D-95

Neuropsychologia, 1977, Vol. 15, pp. 329 to 340. Pergamon Press. Printed in England.

INFORMATION SOURCES IN THE DELAYED ALTERNATION TASK FOR NORMAL AND "FRONTAL" MONKEYS

KARL H. PRIBRAM*, HENRY C. PLOTKIN†, ROBERT M. ANDERSON‡ and DEMETRIA LEONG§

(*Received* 23 *April* 1976)

Abstract—Two studies are reported which demonstrate that in delayed alternation the spatial factor, though essential, serves primarily the sequential aspects of the task. Experiment 1 replicates with computer and additional controls an earlier study in which the ordinarily symmetric intertrial intervals were made asymmetric. Experiment 2 studies the effects on performance strategies of moving the placement of reinforcement from a neutral location to one spatially related to the stimulus panels. The results are contrasted to those obtained with delayed response where the temporal factor in the form of delay, while essential, serves primarily the spatial aspect of that task.

DELAYED response and delayed alternation have long been among the principal methods of investigating the behavioral impairment of monkeys with lesions of the dorsolateral frontal cortex [1–3]. Yet, despite a great number of experimental analyses, surprisingly little has been concluded about the information sources utilized by either the normal or the monkey with frontal lesions in arriving at the strategy necessary for the successful execution of these tasks. Most of the results of these analyses are currently conceptualized under two major hypotheses: the temporal and the spatial, and considerable controversy exists between those who hold to one or the other. Thus PINTO-HAMUY and LINCK [4] found in our laboratory that sequential performance is defective following frontal lesions; PRIBRAM and TUBBS [5] demonstrated that making the ordinarily symmetric intertrial intervals asymmetric would dramatically improve the performance of monkeys with frontal lesions; and MILNER [6], [7] discerned a deficiency in "temporal tagging" on the part of frontally damaged patients. On the other hand, PRIBRAM and MISHKIN [8] and PRIBRAM [9] found that frontal lesions produce a greater disturbance in spatial than in non-spatial (go/no-go) problems, which led MISHKIN [10] and GOLDMAN, ROSVOLD, VEST and GALKIN [11] to further experiments demonstrating the importance of spatial factors in accounting for performance of the alternation task. POHL [12] took this analysis one step further to show that monkeys with frontal damage could perform tasks in which the spatial cues served as external markers while failing those where such markers were not supplied. Also, GENTILE and STAMM [13] showed the efficacy of supplementary articular-somesthetic cues in improving the performance of delayed alternation by monkeys with frontal lobe resections,

*Departments of Psychology and of Psychiatry and Behavioral Sciences, Stanford University, Stanford, California, U.S.A.

†MRC Unit on Neural Mechanisms of Behavior, Department of Psychology, University College, London, England.

‡Department of Philosophy, Rensselaer Polytechnic Institute, Troy, New York, U.S.A.

§Department of Psychology, Northeastern University, Boston, Massachusetts, U.S.A.

and a not uncommon line of argument implicates both spatial and temporal factors in terms of a spatial mnemonic deficit (e.g. STAMM and ROSEN [14]) on the basis that the alternation task imposes specific spatial differentiation between right and left locations, as well as a delay.

There thus seems to be good evidence that the deficit following resection of the anterior frontal cortex involves both a temporal and a spatial factor. What remains to be specified is the nature of these factors and the possibility that they are separately represented in different locations within the extent of frontal cortex. In another report [15] we have analyzed the delayed response test to show that this task involves primarily the ability to respond to spatial context. Thus the temporal factor in the form of delay, while essential, serves primarily the spatial aspects of the task which are its distinctive features.

In this paper, we report on two studies which demonstrate that in delayed alternation the spatial factor, though essential, serves primarily the sequential, i.e. temporal aspect, which is the distinctive feature of alternation. Experiment I replicates an earlier study by PRIBRAM and TUBBS [5] in which the ordinarily symmetric intertrial intervals were made asymmetric. However, instead of using a hand-operated apparatus, monkeys in the current study were tested in a computer-controlled automated device (DADTA III, [16]) to eliminate experimenter bias. A further improvement in design added the control of varying the short and long intervals from side to side over each day of testing in the asymmetric condition. This effectively eliminates the possibility that asymmetry *per se* could change the task into a simple successive discrimination. The order of presentation for the two groups was counterbalanced across problems.

