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MOVEMENT ORGANIZATION AND DELAYED ALTERNATION BEHAVIOR OF MONKEYS FOLLOWING SELECTIVE ABLATION OF FRONTAL CORTEX

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Abstract. The delayed alternation problem was tested in monkeys either according to the routine procedure (*SS* test), or when additional cues were added which were operating in the moment of executing the response. These additional cues involved different sensations in effort of the performed movement — sliding heavy object vs. sliding light object (*sS* test), as well as different sensations in pattern of movement and joints — sliding vs. lifting of an object (*SL* test). In normal the training of *SL* task was the easiest one, whereas the *sS* task was in some animals much more difficult than the *SS* task, and in others equivalent to this task. Removals in dorsolateral prefrontal cortex were made: total, only principalis sulcus, and only the rest of the area. Total and principalis lesions produced a severe impairment of all three tasks, while the third lesion produced only a slight deficit. The character of the impairment in the first two groups largely depended on the order in which the animals learned the three tasks in the pre-operative training.

The main thesis underlying the experiments to be reported is that the long-term impairment of monkeys following ablation of dorsolateral frontal cortex represents a disturbance of high level kinesthetic-motor processes. Specifically, the deficit of frontally-ablated monkeys is regarded as an inability to make complex motor differentiations when kinesthetic cues, removed in time from response execution, constitute the only relevant sensory information in the task. The term "kinesthesis" is used to denote functions associated with movement-produced information from muscle receptors (that is, from the spindle and tendon golgi body). The complex motor differentiations referred to are of the Movement$_1$ vs. Movement$_2$ (M_1 vs. M_2) type, as classified by Konorski (1967), in which an animal must choose between two different responses, each one of which, when selected correctly, would be reinforced. Usually, differentiations of this type involve a choice between "go-left" vs. "go-right" movements as in the delayed alernation (DA) and delayed response (DR) tasks. The impairment of frontally-ablated monkeys in situations of this type, involving an M_1 vs. M_2 differentiation, has led some investigators, such as Mishkin (1964) and Miles (1964), to suggest that the deficit is associated with a "spatial factor" inherent in the task. It is here proposed that the sensory basis of this general spatial factor is specifically related to the kinesthetic modality.

These formulations are not new. The involvement of prefrontal cortex with kinesthetic processes has been advanced by Konorski (1967). Through elaboration of kinesthetic input, Konorski (1967) has suggested that areas of prefrontal cortex in animals and man become organized functionally as "fields" for kinesthetic gnosis of spatial relations. In accord with Konorski's (1967) formulations, Stamm (1970) has interpreted the long-term impairment on DA and similar tasks as a severe form of "kinesthetic agnosia" which constitutes the disturbance underlying the "spatial factor" proposed by Mishkin (1964).

The experiments summarized in this paper, undertaken in association with John Stamm, examined these proposals. All of the experiments reported here involved training of rhesus monkeys (*Macaca mulatta*) in a modified Wisconsin General Testing Apparatus (WGTA) on several variations of the DA task. In our analysis of the DA task, it was assumed that the movement-produced feedback from prior response is used as the relevant cue for subsequent response selection. Thus, the general strategy was to vary the movement organization used for the two responses, thus varying the nature of the movement-produced stimulation, and to observe the effects on performance of monkeys following prefrontal ablations. It is suggested that the long-term impairment of frontal monkeys on DA results from: (i) an inability to discriminate in time between the kinesthetic consequences of prior movements to the left from those to the right, or (ii) an inability to utilize kinesthetic cues to select correctly between the two response alternatives.

EXPERIMENT I. SUPPLEMENTARY CUES AND DA PERFORMANCES

In structuring the DA task, it is common to have responses involve very similar movements. The manipulanda are usually objects of the same size, shape and weight. Thus, the intrinsic spatial organization of the motor pattern used for the two responses is basically the same. As a consequence, somesthetic cues from the receptors located around articular surfaces (Konorski 1967), normally utilized in movement differentiation processes, are minimized. In contrast to the usual procedure, articular-somesthetic cues (reffering specifically to input from *joint receptors*) were added to the DA task by imposing differences in the spatial organization of the motor patterns used for left and right responses. In this first preliminary study (Gentile and Stamm, in press), it had been hypothesized that the introduction of supplementary articular-somesthetic cues in the DA task would provide an alternate means for response selection and, therefore, would reduce the impairment of frontal monkeys.

In the second phase of this experiment, supplementary kinesthetic cues from *muscle receptors* were introduced into the DA task by having different force requirements for right as compared to left responses. It had been hypothesized that the force variation would not improve the DA performance of monkeys with total lesions of dorsolateral frontal cortex. If prefrontal cortex is involved in higher-level processing of kinesthetic input, then the totally-ablated frontal monkeys should be unable to utilize supplementary kinesthetic cues. Although impairment on DA has been demonstrated following ablation in and around principalis sulcus (Blum 1952, Mishkin 1957, Butters and Pandya 1969), this type of ablation may impinge only partially upon kinesthetic gnostic areas. Thus, it was of interest to determine whether the effects of supplementary kinesthetic cues provided in a force variation of the DA task differed following partial as compared to total ablation of prefrontal cortex.

The general testing procedure was the same for all experiments reported in this paper. Before the first trial, both foodwells were baited with half a peanut. Using the correction procedure, reinforcement was maintained on the same side until a correct response was made. The first error to one side was scored as an initial error; successive errors to the same side were scored as repetitive errors. The sum of the two error measures was used as a total error score. In the first experiment, 30 reinforced trials were administered in each session. For all other experiments, 50 reinforced trials were administered.

The subjects in the first experiment were seven rhesus monkeys which had extensive previous training on DA and visual discrimination tasks (Stamm 1970). Four of the animals had received TOTAL ablation of dorsolateral frontal cortex (that is, bilaterally from the anterior bank of arcuate sulcus to the frontal pole including the banks and depths of principalis sulcus). The remaining three subjects, which had previously served as unoperated controls, were administered partial frontal lesions. For two of these subjects, bilateral ablation of the banks and depths of principalis sulcus with sparing of the surrounding cortex (PRIN) was performed. The other partial lesion, administered to one monkey, involved bilateral ablation of the anterior bank and depth of arcuate extending the sulcus dorsally and laterally to all portions of the dorsolateral convexity except for the banks and depths of principalis (DAL).

Supplementary articular cues

The DA variation used to introduce supplementary articular cues (that is, supplementary "joint" input) required two responses in which the movements used differed markedly in the intrinsic spatial organization. This first variation was referred to as Block/Slide (*BS*). The motor pattern used for response to the left involved sliding an aluminium foodwell cover diagonally upward. The right manipulanda, a wooden block covering the foodwell, were displaced by pushing sideways. To control for the differences in the shapes of objects used as manipulanda in the *BS* task, another DA variation was tested in which two blocks of different shapes were employed. In this second variation, referred to as Block/Block (*BB*), a wedge-shaped block covered one foodwell, a rounded block covered the other. The third variation tested involved the standard DA task conditions in which manipulanda were visually identical and displacement movements to the left were the same as those to the right (sliding an aluminum foodwell cover diagonally upward) (*SS*).

The TOTAL frontal monkeys had been previously trained on the *SS* task pre- and post-operatively (Stamm 1970). In the present experiment, they were retrained on *SS* followed by initial training on *BB* and *BS* for 630 trials each. The median per cent correct over seven blocks of 90 trials each under the three DA tasks is presented in Fig. 1. For these TOTAL monkeys, performance was superior under the BS task that provided supplementary articular cues (Friedman's two-way analysis of variance, $p \leqslant 0.01$). The three monkeys which had served as unoperated controls in prior experimentation were retrained, prior to operation, to criterion-performance on *SS* and then on *BB*. The post-operative testing of *SS* indicated a marked decrement in performance following both types of partial frontal lesions (PRIN: 48% and 51%, DAL: 50% correct). With continued testing on the *BB* task, the DAL monkey attained the 90% correct criterion-level. In contrast, the highest per cent correct within a 90-trial block on *BB* was 57 and 61 for the two PRIN monkeys. However, these PRIN monkeys improved substantially when tested on the *BS* task (66 and 86% correct). Apparently, the DAL ablation had less effect upon long-term impairment than PRIN. And, more importantly, PRIN, as with TOTAL monkeys, were less impaired on the *BS* than the *BB* task.

