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PRIMATE FRONTAL LESIONS AND THE TEMPORAL STRUCTURE OF BEHAVIOR[1]

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Removal of the frontal cortex of primates results in a psychological deficit usually classified in terms of short-term memory. This classification is based on impairment in performance of delayed response or alternation type tasks. The present experiments were undertaken in order to utilize this frontal preparation to learn more about the short-term memory process as well as to delineate more precisely the frontal lobe deficit. Rhesus monkeys with lesions of the dorsolateral frontal cortex were tested in a situation where the classical alternation task with 5 second delay (Right-Left-Right-Left) was modified by interposing a 15 second interval between each R-L couplet (R-L . . . R-L . . .). This modification made it possible for monkeys with frontal lesions who had failed the classical task to perform with very few errors. Two additional alternation experiments, one interposing light and one interposing sound between trials, failed to produce such effective performance. These experiments suggest that proper temporal structuring, or parsing, of the stream of stimuli to which the organism is subject, is a more important variable in the mechanism of short-term memory than is the maintenance of a neural trace per se. They also suggest that the frontal cortex of primates is critically involved in the temporal structuring of behavior.

THE experiments contained in this report were designed to take a new look at an old problem. Interest in the problem of short-term memory has recently revived. Psychologists have become adept at manipulating verbal learning (Melton, 1963), and biologists have used intracerebral injection of drugs to good advantage (Flexner, Flexner, and Roberts, 1967). Meanwhile, a time-honored approach to the problem has apparently lagged; that is to say, very few advances in understanding have recently come from the use of primates with frontal lesions. An opportunity seems to have been neglected, since a lesion of the frontal eugranular isocortex inflicts a very specific psychological loss that has been regularly characterized as a deficiency in short-term or working memory (Jacobsen, 1936; Pribram, Ahumada, Hartog, and Roos, 1964). Such preparation of a primate thus provides a good laboratory model for the study of the

results of impairment of the short-term memory process.

The present experiments were undertaken in the context of earlier work suggesting that the impairment shown by primates with frontal lesions centers on failure to properly code input. These early experiments had shown that defective performance in a task, in which response was delayed for some time after presentation of a cue, could be countered by enhancement of S's attention to the cue (Pribram, 1950), and that a variety of cue manipulations were more effective in ameliorating the deficit than were manipulations of the response contingencies (Mishkin and Pribram, 1955, 1956). Later experiments extended these results to show that the relative ambiguity of the cue was an important parameter in the situation (Pribram, 1961), and that the defective performance of primates with lesions of the frontal cortex (both subhuman and human) concerned reinforcing as well as cuing stimuli (Pribram, 1960; Poppen, Pribram, and Robinson, 1965).

Electrophysiological data support the neurobehavioral ones. Yoshii (1965) showed that normal Ss display a characteristic

electroencephalogram (*EEG*) at the time of cue presentation in the delay task, and that *S*s with frontal lesions who fail the task also fail to show this *EEG* response. Indirect neurophysiological evidence also has been adduced: electrical stimulation of the frontal cortex is effective in altering the organization of the visual input system (Spinelli and Pribram, 1967); this alteration makes it plausible that in a primate deprived of frontal cortex there is interference between successive inputs due to insufficient temporal resolution in the channel (Pribram, 1966).

All of these experimental results point to the suggestion that normally the frontal cortex plays a critical role in sustaining the organism's ability to make some kind of effective structural differentiation in the stream of stimuli with which it is faced. The present experiments sought to test this hypothesis, to test some new methods of overcoming deficits due to frontal lesions, and to evaluate any variation of efficacy between these methods. Preliminary accounts of some of the initial findings have been reported elsewhere (Pribram and Tubbs, 1967).

EXPERIMENT I

A delayed alternation task was used to provide a baseline for evaluating the classification of Jacobsen and others regarding the relationship of short-term memory to this kind of task.

Method

Subjects. The *S*s were nine preadolescent monkeys (Macaca mulatta) weighing 3.5–4.5 kg. at the beginning of the experiment; age was about three years. They were divided into two groups: five *S*s with dorsolateral frontal lesions made about 2.5 years earlier and four unoperated control *S*s from the same age group.