While Experiment I investigated the influence of temporal factors in delayed alternation, the second experiment manipulated the spatial factor in a classical (symmetrical) delayed alternation task. In this experiment the placement of the reinforcement chute was either spatially neutral or spatially related to the stimulus panels. In earlier studies which utilized two-choice situations, two possible sources of information are confounded, either of which could generate a correct response on the subsequent trial. These are the response location and the position of reinforcement. If the animals with frontal resections are facilitated by spatial cues then it is of some theoretical importance to separate these. This can be achieved either by delivering the reinforcement to a neutral uniformative position midway between the response panels, as in the Discrimination Apparatus for Discrete Trial Analysis (DADTA III [16]) or to separate response and reinforcement locations, but to retain the left–right congruence of each, as in DADTA IV [17], [18]. Here a left response is reinforced by the delivery of a food pellet to the left of two reward locations, and right responses result in delivery of reinforcement to the right. Such an arrangement might, if spatial mnemonic factors are central to the solution of the task, be expected to improve delayed alternation performance. Comparisons of the performance of both intact and frontally lesioned monkeys on DADTA III and DADTA IV can provide some insight into the relative importance of the location of the reinforcer.

The data from Experiment 2 were also assessed to compare the spatial aspect of the reinforcer with its sign. This analysis extends an earlier study from our laboratory [19] which indicated that normal monkeys tend to alternate more on trials which follow non-reward than on those following reward, and that monkeys with frontal lesions appear to be unresponsive to negative reward outcomes. Wilson's data were gathered over only 200 trials in any one of four possible conditions, these latter being intermixed in 10 trial blocks on any one day of training. For this reason, his animals did not appear to alternate at levels

substantially above chance. An additional purpose of this present report, therefore, is to verify Wilson's original suggestion by observations over prolonged training periods.

In summary, two experiments were carried out. In Experiment 1, monkeys with frontal lesions and normal controls were run in asymmetric and symmetric delayed alternation tasks in a counterbalanced design. In Experiment 2, experimental and control groups were tested on the symmetrical task alone in two types of apparatus, one in which the food cup was in a central position (DADTA III) and another in which two food cups were directly below the two stimulus panels (DADTA IV). The data from this study were also used to determine the probabilities of both groups to adopt win–stay, win–shift, lose–stay, or lose–shift strategies following reward or non-reward.

METHOD

Subjects

The subjects were sixteen mature irus monkeys (*Macaca fascicularis*) ranging in age from approximately 4 to 6 yr. Eight were males and eight were females. All animals were experimentally naïve. With the exception of early shaping and training procedures, all animals were maintained under conditions of mild food deprivation.

Surgery

Following response shaping and initial training of all animals on a simple color discrimination, the monkeys were divided into two major groups and an additional control group (D) of three subjects. Group SA consisted of six subjects (two males and four females) of which three females received frontal surgery. The second group, Group AS, consisted of seven subjects (three males and four females). Three males and one female of this group were given frontal resections. Thus a total of three of the males and four of the females underwent single-stage bilateral subpial resection of dorsolateral frontal cortex centering on the sulcus principalis and extending from the arcuate sulcus posteriorly to the lip of the hemisphere ventrally, and including the frontal pole. Recovery from surgery was uneventful.

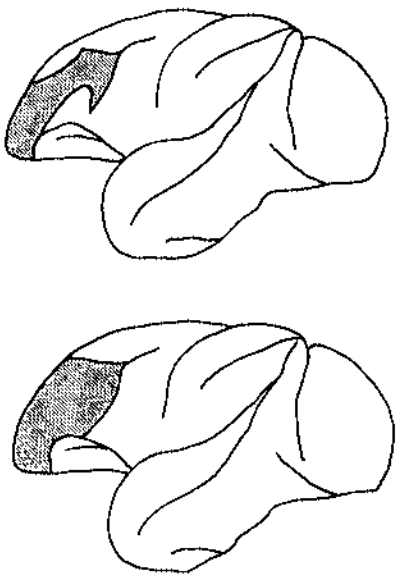

FIG. 1. Composite diagram of reconstructions of the frontal lesions indicating maximum and minimum extent over all hemispheres.

Following the 4 yr of testing, all monkeys with lesions were sacrificed, their brains perfused with formalin and imbedded in albumin. Serial sections (50 μ) were cut and stained with cresyl violet. From these, reconstructions of the lesions were made and thalamic degeneration assayed. Figure 1 shows a composite

diagram of these reconstructions indicating the maximum and minimum extent of the lesions. Complete reconstructions of individual brains are on file with the senior author.

Apparatus

The DADTA III apparatus has been described in detail elsewhere [16]. A stimulus display of *O* was used to indicate the two response panels. These were held constant in position and were separated by a distance of 15 in (38·1 cm). Reinforcement consisted of standard banana-flavored pellets delivered to a food cup situated below and midway between the response panels. The stimulus display used for DADTA IV (fully described by DRAKE and PRIBRAM [18] was also an O. But in this latter apparatus, two food cups were present. The DADTA IV response panels were 5 in (12·7 cm) apart, the food cups were 2·5 in (6·35 cm) below these panels, and were spaced 8 in (20·3 cm) apart. In DADTA IV, if the correct response was on the left panel, reinforcement was delivered to the left food cup; if the right panel response was correct, reinforcement was delivered to the right food cup.