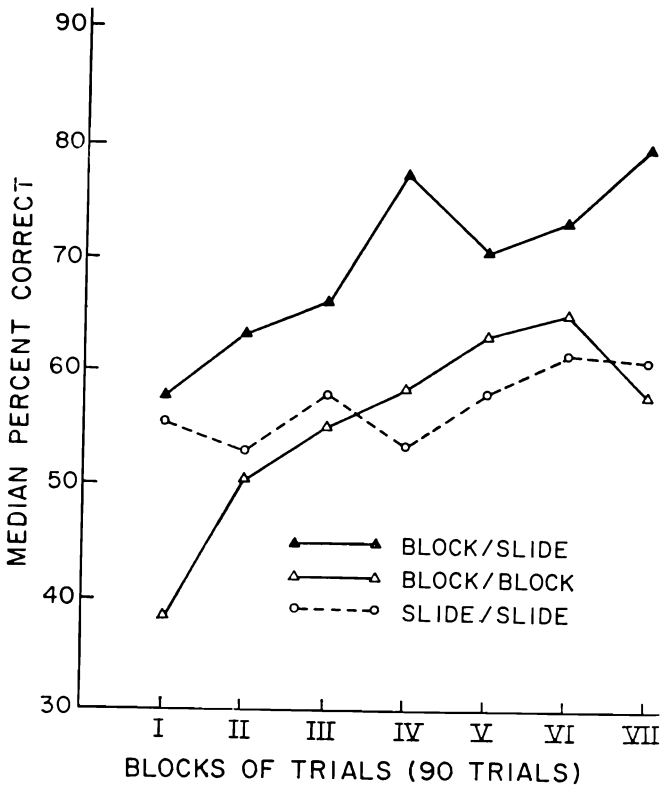

Fig. 1. Median per cent correct response of TOTAL monkeys on three DA task variations during retraining.

The observed improvement in the performance of the PRIN and TOTAL monkeys on *BS* during successive testing of the three DA tasks could have been attributed to time or order in training. To evaluate the effects of the supplementary articular cues without these confounding variables, a shifting-task procedure was next employed for both TOTAL and partially-lesioned groups. Each task was administered for 150 trials in the following order: *BS* — *BB* — *BS* — *SS* — *BS*. The mean total error per trial and median per cent correct response during the series of shifting-tasks is presented in Fig. 2. Although the mean total error appears higher for PRIN than TOTAL monkeys (Fig. 2), the post-operative interval was not comparable. Differences in mean total error and per cent correct were statistically significant for TOTALs (analysis of variance, $p \leqslant 0.05$; and Friedman's two-way analysis, $p \leqslant 0.042$). Although no further statistical evaluation was undertaken, the same pattern of shifts in error measures was observed for partially lesioned monkeys. In summary, monkeys that had sustained total or

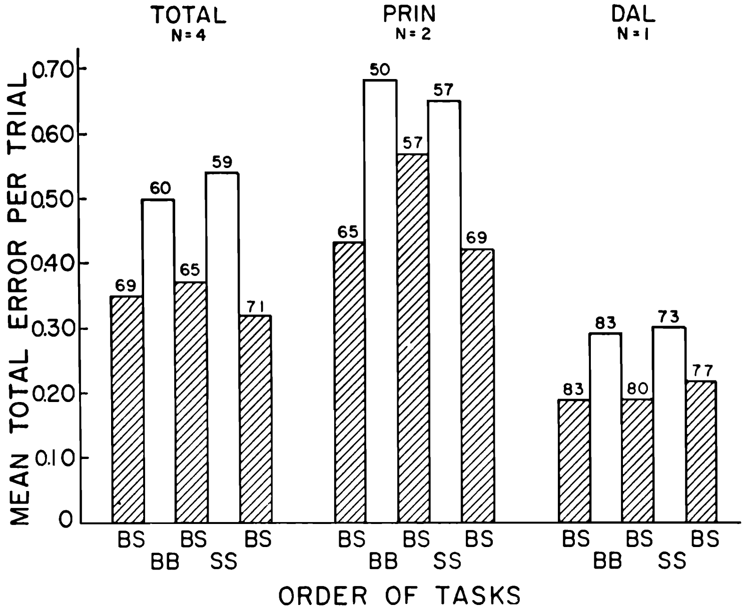

Fig. 2. Mean total error per trial on delayed alternation during series of shifting-tasks (entry above bar indicates median per cent correct response).

partial ablation of dorsolateral frontal cortex improved on DA when supplementary articular somesthetic cues were introduced in the task.

Supplementary kinesthetic cues

In the second phase of this experiment, supplementary kinesthetic cues were provided in the DA task by weighing the wedge-shaped block previously used in the *BB* task. First, the seven monkeys were trained using the heavier wedge-shaped block (489.0 g) to cover one foodwell and the lighter rounded block (141.5 g) to cover the other. Thus, there were differences in both weights and object-shapes of the manipulanda. Then, testing was carried out using two identical, wedge-shaped blocks of different weights (489.0 and 141.5 g). The results indicated that when supplementary kinesthetic cues were introduced into the DA task, the performance of TOTAL monkeys did not change whereas that of PRIN improved. Performance changes of the DAL monkey were not consistent and appeared influenced by the absence or presence of visual cues. Thus, there appeared to be some preliminary evidence of a functional dissociation between TOTAL and PRIN monkeys: they respond differently to kinesthetic cues. Whereas both PRIN and TOTAL monkeys utilized supplementary articular cues ("joint" input) to improve DA performance, only PRIN animals appeared able to utilize supplementary kinesthetic cues ("muscle" input).

Comments

The improvement on DA when articular-somesthetic cues were added to the task. indicated that all frontal monkeys could utilize other cues to affect some compensation for the proposed kinesthetic deficit. The improvement under *BS* was related specifically to the addition of another form of movement-produced cues: no effect was observed when supplementary visual cues alone were provided as in the *BB* task. However, there were two limitations to these findings. First, although the intent of the present study was to introduce articular-somesthetic cues to the task, it was unavoidable that concommitant alteration of kinesthetic feedback occurred. Thus, the task really provided a combination of supplementary articular and kinesthetic cues. That the observed improvement was attributed to articular cues still seemed to be the most reasonable interpretation. When kinesthetic cues alone were added to the task, as in the two force variations, no effect was observed upon the performance of TOTAL frontal monkeys. The second limitation of this study related to the presence of visual cues. Under the conditions of this study, it was not possible to determine if the frontal monkeys' improvement on DA was the result of articular cues alone or these cues in the presence of visual differences between manipulanda.

EXPERIMENT II. MOVEMENT ORGANIZATION AND DA PERFORMANCE

The purpose of the second experiment was to eliminate the methodological limitations of the first and to continue in the same, general line of inquiry. Again, three types of DA tasks were used: a standard task and two variations which provided either (i) supplementary kinesthetic cues alone or (ii) a combination of supplementary articular and kinesthetic cues. In all three tasks, the manipulanda were of the same size and shape, thus eliminating the concommitant visual cues present in the previous experiment.

Another important aspect of the second experiment concerned a more thorough analysis of DA which took into account the sequential aspects of the task. As many trials are administered within one experimental session on the DA task, obtaining the relevant cues seemed to involve more than distinguishing between patterns of movement-produced input from right and left responses. Rather, as successive patterns of input occur within a relatively brief interval of time, it appeared necessary for the animal to determine which of the residual aftereffects of various movements occurred last. A representation of the analysis to follow is given in Fig. 3. In the standard DA task, it is suggested that the relevant kinesthetic cue is obtained by "partitioning" (Pribram 1960) overlapping sets (circles in Fig. 3) of movement-produced input into non-intersecting subsets ordered on the basis of recency. The intersect or area of overlap would contain the consequences of motor components common to the left and right responses. The two non-intersecting subsets would represent the kinesthetic aftereffects restricted to one or the other of the two responses. Abstracting the kinesthetic cue from the subset associated with the most recent response (stippled circle in Fig. 3) would provide for the left versus right movement differentiation required in the DA task.