Apparatus. All testing was carried out in a Wisconsin General Testing Apparatus (*WGTA*) placed in a darkened, sound-shielded room. The *S* sat in a transport cage facing an opaque screen which could be raised or lowered by *E*. In the raised position, the screen revealed two identical foodwells (covered), equidistantly 16 inches apart from center to center, in which peanuts

could be placed. When *S* uncovered a food-well, the screen was immediately lowered, whether the choice was correct or incorrect. If correct, a peanut was then placed in the other foodwell, both were covered, and the screen raised for the next trial. If *S* chose incorrectly, the usual correction procedure was instituted: the trial was repeated to the same foodwell until *S* chose correctly. The intertrial procedure took about 5 seconds, and a set pattern of performing it was avoided to prevent offering audible cues. A small lamp provided illumination for *E* and the foodwells; radio music and announcements masked extraneous sounds.

Pretraining. The *S*s were trained to enter transport cages from their home cages and were gradually shaped in the *WGTA* to take peanuts from open, then covered, foodwells. Pretraining was continued only until *S*s tested well (that is, actively) in a random series of trials, irrespective of how correct their performance; this took about five days.

Throughout testing, *S*s were on a mild deprivation diet of 8–10 standard laboratory pellets per day, fruit twice a week, and of course the peanuts obtained during testing.

Training. Fifty trials were given per day with the exception of the first three days after pretraining, when 30 trials per day were given, and an occasional day when an *S* would refuse to test. Following the usual classical alternation paradigm, *S* sat in the transport cage in front of the *WGTA* opaque screen. For the first trial of each run, both foodwells were baited; when *E* raised the screen, *S* could obtain a reward (a peanut) by uncovering either the Right (*R*) or Left (*L*) foodwell. Whichever choice was made, *E* lowered the screen as soon as *S* secured the reward, and before *S* had a chance to try the other foodwell. After making sure a peanut was in the alternate foodwell, *E* replaced both lids and raised the screen for the next trial. The *S* was thus required to go Right-Left-Right-Left (*R-L-R-L*) and so on through a given run. The intertrial procedure took about 5 seconds; daily sessions were run until 50 rewarded trials had been accomplished. Criterion was 90 percent correct over trials.

Surgery. The five "frontal" monkeys had been operated on about 2.5 years earlier.

All operations were single-stage, bilateral surgical procedures carried out in aseptic conditions under intravenously administered Diabutal anesthesia; they required about three hours to perform. A linear scalp incision was made extending from one temporal region to the other across the vertex. A full calvarium osteoplastic flap was then turned on the left temporal bone, exposing both cerebral hemispheres forward of the central sulcus. The dura was opened bilaterally in all instances. The cortex was subpially resected in scar-minimizing fashion with an 18-gauge metal Pribram sucker designed for the purpose. Symmetrical bilateral removals were performed in one stage, and white matter was not intentionally invaded. The lesions extended from the arcuate sulcus forward to the pole, and included the depths of the *sulcus principalis*. Wounds were closed in anatomical layers with silk. All *S*s recovered without complications.

Histological procedures. *S* 188 died from intercurrent gastrointestinal disease several months after the experiment was completed and before sacrifice and perfusion could be instituted. (His performance had been indistinguishable from that of the others.) All other brains were perfused, fixed, cut, and stained according to the procedure described by Sherer and Pribram (1962).

Results

There was a marked difference in performance between the frontally-lesioned and normal groups. All of the control *S*s learned the task (Mean = 440 trials, inclusive of criterion, with a range of 370 to 590 trials). The frontal *S*s all failed to learn in over 1000 trials.

EXPERIMENT II
Method

Subjects. The *S*s were nine preadolescent monkeys (Macaca mulatta) weighing 3.7–4.8 kg. at the beginning of the experiment. The same frontal group (5 *S*s) as in Experiment I was used; the control group, however, consisted of four sham-operated *S*s similar in background of laboratory experience to the earlier group (obviously the initial control *S*s could not serve as controls for this experiment since they had already achieved criterion performance in alternation).

Apparatus. Exactly the same equipment and experimental environment as described in Experiment I was used.

Pretraining. Since the frontal group had already been trained to take peanuts from the covered foodwells of the *WGTA*, only one partial day of pretraining in a random series of trials was necessary to initiate active testing. The control group, having had previous experiences in the *WGTA* (but not in the alternation task), required only one full day of shaping in the *WGTA* to take peanuts from open, then covered foodwells.