Procedure

All monkeys, following a 2 week recovery period from the date of surgery of the operated *S*s, were trained on a color discrimination. As soon as a 90% criterion in 100 consecutive trials had been reached, the experimental trials began.

Experiment 1. Animals were divided into two categories: one group of monkeys (SA) consisted of three controls and three with frontal resections. All were trained initially on the symmetrical task and then on the asymmetrical task in DADTA IV. The second group (AS) consisted of three controls and four monkeys with frontal lesions and were trained (also on DADTA IV) initially on the asymmetrical task followed by the symmetrical. Fifty reinforced trials per day were run, using a correction procedure. The first response to either of the response panels was reinforced at the beginning of each session. In the symmetrical form of the task a correct response was followed by the immediate delivery of a food pellet and the response panel lights were extinguished for a 5 sec period. In the asymmetric form the response panel lights were extinguished for 5 sec and 15 sec in an alternating fashion. The position of the long and short duration stimuli was altered on each day. Thus on day 1, the 5 sec period preceded to go-right placement of the reward while the 15 sec period preceded the go-left placement. On the following day the timing was reversed (i.e. the 5 sec intertrial interval preceded the go-left condition while the 15 sec interval preceded the go-right trials).

Following the intertrial interval, both panel lights reappeared and the next trial began. In the event of an incorrect response, both panel and house lights were extinguished for a 5 sec or a 15 sec period depending on the delay interval. The position of the reinforced panel was alternated only after a correct response. Training continued until an 85% ciriterion was met.

Experiment 2. Group SA and an additional three control *S*s were also trained on the classic form of the delayed alternation task 'symmetrical only' on the DADTA III (food cup center) for comparison with their performance on DADTA IV (adjacent food cups). The training continued until 85% criterion was achieved. An animal was considered to have failed the task if a 65% criterion had not been achieved by 5000 trials. The data from this experiment were utilized in two ways, first to assess the effect of spatial cues on the performance (trials to criterion) of frontally lesioned animals, and secondly to assess the response strategies of the two groups under the two conditions. A computer controlled analysis calculated all response position information following both rewarded and non-rewarded trials on both the DADTA III and DADTA IV.

RESULTS

Experiment 1

Table 1 and the left panel of Fig. 2 show the scores of the monkeys in Group SA. The performance of both frontal and control subjects on the asymmetrical version of delayed response is comparable and the groups do not differ significantly at the higher criterion levels, while the usual severe deficit is shown on the symmetrical task by the frontal subjects at all but the lowest criterion levels (Mann–Whitney $U = 0$ in all cases, $n_1 = n_2 = 3$, $P = 0{\cdot}05$).

By contrast, the scores of Group AS are shown in Table 2 and in the right panel of Fig. 2. When the asymmetrical form of delayed alternation is presented as the initial task, a certain difference appears. Monkeys with frontal resections appear somewhat retarded, but they reach the highest criteria and are not significantly impaired with respect to the controls on the asymmetric version (85% criterion $U = 5$, $n_1 = 3$ $n_2 = 4$, $P = 0{\cdot}429$; 80% criterion $U = 4$, $P = 0{\cdot}314$; 75% criterion $U = 3$, $P = 0{\cdot}2$; 70% criterion $U = 1$,

Table 1.

Control subjects	Asymmetrical					Symmetrical				
	65%	70%	75%	80%	85%	65%	70%	75%	80%	85%
Dee	944	1014	1151	1214	4898	62	62	62	62	370
Mal	836	836	2686	2686	2913	60	60	60	60	119
Isa	1791	4250	8083	13436	13436	242	473	473	2362	3552
$\bar{X}$ =	1190	2033	3973	5779	7082	121	198	198	828	1347
Frontal subjects	65%	70%	75%	80%	85%	65%	70%	75%	80%	85%
Whi	1994	1994	2675	2889	4073	126	126	126	126	182
Pat	5857	6604	6759	8004	8004	58	58	58	58	58
Gri	8283	8283	8436	10381	10381	152	152	152	1361	4212
Pet	8256	8256	8760	11793	11793	685	757	4605	5504	6614
$\bar{X}$ =	6098	6284	6657	8267	8563	255	273	1235	1762	2767