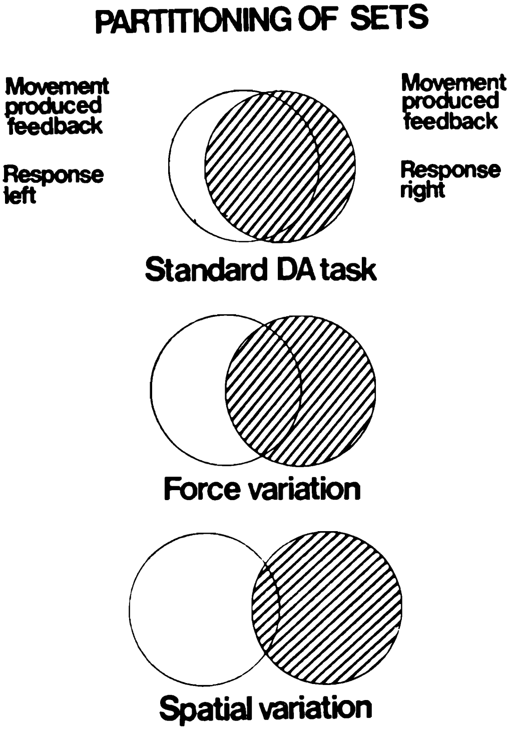

Fig. 3. Schematic representation of the processing of movement-produced feedback required in the standard DA task and in two variations.

If the DA task was structured so that the *force* requirements of movements to the left differed from those to the right, then it was hypothesized that there would be less similarity between patterns of kinesthetic feedback from the two responses. In other words, the area of intersect representing the overlap between sets of kinesthetic input from the left and right movements would be reduced (Fig. 3). Thus, abstracting the relevant kinesthetic cue would be easier and, consequently, the movement differentiation process would be facilitated.

If the DA task was structured so that the intrinsic *spatial* organization of movements to the left was markedly different from movements to the right, then two events would be predicted to occur: (i) the commonalities in the patterns of kinesthetic input from the two responses would be markedly reduced and (ii) articular-somesthetic cues not usually relevant in the DA task would become available. Both of these events would result in less overlap of movement-produced input from right and left responses (Fig. 3). Thus, abstracting and utilizing cues for movement differentiation processes would be markedly facilitated.

On the basis of the previous findings, it was hypothesized that the acquisition of DA by normal monkeys and the long-term impairment of frontally-ablated monkeys would be a function of the type of movement-produced cues provided in the task. It was predicted that processing and utilizing cues would be easiest in the spatial variation of DA, of moderate difficulty in the force variation, and most difficult under the standard DA conditions. This order was expected to be reflected in the acquisition rate of normal monkeys, with the spatial variation fastest and the standard DA task slowest. The performance on DA immediately following prefrontal ablation was expected to correspond to the extent and locus of the lesion: (i) total ablation of dorsolateral frontal cortex yielding the most pronounced impairment with characteristically high rates of repetitive error, (ii) ablation of principalis sulcus yielding almost as marked a disruption as the TOTAL lesion but with less repetitive error, and (iii) ablation of anterior arcuate extending the lesion dorsally and laterally but sparing principalis sulcus and surround yielding least and most short-term disruption of performance. Differences between the three DA variations were not expected during the initial post-operative testing interval as all ablations of prefrontal cortex were expected to disrupt kinesthetic processes. However, with continued training post-operatively, the performance of TOTAL monkeys was predicted to improve most on the DA task providing supplementary articular cues (that is, the spatial variation). Similarly, PRIN animals also were expected to be least impaired on the spatial variation of DA during post-operative retraining. However, in contrast to the totally-ablated monkeys, it was predicted that PRIN monkeys would recover use of kinesthetic cues as areas of prefrontal cortex were intact. Therefore, during retraining, it was predicted that PRIN would have better performance on the force variation of DA than on the standard task.

The subjects were 10 experimentally-naive rhesus monkeys. Nine animals were administered one of three types of frontal ablation: (i) TOTAL (all of dorsolateral frontal cortex from anterior arcuate to the frontal pole), (ii) PRIN (primarily the lower portion of the banks to the depths of the sulcus from anterior arcuate to the frontal pole), and (iii) DAL (smaller than in the previous experiment, including banks and depths of anterior arcuate extending the lesion dorsally and laterally but sparing principalis and a greater extent of its surround).

For the three DA tasks, the manipulanda were of the same size, shape and orientation. The tasks varied in terms of the displacement movements used for right and left responses. In the standard task (Slide/Slide), the objects covering the left and right foodwells had to be displaced by pushing sideways to the left with the left hand against an upright post between a circular disc and a metal base (Fig. 4). In the force variation, the objects covering the foodwells had to be displaced in the same manner as the Slide/Slide (*SS*) task except that the right manipulandum was substantially heavier than the left (625.5 compared to 296 g). The force variation was denoted as the Heavy Slide/Light Slide (*sS*) task. The third variation in DA was structured so as to affect as

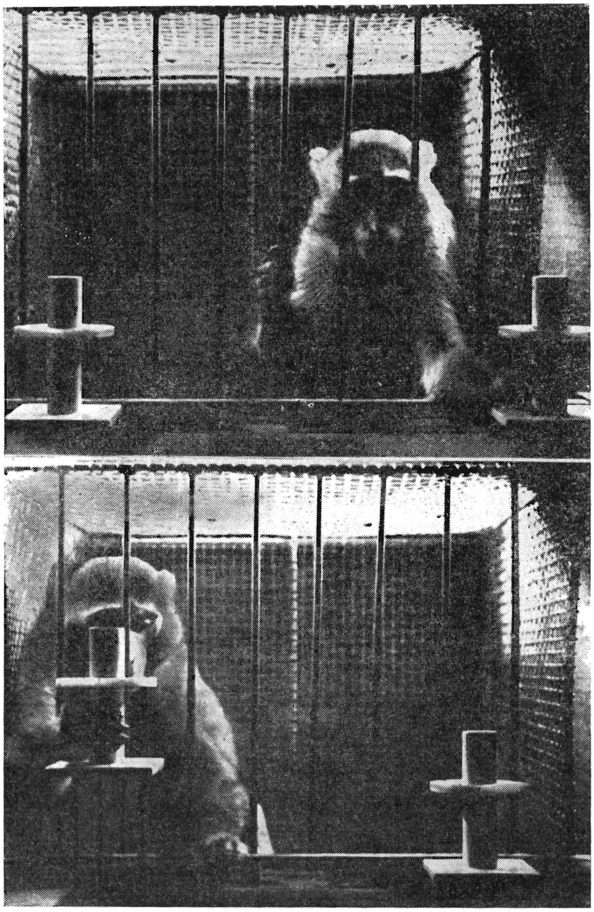

Fig. 4. Movements used for lift and slide manipulanda.

much dissimilarity in the spatial organization of left and right movements as possible. The left manipulandum was displaced by pushing sideways with the left hand as the *SS* task. The right manipulandum was a lifting apparatus. To attain the peanut located in the foodwell, the animal had to grasp the upright post between the base and circular disc with the right hand and lift the object directly upward (*SL*, Fig. 4).

For pre-operative training, nine subjects were randomly assigned to initial acquisition on one of the three DA task: *SS*, *sS* or *SL*. After acquiring the first DA task to a 90% correct level or after 1,200 training trials, monkeys were trained to criterion on the other two tasks in a counterbalanced order. Thus, there was a group of three monkeys tested under each of three order conditions: (i) *sS* — *SS* — *SL*, (ii) *SS* — *SL* — *sS*, (iii) *SL* — *sS* — *SS*. Reference to the task administered first during acquisition has been used to identify a particular order group. Thus, the "*SL*" group consisted of the three monkeys which acquired the DA variations in the *SL* — *sS* — *SS* order. To evaluate possible transfer effects between tasks, 400 trials of additional testing were carried out after acquisition of the third DA task.

