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LOCOMOTOR DELAYED RESPONSE IN FRONTALLY ABLATED MONKEYS

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Monkeys which had been trained on a locomotor task, in which they were rewarded for approaching a food cup located in a direction opposite to that of the stimulus, became severely impaired after bilateral ablations of dorsolateral prefrontal cortex, but not after damage to other frontal lobe structures (Stępień and Stamm 1969). The marked impairment, which was exhibited by responses indicative of "magneto-reactions", was also seen after resections restricted to cortex surrounding sulcus principalis, whereas ablations of cortex only in the depth and banks of this sulcus did not result in appreciable behavioral deficits. This finding appears of significance in view of the reports (Mishkin 1957) that cortex in sulcus principalis is of crucial importance to performance of delayed alternation and delayed response tasks. Since our findings had been obtained with presentation of the stimulus while the monkey was making the locomotor responses, it seems important to examine the consequences of introducing a delay between stimulus presentation and initiation of the response process. The results of such tests with frontally ablated monkeys are presented in the present report.

METHOD AND PROCEDURE

Subjects. 14 immature monkeys were selected from the previous experiment (Stępień and Stamm 1970). The subjects had been trained on the task of spatial opposition between stimulus and reward and then had received bilateral frontal ablations, as indicated by Fig. 1 and Table I. Monkey 127 had received ablations of "supplementary motor cortex" only and M 131 of this area and also of the dorsolateral aspects of premotor cortex; in five monkeys the total areas of dorsolateral prefrontal cortex, including the depth and banks of sulcus principalis were

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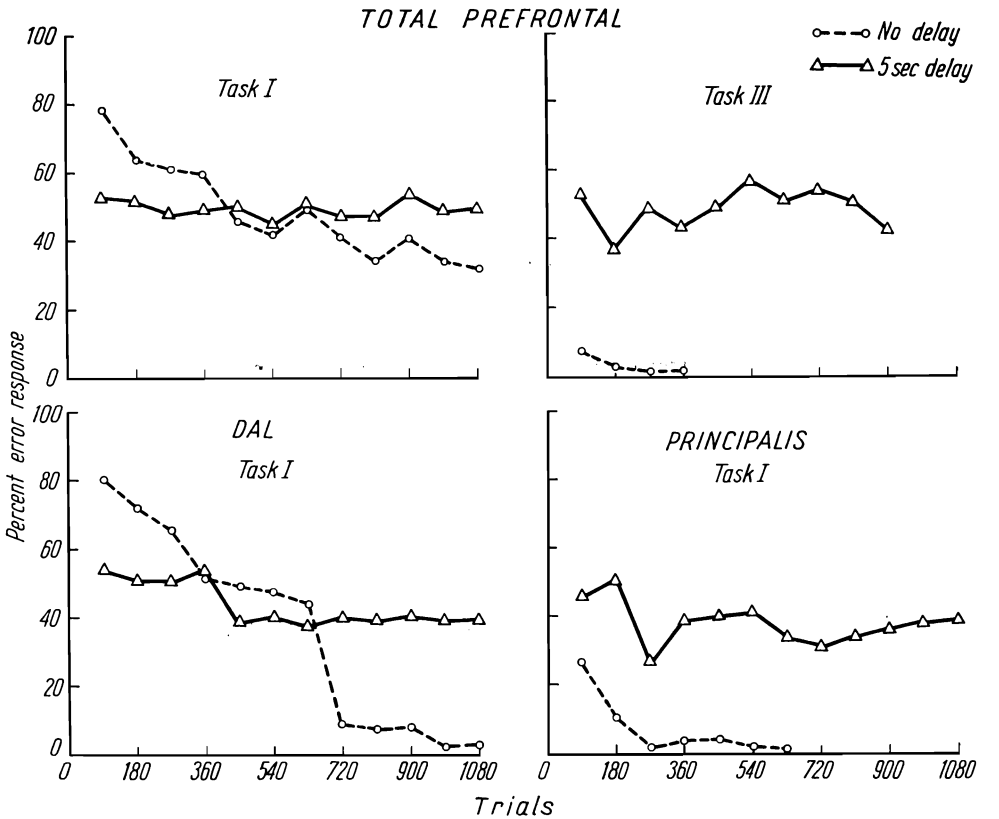