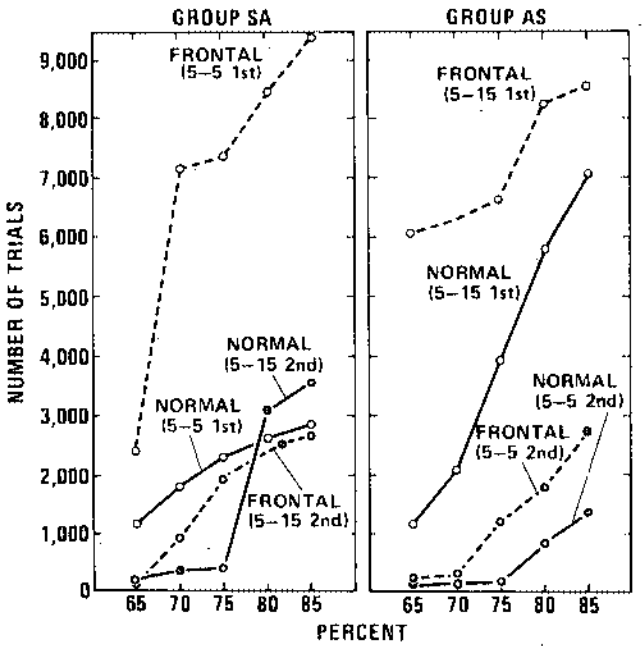

FIG. 2. Comparison of the performance on variations of the delayed alternation task of groups SA (symmetrical version of delayed alternation followed by the asymmetrical version) and AS (asymmetrical version followed by the symmetrical version). Note the relative difficulty of the asymmetric version for both groups and that despite this, the monkeys with frontal lesions perform this task remarkably well.

$P = 0{\cdot}057$). But unlike Group SA, group AS monkeys with frontal resections are also not impaired with respect to controls on the symmetrical version. Observation of these monkeys revealed that in all cases they had learned some sort of mnemonic in the asymmetrical task—such as circling the cage in different directions for different locations of reward, or holding themselves in a strategic position vis-à-vis the next correct choice. These mnemonics were

carried over from the asymmetric to the symmetric condition and account for the remarkably good performance in a task classically failed by monkeys with frontal lesions.

A close inspection of the mean values for the control animals in Tables 1 and 2 shows the asymmetric task as consistently appearing to be more difficult than the symmetric version, whatever the order of task presentation and at almost all criterion levels. Unfortunately the very small group sizes do not make reliable statistical testing of this possible.

Table 2.

Control	Symmetrical					Asymmetrical				
subjects	65%	70%	75%	80%	85%	65%	70%	75%	80%	85%
Hen	1258	1330	1472	1472	1468	258	258	489	489	610
Gio	888	1284	2248	2248	2843	266	595	595	1574	1708
Pon	1320	2685	3082	4170	4170	157	157	157	7204	8251
$\bar{X}$ =	1153	1766	2268	2630	2827	227	337	414	3089	3523
Frontal										
subjects	65%	70%	75%	80%	85%	65%	70%	75%	80%	85%
Jer	77	6053	6053	6776	7250	75	569	2493	2769	3133
Nam	1770	2884	3412	4732	8354	74	228	607	2403	2403
Fri	5615	12498	12562	13913	14040	303	1799	2353	2353	2353
$\bar{X}$ =	2487	7145	7342	8474	9881**	151	865	1818	2508	2629

Experiment 2

Positional data. The data from the monkeys trained on both DADTA III and DADTA IV are presented for both performance in 50 and 100 consecutive trial blocks from 65–85% criterion. Figure 3 illustrates the results for the symmetrical alternation task for both the monkeys with frontal resections and their controls in both types of apparatus. The information for the monkeys with frontal lesions on DADTA III (food cup center) is omitted as these animals failed to reach the 65% criterion in 5000 trials. No significant differences for either of the control groups on either type of apparatus, in the 50 and the 100 consecutive trials could be demonstrated. The frontally lesioned group is significantly impaired in both cases ($U = 0$, $P < 0{\cdot}05$). Compared to their performance on DADTA III, however, frontal animals were successful in achieving 85% correct for both the 50 and 100 trial block criteria. This illustrates that monkeys with frontal lesions are aided by the positional cues provided by the placement of the food cups.

Probability data. The data from this study were further analyzed to determine whether any differences could be found between experimental and control groups in their win–stay, win–shift, lose–stay, or lose–shift strategies following reinforced and non-reinforced trials. Conditional probabilities (in the form of percentages) were computed for the four major parameters:

Shift following reinforcement on the right
Shift following reinforcement on the left
Shift following non-reinforcement on the right
Shift following non-reinforcement on the left.

(A stay strategy is inferred by the absence of shift and need not be considered separately.)