Pre-operative retention testing involved administration of 100 trials on each of the three DA tasks. Immediately after pre-operative retention testing, animals underwent surgery receiving one of the three lesions described previously. One animal within each order group was randomly assigned to one of the three types of frontal ablations. Post-operative retention testing involved the administration of 100 trials on each of the three DA tasts followed by a second series of 300 trials. To provide for examination of each task during various recovery stages in retraining, each task was tested for 200 trials within each 600 trial block (order counterbalacend across blocks). Over all post-operative testing, each of the three DA tasks was administered for 1,000 trials: 200 trials during the initial post-operative period and 800 retraining trials. Thus, each animal was tested for a total of 3,000 trials post-operatively.

Pre-operative training

Acquisition of *SL* appeared to be faster than the standard DA task (Fig. 5). By the third block of trials, the three monkeys under *SL* were performing above the 70% correct level: whereas the highest level attained on *SS* was 63% correct (Fisher's Test, $p \leqslant 0.5$ at blocks 2 and 3). The learning curves overlapped after 400 trials of training; the performance of the poorest monkey on *SL* (83% correct) was matched by the best monkey on *SS*. Although no difference was evident between the mean number of trials to criterion on the two tasks, acquisition to the 80% correct level was more rapid on *SL* than *SS*.

As soon as performance on *SS* exceeded 60% correct, rapid acquisition to criterion-level was evident. In contrast, two of the three monkeys originally trained on *sS* failed to attain the learning criterion after 1,200 trials although performance levels were above 60% correct at some point in training for both monkeys. An additional monkey was trained on *sS* (Monkey 2). Again, the task was not learned after 1,200 trials. The likelihood of having six animals under the other two tasks (*SL* and *SS*) reach criterion and three-fourths of the monkeys on *sS* fail to do so is 0.03 (Fisher's Test). Thus, acquisition of *sS* beyond the 60% correct level appeared mode difficult than *SS* and *SL*.

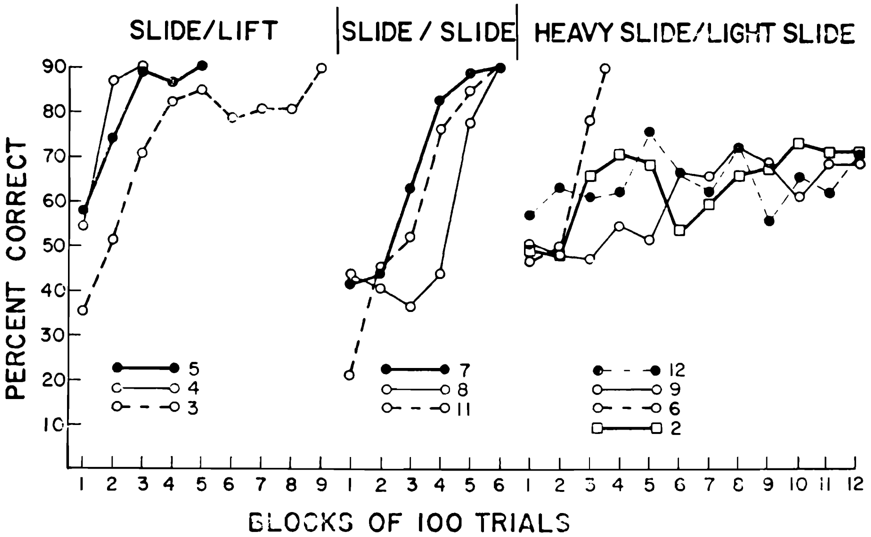

Fig. 5. Per cent correct response during acquisition of three DA tasks for the 10 monkeys trained pre-operatively.

The three animals that failed to learn *sS* were transferred to the *SS* task and reached criterion-level in a mean number of 283 trials. During the first 100 trials on the task these monkeys averaged 70% correct response which was significantly (Fisher's Test, $p \leq 0.05$) better performance than the first 100 trials of monkeys originally trained on *SS*. Thus, switching to *SS* did not constitute acquisition of a new task for these "*sS*" monkeys. Rather, training on *SS* either (i) provided the additional trials required by these monkeys to reach 90% correct or (ii) altered the task conditions in some way to make continued improvement possible.

The monkeys initially trained on *SS* and on *SL* acquired the second and third DA tasks in a mean number of 54 trials. Thus, learning of the *sS* task after acquisition of *SL* and *SS* presented no difficulty to these animals. The one monkey in the "*sS*" group which had initially acquired that task (Monkey 6) also transferred easily to the other two DA variations. The remainder of the "*sS*" group, after finally having learned *SS*, took a mean number of 383 trials to acquire *SL*: a significantly greater number of trials than either of the other two groups on either the second or third DA tasks (Fisher's Test, $p \leqslant 0.05$). This observation may have reflected one of several factors: (i) intellectually-disadvantaged monkeys, (ii) an accommodation factor of prolonged low level performance on prior tasks or (iii) a particular transfer effect inherent in the order of task administration.

To summarize the pre-operative data: acquisition of DA with the combination of articular/kinesthetic cues added to the task (*SL*) seemed faster than the standard task, as had been hypothesized. No support was provided for the prediction concerning supplementary kinesthetic cues. Quite unexpectedly, acquisition of *sS* appeared to be more difficult than the other two DA task conditions.

Initial post-operative testing

Both TOTAL and PRIN ablations disrupted DA performance (Sign Test, $p \leqslant 0.03$); while DAL lesions seemed to have little effect. The mean per cent correct over all tasks during the post-operative retention tests was 58% for TOTAL monkeys, 61% for PRIN and 88% for DAL monkeys. For specific tasks (Fig. 6), TOTAL monkeys had significantly higher mean total error on *SL* than PRIN monkeys (Friedman's two-way analysis, $p \leqslant 0.028$). The difference was primarily attributable to the rate of repetitive error. Generally, on the other two tasks, TOTAL monkeys were more impaired than PRIN animals but these smaller differences were not statistically reliable. By the second block of 300 trials post-operatively, initial and repetitive error had decreased significantly for both PRIN and TOTAL monkeys (Sign Test, $p \leqslant 0.02$) for each measure (each lesion group). Task differences between lesion groups were not evident at this point.

In summary, task differences between lesion groups had not been hypothesized immediately following frontal ablations. However, during post-operative retention tests, a difference in repetitive error between TOTAL and PRIN monkeys on the *SL* task was observed. Performance on the DA variation which had been acquired most rapidly by normal monkeys (*SL*), apparently because of the supplementary articular/kinesthetic cues, was most markedly disturbed following TOTAL ablation and least disrupted following PRIN lesions.

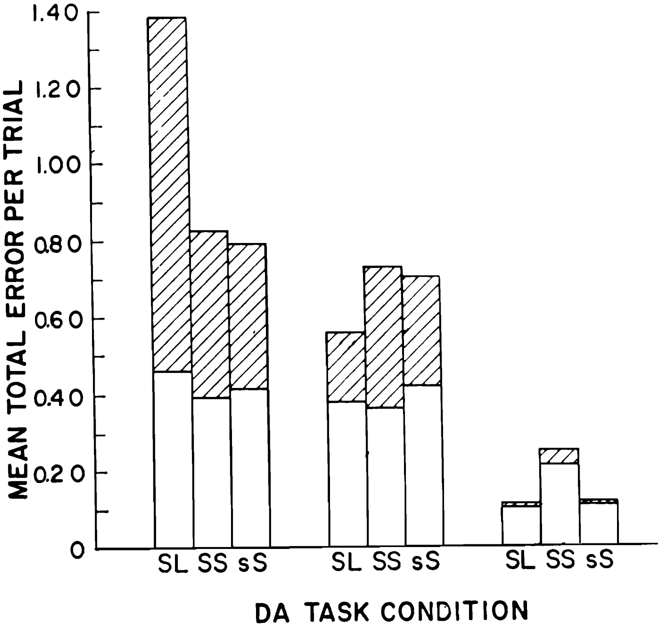

Fig. 6. Mean total error per trial during post-operative retention tests for the three lesion groups (TOTAL, PRIN, DAL) on each DA task. Stippled portion of bar indicates repetitive error.