Fig 1. Means of error response rates (two monkeys per group) for post-operative testing under no-delay and delayed response conditions. Task I, spatial opposition; Task III, spatial contiguity between stimulus and reward locations. Cortical lesion groups as indicated

resected; two monkeys had resections only of cortex in depth and banks of sulcus principalis, and two others of the surrounding dorsal, anterior arcuate, and lateral strips (DAL cortex). In one monkey only the dorsal portion of this area, and in two subjects only the lateral cortical strips were ablated.

Apparatus. The "open field" apparatus has been described in the previous communication.

Procedure. 12 monkeys were trained on the task of spatial opposition between stimulus and reward, one to auditory and the others to visual cues. This task (Task I) required the monkey to approach a food cup in response to the stimulus which was located in the opposite direction. After adaptation to the apparatus each animal was trained at 30 trials per session until it attained the criterion of 81 correct responses in 90 trials. Then the monkey was restricted to the starting compartment by a wire mesh screen that was placed between the two compartments of the apparatus. The screen was raised, first at the onset of the two sec cue (no delay),

Table I

Summary of results

Ablation group	Monkey	Task[a]	Total trials[b]		Errors[c]	
			Pre-op	Post-op	Pre-op	Post-op
Premotor	127	I—Vis	270	90	37	7
	131	I—Ac	270	1260F	38	178
Prefrontal	127	I—Vis	(270)	900	(37)	295
(total dersolateral)	134	I—Vis	360	1170F	49	457
	135	I—Ac	450	990F	61	466
	142	III—Vis	540	810F	87	412
	162	III—Vis	540	900F	94	413
Principalis	113	I—Vis	540	1260F	80	200
	170	I—Vis	270	990F	42	427
DAL[d]	161	I—Vis	900	990F	152	425
	164	I—Vis	630	990F	78	322
Dorsal	168	I—Vis	180	450	12	51
Lateral	172	I—Vis	360	900	650	140
Lateral	174	I—Vis	630	270	137	33

[a] Task I, Spatial opposition between cue and reward; Task III, Spatial contiguity between cue and reward; Vis, visual cue; Ac, acoustic cue.
[b] Including criterion trials; F, failure to meet criterion.
[c] Total, including criterion trials, or for 900 trials.
[d] DAL, dorsal, arcuate and lateral segments of prefrontal cortex.

subsequently at termination of the cue, then after delays of two sec and finally of five sec. After attainment of criterion performance 10 days of rest were given and then the retention testing was performed consisting of three successive sessions in which the animals would react immediately to the presentation of the S-s, succeded by three sessions with 0 sec of delay and three senssions with 5 sec of delay. Thereafter surgery was performed, and after a 10 day recovery period, post-operative training commenced, according to the retention test procedure. Training was terminated after reattainment of criterion performance, or after at least 900 trials.

Two monkeys M 142, M 162, were tested on the delayed response task (Task III) when rewards were presented to the food cup adjacent to the visual cue. The same training procedure was followed as for the other subjects and after attainment of criterion performance the monkeys received ablations of total dorsolateral prefrontal cortex.

RESULTS

The results for delayed response tests are summarized in Table I and Fig. 1. Ablations of only supplementary motor cortex (M 127) had no effect on correct performance on the task. The monkey with more extensive damage to premotor cortex (M 131), including the dorsolateral areas,

responded at the 90% correct criterion level during the third block of 90 post-operative trials, but its correct performance deteriorated during subsequent testing and remained below 75% correct.

Four of the monkeys with total dorsolateral lesions remained severely and permanently impaired on delayed response Tasks I and III, and their correct performance did not rise appreciably above chance level throughout post-operative training. No appreciable differences were found in performance scores between Tasks I and III, the latter corresponding to the traditional delayed response task. The one prefrontal monkey (M 127) which eventually reattained criterion performance achieved this by developing a pronounced stereotyped habit of circling movements in the starting compartment after presentation of the left stimulus and sitting quietly following presentation of the right stimulus. Similar stereotyped behavior patterns were not observed in any of the other monkeys.