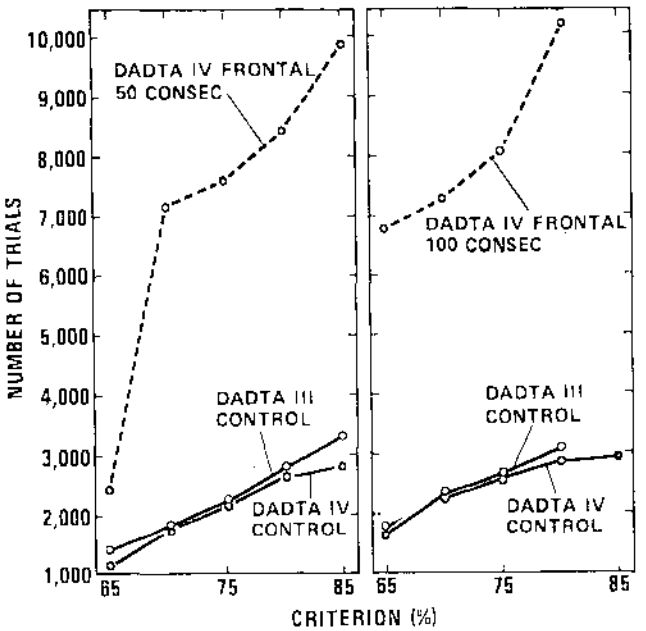

FIG. 3. Graph of a the number of trails taken by control and frontally operated monkeys to reach various criterion levels for 100 consecutive trials (right graph). Performance for the frontal group in DADTA III is not graphed since these monkeys did not reach the 65% level of performance in 5000 trials and were therefore not continued in this apparatus.

The probability scores for individual animals gave no indication that any consistent position bias was operating. Therefore the data were collapsed across position and all analyses were carried out on reinforced and non-reinforced trials only.

Regression coefficients were computed [20] and the coefficient significance levels along with the between-groups significance levels are illustrated in the graph of the regressions in Fig. 4 together with the F values from the analyses of regressions. The significant results for all the groups regression coefficients ($P < 0{\cdot}005$–$0{\cdot}025$) indicate that all animals have a consistent pattern of performance over trials. However, the analysis for the between-groups effect illustrates that the control groups in all cases are significantly more inclined to adopt an alternating (shift) strategy, while the frontals remain near the 50% level, showing no characteristic response strategy.

It was felt that this analysis may have obscured certain trends in the data, and a second analysis was computed for within-group performance over all conditions. These data are illustrated in Fig. 5. Once again all regression coefficients are significant showing consistent trends in performance over trials for all groups. Panels A, B, C, D show the results for the control groups, first comparing reinforced and non-reinforced trials (A, B) and secondly their performance on the two types of apparatus (C, D). The results are clear. The non-reinforced trials produce significantly more alternation in responding ($P = 0{\cdot}005$) while the type of apparatus has no effect on this strategy.

Equally straightforward is the finding that the performance of the monkeys with frontal lesions is significantly affected by the apparatus. They increase alternation, albeit slightly, for non-reinforced trials ($P < 0{\cdot}01$) but only in DADTA IV (panels F, H). The apparatus has no effect on their response strategy for reinforced trials.

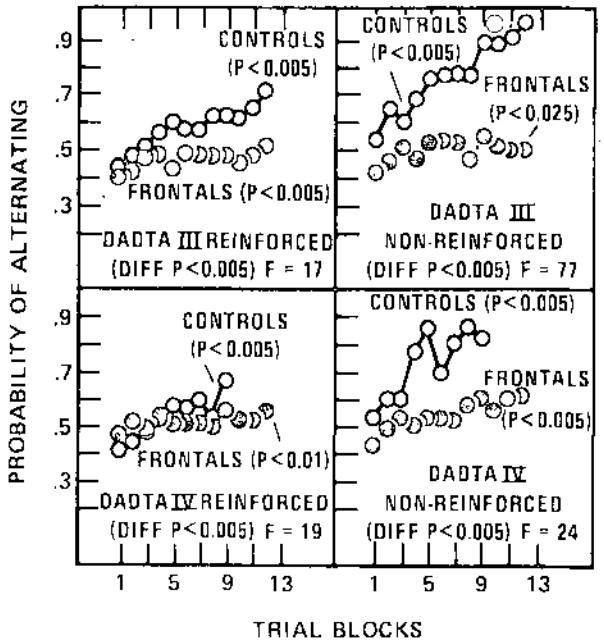

FIG. 4. Graph of the probability of alternating following a reinforced or a non-reinforced response for frontally lesioned and control animals in DADTA III (upper graphs) and DADTA IV (lower graphs). Each point on the figure presents the mean value for four consecutive training sessions. The *P* values given in the upper portions of each block refer to the slope of each indicated curve. The *F* and *P* values given in the lower portion of each block refer to differences in the slopes of each pair of curves.