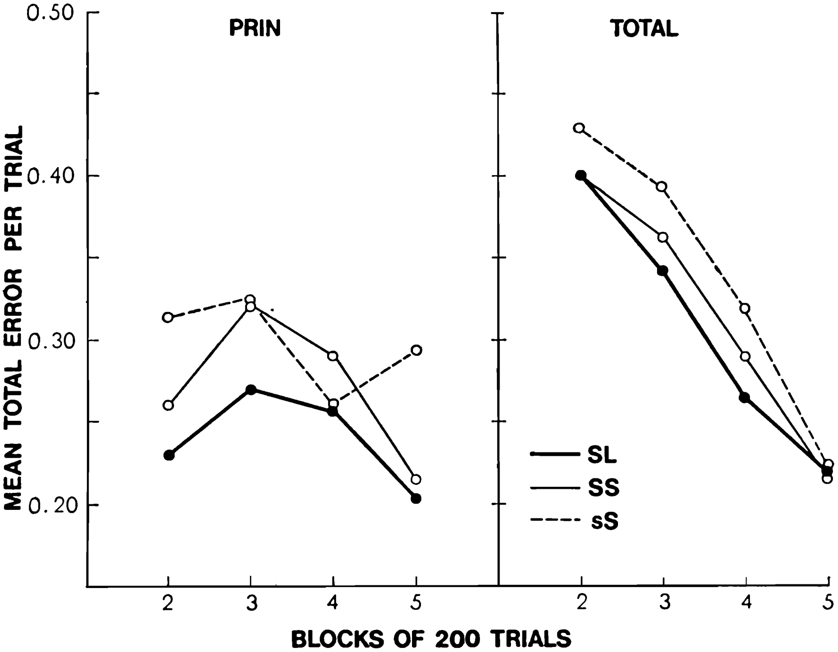

Fig. 7. Mean total error during the 800 retraining trials on each of the three DA tasks for the PRIN and TOTAL groups.

Retraining

Two findings were made from the retraining data. First, as had been hypothesized, DA performance seemed better for TOTAL and PRIN animals on the task in which articular cues were added (*SL*). Figure 7 shows mean total error for the two lesion groups during the 2,400 retraining trials (800 on each task). Differences between curves were statistically reliable at the third and fourth blocks for TOTAL monkeys (Sign Test, $p \leqslant 0.006$). For PRIN monkeys, error on *SL* was significantly less than the other two tasks at the second and third blocks (Sign Test, $p \leqslant 0.006$). Group data for PRIN monkeys were not reliable after the third block: the curves are an averaging effect as individual monkeys had very different error patterns over the terminal phase of training.

The second finding was that the magnitude of impairment following frontal ablation seemed related to the pre-operative order of task administration, that is, one monkey in each lesion group having been trained first on one of the three DA tasks. Figure 8 indicates total error *averaged over the three tasks* and arranged by lesion and order group.

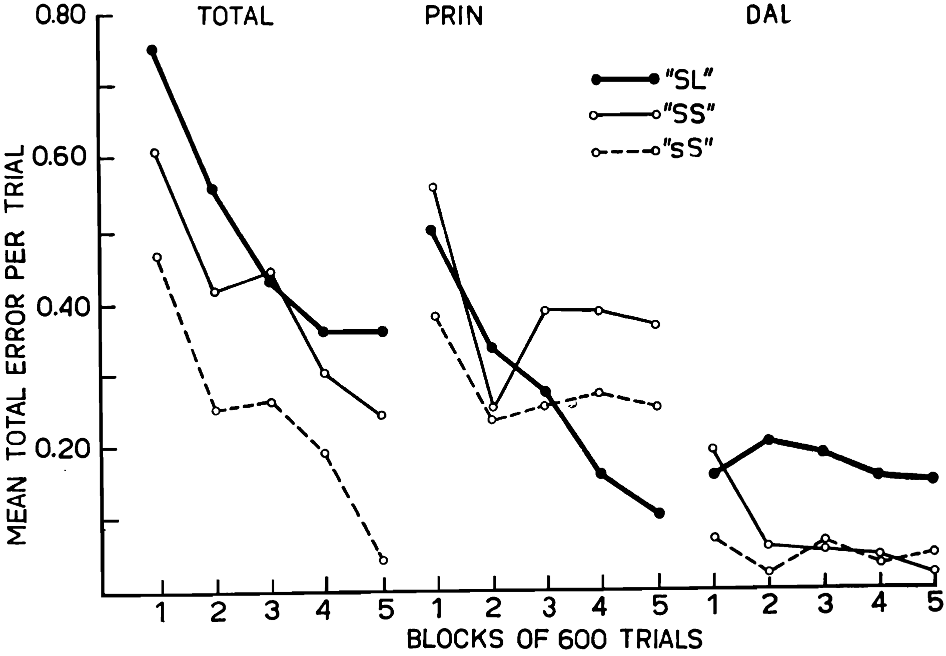

Fig. 8. Mean total error averaged over the three DA tasks for the 3 000 trials of post-operative training for the three lesion groups. Order group indicates DA task administered first during pre-operative training.

Monkeys that acquired *sS* first during pre-operative training were less impaired than those that initially acquired the standard task (*SS*) regardless of lesion-type. Indeed, the TOTAL monkey in the "*sS*" group relearned all tasks to the 90% correct level during the last block of trials. It seems unlikely that by chance the brighter monkeys were in the *sS* group as the TOTAL and PRIN animals were the ones that had failed to acquire the *sS* task pre-operatively after 1,200 trials. The additional training could have been a determining factor but these added trials were administered before having acquired any DA task. The post-operative order of testing might be considered a variable but this seemed unlikely also as under all order conditions each task was tested following every other task. Thus, no one of these possibilities seemed to

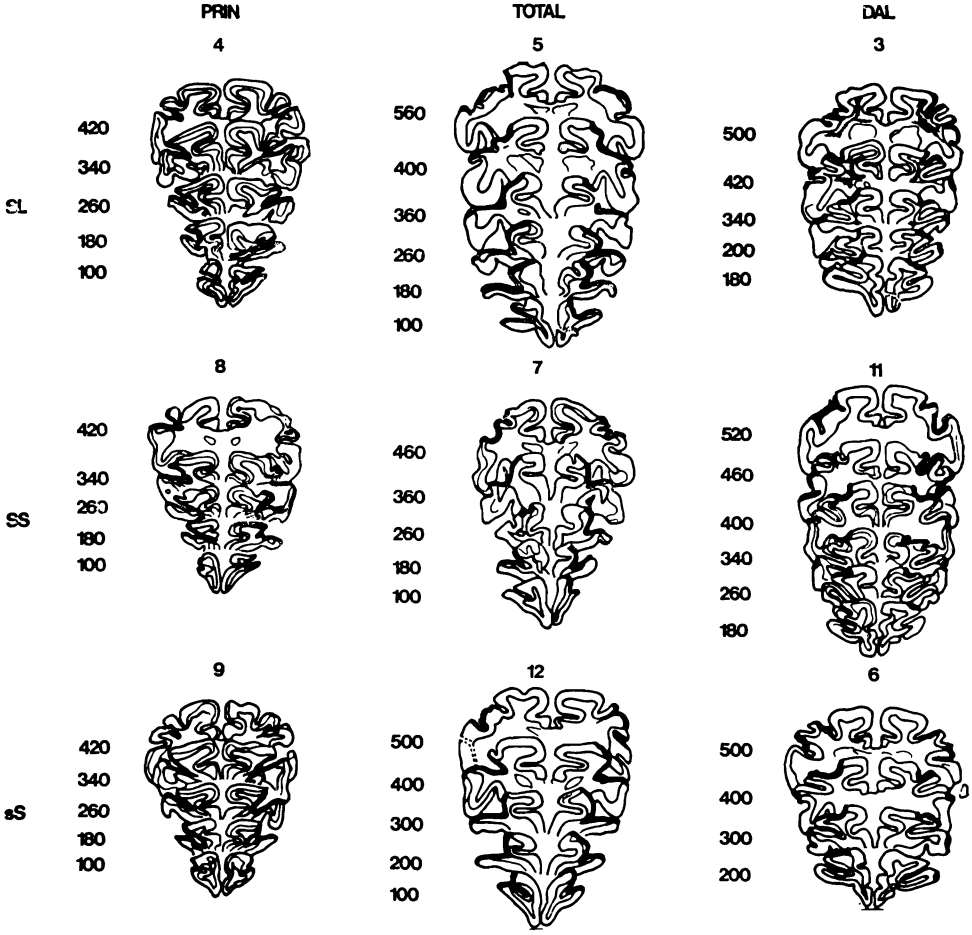

Fig. 9. Recontructions of lesions for nine monkeys.

account for the finding. Of further interest were the performance levels of monkeys first trained pre-operatively on the *SL* task: the TOTAL and DAL monkeys were the most impaired within their lesion groups, the PRIN monkey was terminally least impaired within that group relearning all tasks to criterion-level by the last block of trials. The pre-operative data had indicated that *SL* was the easiest task and *sS* the most difficult task to acquire. It seemed as though the degree of difficulty in initially acquiring a DA variation was related to the magnitude of impairment post-operatively.