Training. Several modifications were made from Experiment I. The *S* sat in the transparent cage in front of the opaque *WGTA* screen. But in this task trials were presented as Right-Left (*R-L*) couplets and a 15-second delay—"temporal parsing"—was interposed between each couplet: *R-L* ... *R-L* ... *R-L* .... When *E* initially raised the screen, *S* could obtain a peanut by uncovering either the Right (*R*) or Left (*L*) foodwell, and the screen was immediately lowered. If *S* chose Right, the screen was lowered, the usual 5-second intertrial procedure was instituted, and the screen raised for the alternation. If *S* chose the Left foodwell (on the first or any subsequent couplet), the 15-second delay was instituted, in essence initiating the couplet. Daily sessions were run until 40 rewarded trials (20 couplets) had been accomplished.

Results

As can be seen in Figure 2, there was a dramatic improvement in performance over Experiment I. While the frontally lesioned *S*s previously did not learn within 1000 trials (dotted line shows average errors) and lagged far behind their controls, in the temporally parsed alternation task their performance improved at essentially the same rate as that of the normals. They took only a slightly greater number of trials to reach criterion (Range: frontal 400 to 520, normals 240 to 480; $p \leq .10$, Mann-Whitney U test), though they made a reliably greater number of errors to reach criterion (Range: frontals 124 to 256, normals 94 to 154; $p \leq .02$). Error scores for
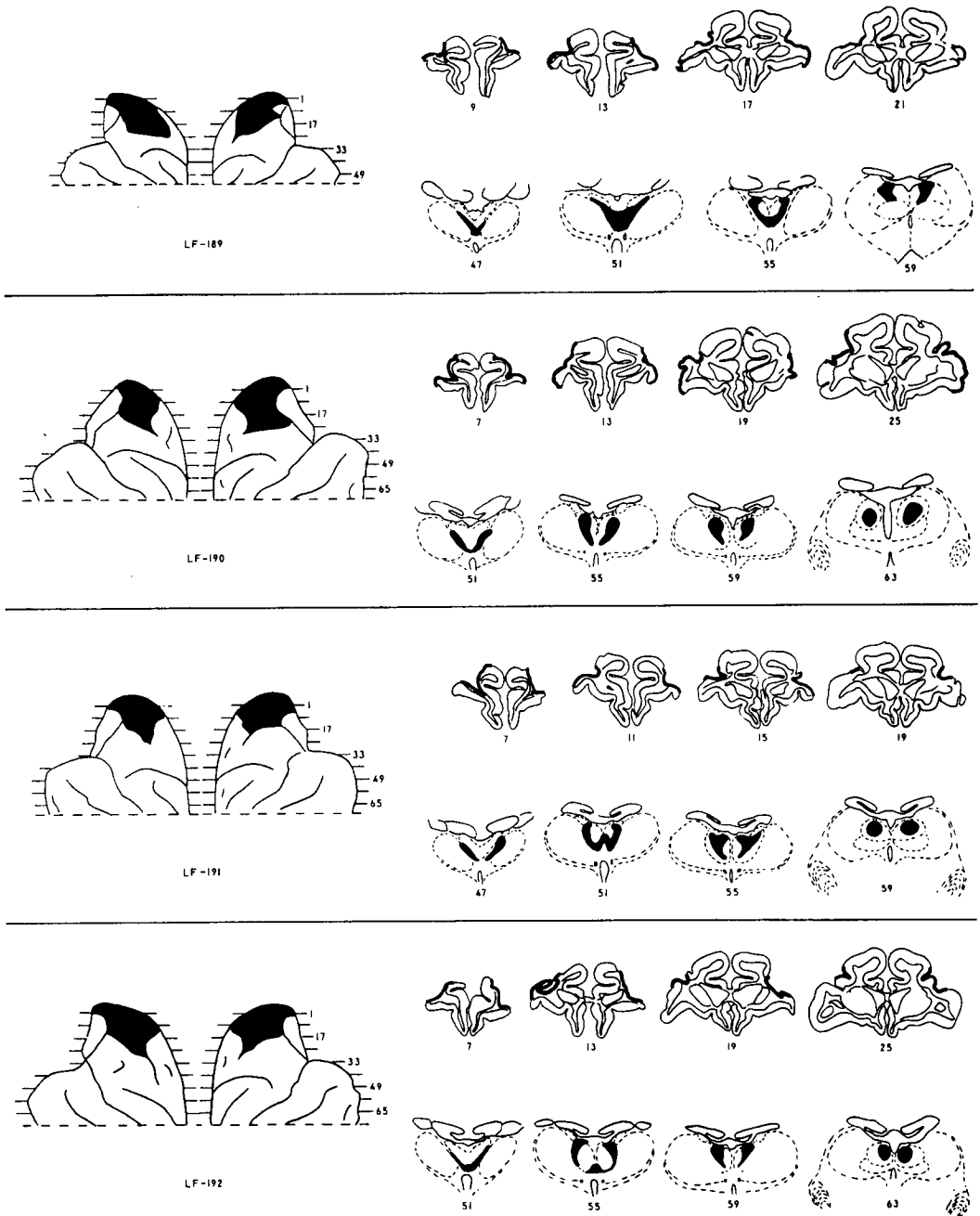
FIG. 1. Reconstruction and cross sections of the extent of ablations of the frontal cortex and of resulting thalamic degeneration.