DISCUSSION

The most striking result of this series of experiments is the effect of making the intratrial interval of the delayed alternation asymmetric. As in an earlier study [5] when the asymmetric condition follows prolonged training in the classical symmetrical form of the task, the performance of monkeys with frontal lesions is indistinguishable from that of their controls. This result is obtained despite varying the sign value of the asymmetry from day-to-day and irrespective of whether the apparatus used for testing is, as in the earlier study, a hand-operated Yerkes type Wisconsin General Testing Apparatus or, as in the current series of experiments, a computer-controlled, fully automated discrimination testing device of the DADTA IV configuration. Further, when the asymmetric version of delayed alternation is presented first, monkeys with anterior frontal lesions also show no statistically reliable deficit with respect to their controls, although their performance is somewhat retarded.

These results are especially significant since the asymmetric form of delayed alternation as presented in these experiments—i.e. with daily variation of the sign value of the asymmetric interval—is initially almost three times as difficult (i.e. took almost three times as many trials to learn) as the classical symmetric task for normal monkeys. Thus the excellent performance of monkeys with frontal resections on this task cannot be related to a difficulty dimension. Further, as in an earlier experiment performed in our laboratory which used colors and sounds as signs to no avail [21], the present results, based on varying the sign value of the asymmetric intertrial interval, make it unlikely that the asymmetric version

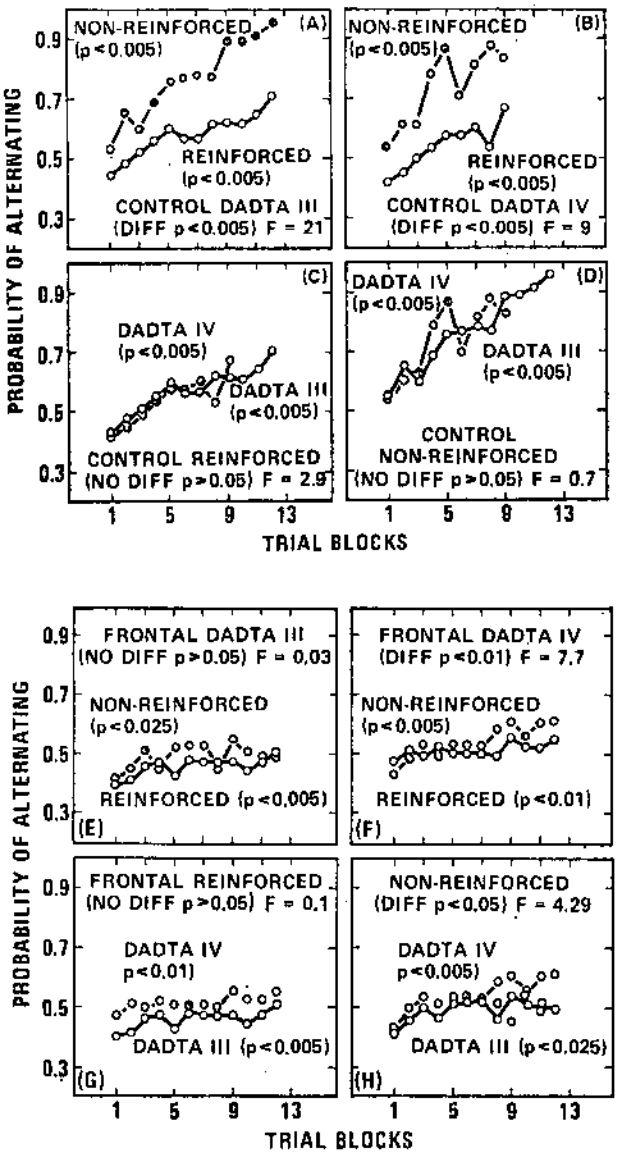

FIG. 5. Graphs of paired comparisons of within and between group and apparatus conditional probabilities. A and B are comparisons between reinforced and non-reinforced responses in DADTA III and DADTA IV; C and D are comparisons between DADTA III and DADTA IV for reinforced and non-reinforced responses, for the control subjects. E, F, G and H are the corresponding comparisons for the frontal subjects. The *P* values given in the upper portions of each block refer to the slope of each indicated curve. The *F* and *P* values given in the lower portion of each block refer to differences in the slopes of each pair of curves.

of delayed alternation is merely a successive discrimination which can more readily be performed by monkeys with frontal lesions [22].

In summary of this part of the report, the results indicate that the delayed alternation contains a temporal factor to which monkeys with frontal resections are especially sensitive.