None of the monkeys with lesions restricted to either sulcus principalis or of the surrounding dorsolateral cortex (DAL group) was able to reattain criterion during the post-operative testing. After 990 trials one subject in each of these groups responded near 60% correct and the two others, which sat more quietly in the starting compartment during the delay period, achieved as high as 75% correct responses. Only monkeys with partial lesions of the DAL area were able to reattain criterion (Table I), but even these subjects required considerable post-operative training.

As indicated by Fig. 1, there were no appreciable differences among the total prefrontal, principalis and DAL groups in error rates on the delayed response task and, for monkeys with total prefrontal lesions, between the two Tasks I and III. The slight reduction in error scores by the total prefrontal group on Task I is the consequence of M 127's eventual reattainment of criterion performance. By contrast during testing under conditions of no delay marked differences among the experimental groups were found. The two groups total prefrontal and DAL which had been impaired on that task exhibited error rates appreciably above chance level during the early post-operative period and a subsequent decline to criterion level, which was reached by all subjects, during the post-operative testing period. On the other hand, the principalis group was not impaired at all in the no delay task.

DISCUSSION

The present results indicate clear differences among lesion groups on both tasks between the no delay and delayed response procedures.

With the former procedures, when the correct response was in the direction opposite to that of cue presentation impairment became evident after ablations of total dorsolateral prefrontal cortex or of the surrounding DAL cortex, but not after resection of the principalis cortex or of segments of the DAL area. The impairment was demonstrated by initial high rates of responses toward the side of the stimulus and a consistent decline in error rates during subsequent training. By contrast, the delayed response procedure resulted in performance near chance level throughout post-operative training in each of the lesioned groups and in less severe impairments after smaller lesions of the DAL area.

The findings from the previous experiment (Stępień and Stamm 1970) suggested a functional dissociation between cortex in sulcus principalis and in the surrounding dorsolateral area (DAL cortex), with only the latter implicated in the task of spatial opposition between cue and reward. Our finding that ablation of principalis cortex results in severe and permanent impairments on both forms of delayed response tasks (Tasks I and III) is in agreement with previous findings of the implication of this restricted cortical area on tasks of delayed alternation in the Wisconsin Test Apparatus (Mishkin 1957) and in the locomotor maze (Stamm, in preparation). However, our results of severe impairments on the delayed opposition task after DAL lesions are unexpected in view of the findings from other experiments that monkeys with lesions in this area exhibit only mild and transitory impairments on delayed alternation tasks in the locomotor maze and in the Wisconsin Test Apparatus (Gentile personal communication). This discrepancy may be the consequence of the extent of lesioned areas, especially along the borders of sulcus principalis and in the rostral segment of the DAL area, which appeared to have been spared in the delayed alternation experiment. A further explanation for the impairment by the DAL monkeys in the present experiment may be that these subjects were tested only on the delayed opposition task. Since they were severely impaired on this task under the no-delay conditions during early post-operative training and only reattained criterion performance after several hundred trials, this functional recovery may not reflect complete compensation of the monkeys behavioral impairment. The inadequate compensation may therefore have contributed to the monkey's inability to solve the delayed task. The inadequacy of this explanation needs to be determined by testing of monkeys with DAL lesions on the standard delayed response task (Task III) and to compare their performance with that of monkeys having lesions restricted to sulcus principalis.

SUMMARY

12 monkeys were tested on the delayed (5 sec) response of spatial opposition between stimulus and reward. The task required the monkey to approach a food cup in response to the stimulus which was located in the opposite direction.

Ablations of the supplementary motor cortex or of the whole premotor area had only litle effect if any on the performance of the task. On the other hand, following dorsolateral prefrontal removals all the animals were severely impaired. There were no appreciable differences among the total prefrontal, pricipalis and DAL (cortex surrounding principal sulcus) groups in error rates on the delayed response task. The lesioned animals were not able to reattain the criterion during the postoperative testing.

Two monkeys had been trained on the delayed response task when rewards were presented to the cup adjacent to the cue. These animals showed similar impairment after ablations of the dorsolateral prefrontal cortex.

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