The extent and locus of lesions were examined to determine if any relationship with the magnitude of impairment was evident (Fig. 9).

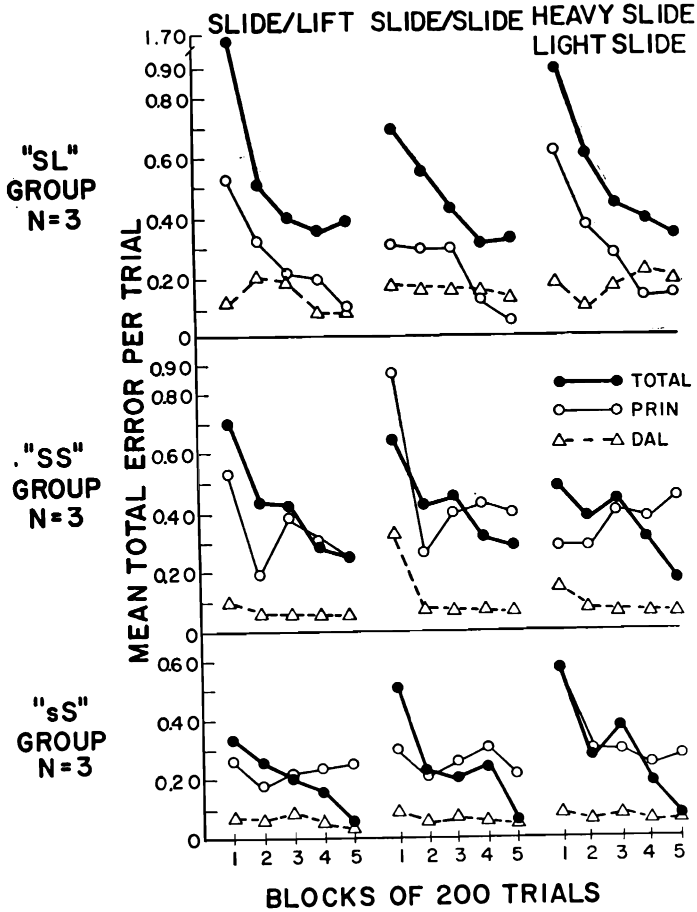

Fig. 10. Post-operative data for individual monkeys within each order group arranged by task and lesion.

Except for the DAL monkey in the *SL* group, no correlation seem evident. In fact, the two monkeys that relearned DA (Monkeys 4 and 12) both ranked in the middle of their lesion groups in extent.

Individual retraining data were examined, particularly the error patterns of PRIN animals (Fig. 10). The PRIN monkey in the "*sS*" group did not improve after 400 trials although the error rate during retraining was comparatively quite low. The PRIN animal in the "*SS*" group sharply increased in error after 400 trials on each task. Both monkeys had higher error measures than the TOTAL monkeys within their order group over the last blocks of training on the *SS* and *sS* tasks. The error pattern for these two PRIN monkeys differed under the *SL* task: the "*sS*" monkey had a gradual increase in error over training; the "*SS*" monkey sharply increased but then decreased error paralleling the error rate for the TOTAL monkey in that order group over the last blocks of trials. These trends, along with the notably different pattern of the "*SL*" monkey, suggested a very speculative hypothesis. The interpretation of these data is presented at this point in some detail as it led to very specific predictions in the next experiment.

Comments

It is proposed that pre-operative training on the first task administered resulted in the functional organization of kinesthetic gnostic areas in prefrontal cortex as well as the organization of other areas of brain, possibly those subcortical structures anatomically associated with dorsolateral frontal cortex, possibly other cortical areas. For ease of discussion, these other brain structures will be referred to as subcortical. However, the involvement of other parts of cortex, especially association sections related to somatosensory functions, may be the critical areas of concern.

The extent of organization resulting from pre-operative training is proposed to be related to the degree of difficulty of the task; *SL* an easier task, therefore, less organization; *sS* a more difficult task, therefore, more organization. Following TOTAL ablation of prefrontal cortex, the level of impairment was determined by the extent of subcortical organization resulting from pre-operative training. Thus, the TOTAL monkey pre-operatively trained first on *sS* was less impaired than the "*SL*" animal. Complex processing or utilization of kinesthetic cues was not possible for TOTAL monkeys, as all kinesthetic gnostic areas of prefrontal cortex had been removed. Therefore, the TOTAL monkey began using the articular-somesthetic cues in the *SL* task and transferred the positive effects of this training to the two other tasks.

Following PRIN ablation, the level of impairment was determined by the extent of subcortical organization *and* the extent of organization within those prefrontal areas left intact. For all PRIN monkeys, complex processing or utilization of kinesthetic cues was disrupted. However, to the extent that intact areas had been functionally organized during pre-operative training, a PRIN monkey would persist in the attempt to use kinesthetic cues instead of the available articular cues. It is suggested that use of one type of cue interfered with the other and this interference increased as the intact kinesthetic areas were reorganized during retraining. Thus, the PRIN monkey trained first on *sS* pre-operatively had the most highly organized prefrontal-subcortical system. While this greater functional elaboration resulted in least impairment post-operatively, it interfered with the use of articular-somesthetic cues. Similarly, the "*SL*" monkey had the least highly organized system and, therefore, had the least interference in the use of articular cues. For the "*SS*" PRIN monkey, interference between the two sources of cues resulted in the increase in error during retraining. Over the last blocks of retraining trials, articular cues were used by the "*SS*" PRIN monkey but the interference from intact cortical areas precluded positive transfer from *SL* to the other tasks. This interference effect was observed also in the "trade-offs" in performance levels between *sS* and *SL* for the most impaired DAL monkey (Monkey 3).

EXPERIMENT III. PRE-OPERATIVE TRAINING AND DA PERFORMANCE FOLLOWING PRINCIPALIS ABLATION

The purpose of the last experiment was to determine how tenable were the interpretations of findings from the second experiment. Three specific hypotheses were formulated. It was predicted that (i) acquisition of *sS* would be more difficult for normal monkeys than the standard DA task (*SS*); (ii) the impairment on DA following ablation of PRIN would be less for those monkeys pre-operatively trained first on *sS* than for those trained on *SS*; and (iii) PRIN monkeys first trained pre-operatively on *sS* would be less able to utilize supplementary articular-somesthetic cues in the DA task during retraining than PRIN monkeys initially trained on *SS*.

Nine experimentally-naive monkeys were used as subjects. However, two died during the experiment: one after completing pre-operative training and one after the first stage of post-operative testing. The eight monkeys available after pre-operative training were all administered PRIN ablations. The same three DA tasks as used in Experiment II were employed again. Monkeys were adapted to the apparatus and trained in the required displacement movements using the same procedures as described previously.