By contrast, with regard to manipulation of other dimensions of the alternation task, the largest observed differences were within the normal group. This was the greater tendency to alternate following nonreinforced trials, irrespective of whether there were one or two food cups. This result represents a substantive extension of WILSON's [19] findings. The correct strategy for the solution of an alternation task with a correction procedure is win–shift/lose–shift, and our data indicate that the acquisition by the normal monkey of the lose–shift component significantly leads that of the win–shift component. However, this cannot be attributed to the appearance of an erroneous win–stay strategy, because had this occurred the conditional probabilities following reinforced responses would have approximated the zero level. This was never observed to occur at any stage of the study. The failure of a troublesome win–stay strategy to appear is the more curious in the light of the very extended training required before the normal animals achieved high levels of alternation.

The frontal groups also present a clear picture. Overall performance is severely impaired in both DATDA III and DADTA IV. However, the impairment is more pronounced in the DADTA III with its centrally located reinforcement cup. Fine-grain analysis shows that when, as in DADTA IV, the centrally placed reinforcement location is replaced by two spatially distinct positions, the frontal animals begin to generate conditional probability profiles similar to those of the normal animals. That is, the tendency to alternate at a higher rate following nonreinforcement appears, albeit very weakly.

We therefore conclude, in agreement with the various other reports based on different analyses and reviewed in the Introduction, that the performance of delayed alternation by frontally lesioned monkeys can be enhanced by furnishing clearly distinguishable spatial cues—in this instance, spatially distinct reinforcement placements congruent with the correct response. Our analysis shows, however, that this effect is weak and is accomplished by potentiating the generation of conditional probability profiles similar to those of normal subjects in attaining the win–shift, lose–shift strategy necessary to criterion performance of the "correction procedure" alternation task. Normal monkeys were shown to solve the alternation problem by first developing the lose- shift, then the win–shift part of the stratagy. Despite earlier training on discrimination problems which demand win–stay, no such strategy appears in the alternation task for either frontally lesioned or control groups. Thus, monkeys with frontal resections remain sensitive to both the location of the reinforcer and its sign. It is important to note, however, that manipulations of these aspects of the delayed alternation task influence the performance of such monkeys only weakly while changes in the temporal organization of the task have a profound effect.

We conclude, therefore, that in our experiments the spatial aspects of delayed alternation, although essential, are serving the more important temporal characteristics of the task. Temporal organization appears to be the primary information source in delayed alternation and forms the context in which spatial and other aspects of the task such as the sign of the reinforcer are processed. In this respect the delayed alternation is markedly different from delayed response as indicated in the introduction to this report. Therefore, the differential involvement of the two tasks by lesions of different parts of the frontal cortex (see reviews by MISHKIN [10], TEUBER [23], and PRIBRAM [24]) suggests some functional localization of the spatial and temporal factors within that cortex.

Acknowledgements—This work was supported by NIMH Grant No. MH 12970 and NIMH Career Award No. MH 15214 to the second author.