the frontal group began with an average of 35 per S on the initial day and fell gradually within two weeks to five errors per S.

The Ss did not maintain positions or show any other evidence of development of new external modes of response during the new testing situation. Some continued to circle in either direction, others somersaulted, still others sat in the rear of the cage and dashed up to the foodwell when the screen
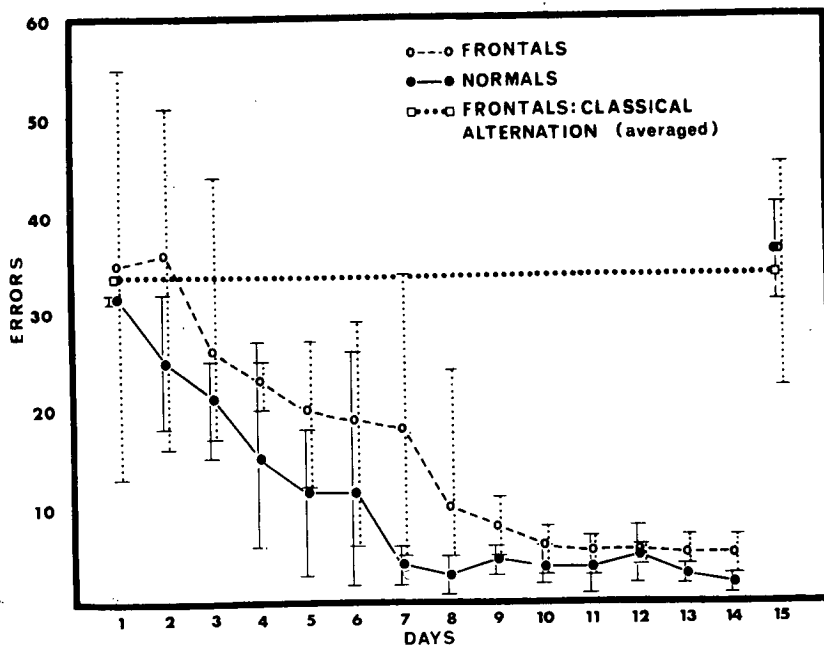
FIG. 2. Graph of the average number of errors made by monkeys having ablations of the frontal cortex and by their controls in the "temporal parsing" situation. Bars indicate ranges of errors made; dotted horizontal line indicates average errors of the frontal group in the classical alternation situation. The points plotted for day 15 show records of the number of errors made on return to the classical 5-second alternation task.

was raised—sometimes to the wrong food-well, only to correct themselves at the last moment. When Ss were returned to the classical alternation task, the performance of both groups broke and an average of about 36 errors was scored per S. This is not too surprising since neither group had ever learned the alternation task in its standard form.

DISCUSSION OF RESULTS OF EXPERIMENTS I AND II

The marked improvement in performance of the frontal group suggests that a critical factor in short-term memory is the proper division, the "chunking" or structuring of the stream of stimulation to which the organism is subjected. Furthermore, the fact that the monkeys were able to perform excellently (Fig. 2) despite the 15-second delay separating the trial couplet suggests it is highly unlikely that some sort of memory decay, per se, is hastened by frontal lesion. On the other hand, a 15-second delay does

not improve delayed alternation when placed between each trial ($R \ldots L \ldots R \ldots L \ldots$); thus it is likely that the temporal organization produced by making trial couplets is critical. When this organization comes from the environment, the anterior frontal cortex appears unnecessary; in the absence of such external structure the frontal lobes become important.

The results of this study support and extend, by recourse to a tried and simple technique, the results of other studies performed with more sophisticated, automated apparatus (Pribram, Gardner, Pressman, and Bagshaw, 1962) and more complex tasks in this laboratory (Kimble and Pribram, 1963; Pinto-Hamoy and Linck, 1965).