For pre-operative training, monkeys were divided into two groups: four were initially trained on *sS* and five on *SS*. Following acquisition of the first task to a 90% correct level, "*SS*" monkeys were trained on *sS* and "*sS*" monkeys were trained on *SS*. Next, both groups were trained to criterion-level on *SL*. For both groups, pre-operative retention tests involved administration of 100 trials on only the *SS* taks. Pre-operative testing began two weeks after surgery. Rather than having an intitial post-operative training schedule in which animals were shifted from one task to another, a simpler procedure was used. First, 700 trials on *SS* was administered to both groups. Then, to determine if supplementary kinesthetic cues in the DA task affected a change in performance in comparison to the standard task, a series of shifting tasks (similar to Experiment I) was employed. Two hundred trials of each task were administered in the following order: *sS* — *SS* — *sS* — *SS*. To evaluate if supplementary articular cues differentially affected the performance of the two groups another series was used; namely, 200 trials of each task in the following order: *SL* — *SS* — *SL* — *SS*.

Pre-operative training

No evidence was produced to support the first hypothesis. The median number of trials to criterion for the "*SS*" group was 750, with a range of 470 to 1,860, and for the "*sS*" group was 685, with a range of 440 to 1,750. Three out of the nine monkeys in the two groups took more than 1,200 trials to learn the task: one in the "*sS*" and two in "*SS*" group. Both groups acquired the second and third tasks rapidly in a median number of 70 trials for the "*SS*" group and 60 trials for the "*sS*" group. Thus, on the basis of pre-operative training, there did not seem to be any difference between acquisition of DA under the standard task or the variation providing supplementary kinesthetic cues.

Initial post-opertive testing

For both groups, DA performance was disrupted following PRIN ablations (Sign Test, $p \leqslant 0.004$). The median per cent correct during the first 100 trials of post-operative testing on *SS* was 52% for the "*SS*" group, and 57% for the "*sS*" group. Figure 11 shows the mean total error of the two groups over the 700 trials of testing on the *SS* task. Throughout the initial post-operative period, total error for the "*SS*" group was significantly higher than for monkeys first trained post-operatively on *sS*. The higher total error rate reflected differences in both initial and repetitive error measures. Thus, the second hypothesis

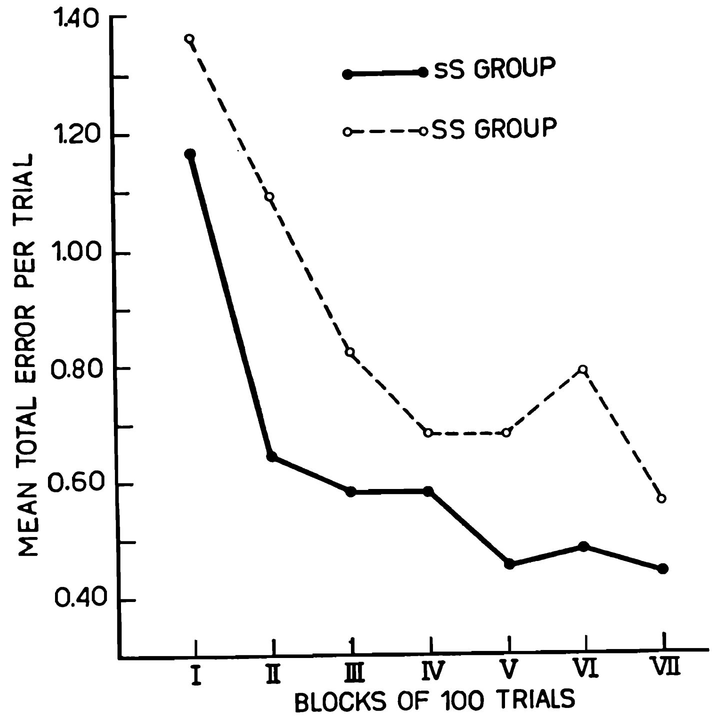

Fig. 11. Mean total error per trial on *SS* task during 700 post-operative trials for two groups of PRIN monkeys differing in pre-operative training.

was confirmed. Monkeys first trained pre-operatively on a force variation of DA providing supplementary kinesthetic cues were less impaired following ablation of PRIN than those first trained on the standard DA task.

Series of shifting tasks

When monkeys were shifted between the *SS* and *sS* tasks, small and not statistically reliable decreases in error were observed (Fig. 12). When transferred into the *SL* task, all monkeys in the "*sS*" group increased error and all monkeys in the "*SS*" group decreased error. The reverse change in error was observed when the two groups were shifted back to the standard task. In the second shift into *SL*, monkeys in the "*SS*" group again decreased error: one of them relearning the task to the 90% correct level. As has been hypothesized, the response of PRIN monkeys to a DA variation providing supplementary articular cues depended upon the nature of pre-operative training. Providing supplementary articular cues to animals initially trained pre-operatively on *sS* disrupted DA performance purportedly because of the interference effect that had been hypothesized.

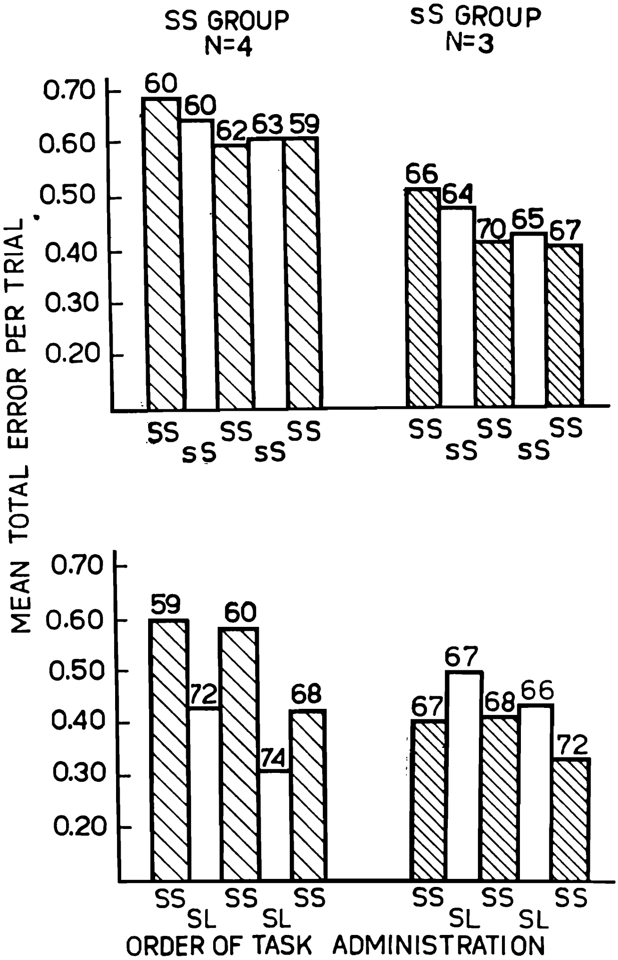

Fig. 12. Mean total error during two series of shifting tasks for two groups of PRIN monkeys differing in pre-operative training schedules. Number above bar indicates median per cent correct.

COMMENTS AND ADDITIONAL ANALYSIS OF PRE-OPERATIVE DATA FROM EXPERIMENT II

The previous findings concerning the difficulty of normal monkeys in acquiring DA under the *sS* task were not replicated. Yet, the basic interpretation did not seem to be supported. Some aspect of the *sS* task when administered first during pre-operative training resulted in less impairment following PRIN ablation and greater interference from supplementary proprioceptive cues than initial pre-operative training on *SS*. There should always be some gain from failure. The benefit in this case was that the duration of pre-operative training could not be considered a determining factor: the two groups were nearly equal in the number of pre-operative training trials. The only difference in training procedure between the two groups was the task administered first. Although the degree of difficulty as determined by the number of trials to criterion on the two tasks appeared equal, some aspect of initial training on *sS* resulted in the post-operative findings. The most reasonable interpretation seemed to be that the *sS* task was more complex whether reflected in acquisition rate or not. It is suggested that processing of kinesthetic cues over time under the *sS* task was different than the standard task because the animal could not determine readily which pattern of kinesthetic input occurred last. Response to the right heavier manipulandum may have resulted in greater intensity of kinesthetic feedback that diminished slowly over time. After response to the left, lighter manipulandum the pattern of kinesthetic input may have been of lesser intensity and, therefore, indistinguishable from the after-effects of the previous response. Thus, the inability to temporally order the areas of no-intersect from the two sets of kinesthetic feedback precluded the abstraction of the relevant cue (Fig. 3). Data from the pre-operative training under *sS* in Experiment II can be offered to support these proposals. If the monkeys could not distinguish between patterns of kinesthetic input after response to the lighter manipulandum, then errors should have been more frequent following left than right responses. During initial acquisition of *sS*, there were significantly more errors following left responses (Sign Test, $p \leqq 0.006$): a pattern very different than that observed under the other two other DA variations. Further, repeated testing within one experimental session should increase the difficulty in temporal ordering of kinesthetic patterns of feedback because of the cumulative interference from prior responses (a form of proactive interference). Therefore, the number of errors in the first 20 trials was compared to the last 20 trials within each experimental session. Only under the *sS* task was there a significantly higher error rate during the last block of trials (Sign Test, $p \leqq 0.006$). Thus, the "parsing" of kinesthetic cues, to use Pribram and Tubb's term (1967) or the ability to make a *recency discrimination* (Yntema and Trask 1963) was disturbed by a biasing factor inherent in the structure of the task. Apparently, the force variation in DA required the animal to develop a more complex program for partitioning sets of kinesthetic input than under the standard DA conditions. The more elaborate organization of kinesthetic gnostic areas for the "*sS*" group resulted in better DA performance following PRIN ablation but interfered with the use of articular-somesthetic cues.

