further training, the performance of this operate continued to improve beyond the 90 per cent level. Anterofrontal resection, on the other hand, produced an abrupt drop in the performance of all three animals in this group; and throughout the subsequent training the performance of these operates (as in the case of the anterofrontal operates in the first experi-

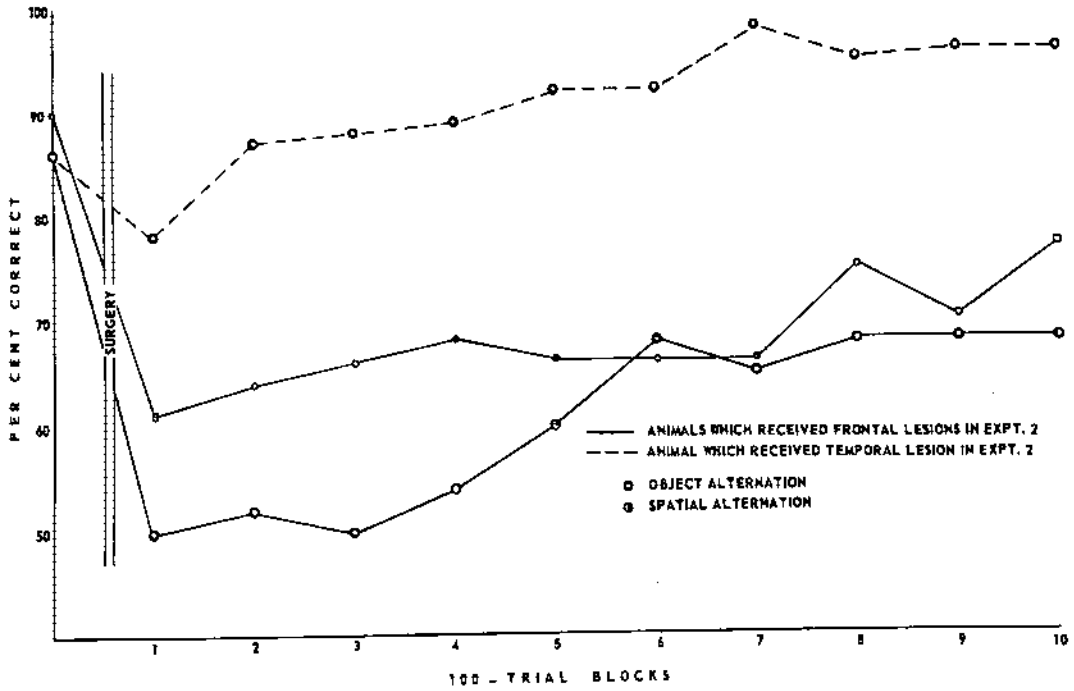

FIG. 3. Performance, scored in blocks of 100 trials, for the four operates in Experiment II. The initial point on each curve represents performance on the last 100 trials of that task preceding surgery.

ment) remained below the 70 per cent level. Their scores on object alternation fell slightly below their scores on spatial alternation, but the difference is not significant.

Because of the peculiar constitution of the groups, a circumstance forced by the difficulty of object alternation for naive rhesus monkeys, these results cannot, by themselves, be considered crucial. They are, however, in the predicted direction, and lend support to the conclusion derived from the findings of the first experiment.

DISCUSSION

The results demonstrate that anterolateral frontal resection interferes as much with performance on object alternation as it does with performance on spatial alternation. Thus, the spatial aspect of traditional predelay cues cannot be responsible for frontal operates' failure in delayed-response–type tasks. The evidence suggests rather that frontal operates have difficulty in responding to a variety of predelay cues, and, thus, an alternate explanation is required to account for their successful delayed-response performance in previous experiments of this series.

One possibility is that the use of nonspatial stimuli in the variations of *delayed response* may have introduced an additional factor that will be labeled, tentatively, "distinctiveness" of cues. The animals had received considerable training on both simultaneous and successive discrimination problems (7) before the series of delayed-response variations were undertaken. Some of these earlier problems involved the same discriminanda that were used later in delayed response, and for a given animal, one object had been consistently rewarded and approached; the other object was consistently unrewarded and avoided. The objects may, thereby, have acquired sufficient distinctiveness to serve as effective cues in the delayed-response variation, particularly since the identical cue-response-reward relationships were maintained. In *object alternation*, where these same cues were used, distinctiveness based on distinctive responses and differential reward should tend to be extinguished, since, in this task, reward is contingent on approaching and avoiding each of the objects on alternate trials.

If this argument is correct, it would suggest that the decrement in performance of frontal

operates on delayed-response–type tasks is a function, not only of the temporal interval between cue and response, but also of the distinctiveness of the predelay cues. In the earlier experiments of this series the distinctiveness of *object* stimuli may have been acquired on the basis of contiguity with distinctive responses and differential reward. (The same explanation would apply to the frontals' successful delayed-response performance with the cues—peanut vs. empty hand—used in the direct method.) In other experiments distinctiveness of *place* stimuli may have been enhanced by presenting predelay rewards in the to-be-correct place (2); by presenting, as the place cue, a spot of light in an otherwise darkened room (3); and by physical and pharmacological manipulations of the motivation of the animal when food was used to signal the correct place (6). In short, increasing the distinctiveness of the predelay cue may enable frontal operates to perform as well as controls even though a delay is interposed between the stimulus and the opportunity for response. A variety of factors which may affect cue distinctiveness has been suggested; the notion of "distinctiveness" needs further experimental specification, however, before a conceptualization of the deficit following frontal lesions can be attempted.

SUMMARY

Four frontal operates were trained approximately one year after surgery on an object alternation task, and their performance compared with (*a*) their own performance on classical spatial alternation and (*b*) the performance of four temporal operates on the object alternation. Results demonstrated that frontal lesions interfere equally with performance on both forms of alternation. This conclusion was confirmed in a second experiment that investigated retention on the two tasks following anterofrontal and inferotemporal lesions. On the basis of the results of the current experiment, the successful performance of frontal operates on delayed-response–type problems observed in earlier experiments was accounted for in terms of the "distinctiveness" which the predelay cues had acquired from contiguity with distinctive responses and differential reward.

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Received December 15, 1954.