REFERENCES

1. JACOBSEN, C. F. The functions of the frontal association areas in monkeys. *Comp. Psychol. Monogr.* **13**, 3–60, 1936.
2. JACOBSEN, C. F. and NISSEN, H. W. Studies of cerebral function in primates—IV. The effects of frontal lobe lesions on the delayed alternation habit in monkeys. *J. comp. Psychol.* **23**, 101–112, 1937.
3. PRIBRAM, K. H., MISHKIN, M., ROSVOLD, H. E. and KAPLAN, S. Effects on delayed-response performance of lesions of dorsolateral and ventromedial frontal cortex of baboons. *J. comp. physiol. Psychol.* **45**, 565–575, 1952.
4. PINTO-HAMUY, T. and LINCK, P. Effect of frontal lesions on performance of sequential tasks by monkeys. *Expl. Neurol.* **12**, 96–107, 1965.
5. PRIBRAM, K. H. and TUBBS, W. E. Short-term memory, parsing, and the primate frontal cortex. *Science* **156**, 1765–1767, 1967.
6. MILNER, B. Interhemispheric difference in the localization of psychological processes in man. *Br. med. Bull.* **27** (3), 272–277, 1971.
7. MILNER, B. Hemisphere specialization: scope and limits. In *The Neurosciences Third Study Program*, F. O. SCHMITT and F. G. WORDEN (Editors), pp. 75–89, MIT Press, Cambridge, Mass., 1974.
8. PRIBRAM, K. H. and MISHKIN, M. Analysis of the effects of frontal lesions in monkeys—III. Object alternation. *J. comp. physiol. Psychol.* **49**, 41–45, 1956.
9. PRIBRAM, K. H. A further experimental analysis of the behavioral deficit that follows injury to the primate frontal cortex. *Exp. Neurol.* **3**, 432–466, 1961.
10. MISHKIN, M. Perseveration of central sets after frontal lesions in monkeys. In *The Frontal Granular Cortex and Behavior*, J. M. WARREN and K. AKERT (Editors), pp. 219–241. McGraw-Hill, New York, 1964.
11. GOLDMAN, P. S., ROSVOLD, H. E., VEST, B. and GALKIN, T. Analysis of the delayed alternation deficit produced by dorsolateral prefrontal lesions in the Rhesus monkey. *J. comp. physiol. Psychol.* **77**, 212–220, 1971.
12. POHL, W. G. Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. *J. comp. physiol. Psychol.* **82**, 227–239, 1973.
13. GENTILE, A. M. and STAMM, J. S. Supplementary cues and delayed alternation performance of frontal monkeys. *J. comp. physiol.Psychol.* **80**, (2) 230–237, 1972.
14. STAMM, J. S. and ROSEN, S. C. The locus and crucial time of implication of prefrontal cortex in the delayed response task. In *Psychophysiology of the Frontal Lobes*, K. H. PRIBRAM and A. R. LURIA (Editors), pp. 139–153. Academic Press, New York, 1973.
15. ANDERSON, R. M., HUNT, S. C., VANDER STOEP, A. and PRIBRAM, K. H. Object permancy and delayed response as spatial context in monkeys with frontal lesions. In preparation.
16. PRIBRAM, K. H. DADTA III: an on-line computerized system for the experimental analysis of behavior. *Percept. Mot. Skills*, **29**, 599–608, 1969.
17. PRIBRAM, K. H., DAY, R., and GLICK, J. Some current methods in neuropsychological research. In *The Future of the Brain Sciences*, S. BOGOSH (Editor), Vol. II. Plenum Press, New York, 1974.
18. DRAKE, K. J. and PRIBRAM, K. H. DADTA IV: a computer-based video display and recording system for behavioral testing. In *Current Computer Technology in Neurobiology* (Proc. Symp. West Virginia Medical Center, April 21–23, 1975), 1976.
19. WILSON, W. A., JR. Alternation in normal and frontal monkeys as a function of response and outcome of the previous trial. *J. comp. physiol. Psychol.* **55**, 701–704, 1962.
20. MOORE, D. and EDWARDS, A. *Standard Statistical Calculations*. Reed Paper Ltd., London, 1966.
21. TUBBS, W. T. Primate frontal lesions and the temporal structure of behavior. *Behav. Sci.* **14**, 347–356, 1969.
22. PRIBRAM, K. H. and MISHKIN, M. Simultaneous and successive visual discrimination by monkeys with inferotemporal lesions. *J. comp. psychiol. Psychol.* **48**, 198–202, 1955.
23. TEUBER, H.-L. Unity and diversity of frontal lobe functions. In *ACTA Neurobiologiae Experimentalis: The Frontal Granular Cortex and Behavior*, J. KONORSKI, H.-L. TEUBER and B. ZERNIKI (Editors). **32**(2), pp. 615–656, 1972.
24. PRIBRAM, K. H. The primate frontal cortex—executive of the brain. In *Psychophysiology of the Frontal Lobes*. K. H. PRIBRAM and A. R. LURIA (Editors), pp. 293–314. Academic Press, New York, 1973.

Résumé :

On rapporte deux études qui démontrent que dans l'alternance différée le facteur spatial, bien qu'essentiel, sert essentiellement les aspects séquentiels de l'épreuve. L'expérience 1 est la replique de l'étude antérieure avec contrôle sur ordinateur dans laquelle les intervalles entre les essais habituellement symétriques étaient rendus asymétriques. L'expérience 2 étudie les effets sur les stragégies de performnce du déplacement du lieu de rëenforcement d'une situation neutre à une autre en raltion spatiale avec les panneaux de stimulus. On oppose les résultats à ceux obtenus avec la rëponse différeé où le facteur temporel sous forme d'un délai, bien qu'essentiel, sert primairement l'aspect spatial de cette épreuve.

Deutschsprachige Zusammenfassung:

Es wird von 2 Untersuchungen berichtet, die zeigen, daß bei verzögertem Wechsel der Raumfaktor dem Sequenzaspekt der Aufgabe dient. Das erste Experiment greift eine frühere Untersuchung unter Verwendung des Computers wieder auf, in der die üblicherweise symmetrischen Intervalle zwischen den Versuchen asymmetrisch gemacht wurden. Im zweiten Experiment wird die Auswirkung auf die Ausführungsstrategien untersucht und zwar bezüglich der Verschiebung des Ortes der Verstärkung von einem neutralen Ort zu einem andern Ort, der in Beziehung zur Reizquelle steht. Die Ergebnisse werden denen gegenübergestellt, bei bei verzögerter Antwort erhalten werden, wo Zeitfaktor und Form der Verzögerung vor allem dem Raumaspekt der Aufgabe zugute kommt.