In contrast, the *SL* task used in the previous experiment seemed to require the simplest program for processing and utilizing kinesthetic cues. After acquisition of *SL*, the monkey may have developed a habitual pattern of action which was atemporal and most likely not a serially-linked S-R chain. Using Bruner's terms (Bruner et al. 1966), the monkey had attained an "enactive" level of development. Apparently, the establishment of the program and mode of representation was dependent initially on the distinctive sets of kinesthetic feedback from the two responses. After development, it seemed that the program for processing kinesthetic cues acted upon output information rather than input held in short-term store, that is, acted upon information held in prospective rather than retrospective short-term memory to use Konorski's (1967) terms. A simplified version of the type of program referred to would be: Given selection of slide, next select lift, and reverse. Evidence for these suggestions can be found in the pre-operative data for monkeys first trained on *SL*. It the representation of the task is in terms of a schemata of action (Bruner 1966, Piaget 1954), then transferring to a task involving new displacement movements (such as *SS*) should result in a specific pattern of position errors. On the *SL* task, response to the slide on the left was followed by response to the lift on the right. On the standard task, sliding left again signals response right. However, sliding right should not be associated with response to the left. Thus, when transferred to the *SS* task, there should have been more errors following response to the right than response to the left and there were (Sign Test, $p \leqq 0.006$). Further evidence was available that *SL* monkeys used a representation of the slide/lift motor schema to mediate performance on the other two tasks. An analysis of "hand errors" indicated distinctly different patterns for the three order groups in Experiment II. A hand error was any instance in which the animal approached a manipulandum and touched the post with the incorrect hand (i.e., right hand on slide, left hand on lift). Although approaching incorrectly, the monkey could displace the foodwell cover only by using the required movement. During pre-operative training, hand errors were evident only when monkeys were shifted into or out of the *SL* task. For the monkeys initially trained on *sS* or *SS*, the first shift into *SL* resulted in the highest number of errors with a steady decrease evident on each successive shift. The pattern for "*SL*" monkeys differed: the number of hand errors remained relatively the same and even increased over successive shifts. Apparently, the "*SL*" monkeys used the same response selection process for the other DA tasks as they did for *SL* and only gradually within the task stopped overt mediation.

DISCUSSION

The findings of these experiments support Konorski's (1967) analysis of prefrontal cortex as a kinesthetic gnostic area and Stamm's (1970) interpretation of the long-term impairment of frontal monkeys on tasks like DA. Apparently, effective performance on DA involves using movement-produced cues for response selection processes. They way in which the task is structured determines the information available and the program required for abstracting and utilizing movement-produced cues. When motor patterns used for the two responses in DA differ in spatial organization and, therefore, result in distinctively different patterns of kinesthetic feedback (as in *SL*), a simple program for processing cues seems to be developed. A more complex program appears required when motor patterns are very similar especially for tasks in which the ordering of kinesthetic input over time is difficult (as in *sS*). Prefrontal and other functionally-related areas of brain (subcortical or cortical) are organized in accord with the complexity of the program required for processing kinesthetic cues. Following TOTAL ablation of prefrontal cortex, the magnitude of DA impairment seems determined by the extent of functional organization that was established pre-operatively. When complex programs have been developed, other functionally-related areas of brain have been elaborated and, therefore, less impairment is observed following TOTAL ablation. Conversely, the development of only simple programs during pre-operative training appears to result in less involvement of other structures and, therefore, greater impairment after complete lesions of dorsolateral frontal cortex. This interpretation would be in accord with the results obtained by Stamm (1970) when monkeys were trained on DA using a locomotor maze, the WGTA, and an automatic panel with monkeys confined to a chair. The left versus right differentiation seemed to involve motor patterns that were most similar in the chair and most dissimilar in the locomotor maze. Thus, the program for abstracting and using relevant kinesthetic cues would be most complex in the chair, of moderate complexity in the WGTA, and simplest in the maze. Stamm (1970) observed that acquisition of DA varied under these three task conditions, with the maze most rapid and the chair slowest. Following TOTAL ablation of dorsolateral frontal cortex, the magnitude of impairment, as reflected by rates of repetitive error, was highest in the maze and lowest in the chair. Stamm's findings would be explained in terms of the present proposals as reflecting the complexity of kinesthetic processing required during pre-operative training and, thus, the extent of functional elaboration of associated brain mechanisms.

The effects of partial ablations of dorsolateral frontal cortex seem determined not only by the degree of elaboration within other brain structures but also by the extent to which intact prefrontal areas were functionally organized by pre-operative training procedures. Further, it is suggested that the locus of prefrontal lesions which will produce the DA deficit may vary as a function of how the task was structured pre-operatively. Perhaps, the identification of principalis sulcus as the crucial area of prefrontal cortex associated with DA deficits reflects only the type of movement differentiation commonly required in the task. Speculatively, it may be proposed that elaboration of higher-level fields within the kinesthetic analyzer proceeds from posterior portions of prefrontal, that is from anterior arcuate region, to more anterior sectors. Performance on tasks requiring simple programs subserving movement differentiation processes would be most impaired following ablation of anterior arcuate areas, as for example has been observed: by Gross and Weiskrantz (1962) using a go–no go testing procedure, by Goldman and Rosvold (1970) on a conditional position response, and by Stępień and Stamm (1970*ab*) in a locomotor task involving a differentiation between orienting and instrumental movements. When the program subserving movement differentiation processes is more complex, as left vs. right required in DA, impairment is evident following ablation of more anterior sectors of prefrontal cortex including principalis sulcus (Butters and Pandya 1969).

In addition to these considerations, the functional organization of kinesthetic areas resulting from pre-operative training seems to be a critical factor influencing post-operative recovery of function. While totally-ablated frontal monkeys seem to compensate for their kinesthetic deficit by using articular-somesthetic cues if they are available, partially-lesioned frontal monkeys may be hindered in the substitution of cues. When prefrontal areas have been highly organized for processing kinesthetic cues, interference in using articular cues is evident following principalis ablations. The performance of PRIN monkeys pre-opertively trained first on "*sS*" was disrupted when supplementary articular-somesthetic cues were provided. In contrast, the PRIN monkey purportedly with the least organization of prefrontal areas ("*SL*" monkey in Experiment II) seemed most able to utilize articular cues and, thus, relearn DA with retraining.

In summary, the deficit following ablation of dorsolateral frontal cortex is proposed to be specifically related to kinesthetic-motor processes. In agreement with the findings of Mishkin et al. (1969), the impairment following frontal ablation does not seem to reflect a memory deficit. Frontal monkeys are impaired on delay-type tasks only when performance is solely dependent upon the use of kinesthetic cues in complex motor differentiations. Thus, the frontal impairment does not seem to represent a "general" spatial deficit (Mishkin 1964). Rather, it seems that the frontal deficit reflects a disturbance of *kinesthetic* gnosis of spatial relations as has been proposed by Konorski (1967).

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