Taken together, the evidence suggests that the frontal lobes in primates are critically involved in the proper programming, the temporal coding, of the stream of stimulation to which the organism is subjected. Another suggestion from these experiments is that the short-term memory mechanism

involves active working processes of input coding and programming (Pribram et al., 1964; Miller, Galanter, and Pribram, 1960; Pribram, 1960), processes which in the "animal literature" are referred to as the development of hierarchies of sets (Brush, Mishkin, and Rosvold, 1961).

Although the above experiments seem to cast some light on the enigma of primate frontal lobe function—a critical role in structuring or "parsing" input—certain questions persist.

Perhaps the dramatic improvement observed in the temporal structuring or parsing is due to changing the problem into a successive discrimination. Two forms of the successive problems have been commonly used (See, for example, Pribram and Mishkin, 1955). In one form (the go-right go-left problem) the cue appears either on both foodwells (Bitterman version) or in between them, and S has to choose the Right foodwell in the presence of one cue and the Left in the presence of the other. The other form is a go no-go task in which only one foodwell is presented. This foodwell is to be opened in the presence of one of the cues and response is to be withheld in the presence of the other. In either form, successive discrimination can be learned by monkeys with lateral frontal lesions (Pribram and Mishkin) although both frontal and unoperated control groups take a considerable number of trails (300–500) to master the go-right go-left problem, despite complete familiarity with the simultaneous differential response to the same cues. Further experiments showed cue-response proximity to be a critical variable determining difficulty (Pribram, personal communication). There is thus some similarity to the problem under examination in this study. It therefore becomes necessary to ask: Does the 15″ temporal interval act as a cue to a go-right go-left successive discrimination? The task was therefore repeated using a bright house light and a loud buzzer to differentiate the Right from the Left response.

EXPERIMENT IIIa

Method

Subjects. The Ss were the same nine preadolescent monkeys (Macaca mulatta)

used in Experiment II. They weighed 3.8–4.8 kg. at the beginning of the experiment; age was about $3\frac{1}{2}$ years. They were divided into two groups, five with dorsolateral frontal lesions made about 3.0 years earlier and four sham-operated controls.

Apparatus. The same $WGTA$ and experimental environment was used as described earlier, but with one modification. A 40 watt red lamp was affixed to the ceiling; depressing a switch convenient to E lit the bulb, effectively bathing the interior of the testing chamber with bright red light.

Pretraining. The Ss were trained to enter transport cages from their home cages. Since Ss had previously been trained to take peanuts from the covered foodwells of the $WGTA$, only one day of pretraining in a random series of trials was necessary to initiate active testing.

Throughout testing, Ss were on the usual mild deprivation diet of 8–10 standard laboratory pellets per day, fruit twice a week, and peanuts obtained during testing.

Training. Again presenting the basic alternation task, E gave forty trials per day in all phases of the experiment with the exception of the first day, when odd numbers of trials were given to a few Ss who refused testing or who did not at first remember how to uncover the foodwells.

Procedure. For the light cue experiment, much the same procedure was followed as in Experiment I. The Ss were brought in transport cages from their home cages. During each run S sat in the transport cage facing the opaque $WGTA$ screen. In this procedure, however, E depressed the light switch on every other trial for three seconds to bathe the testing chamber with a bright red light during the intertrial period. The light was turned off at the same moment the screen was raised to expose the two foodwells. Thus, a cue was provided to the monkey to indicate that he was to go to the right food cup, but this cue did not "temporally parse" the task into couplets: R-L-light-R-L-light, and so on. Basically the same correction procedure as in the classical alternation experiment was used: upon an incorrect choice after L-light, the light was again lit and Right foodwell baited (light-R, light-R) until S chose R, completing the trial. As in

Experiment II, daily sessions were run until 40 trials had been accomplished.

Results

The frontally-lesioned Ss' performance in this experiment corresponded to their performance in the standard alternation task. This is clearly evident when the performance of the frontal and control groups in the temporal parsing situation is compared with the same groups in the Light situation. While temporal parsing enabled both groups to drop from an average of 25 errors per S on the initial day to five per S within two weeks, frontals in the Light cued group were still averaging 20 errors per S at three weeks; Ss in the normal group stayed at an average of 20 errors for two weeks, then dropped within a week to about five errors per S.

EXPERIMENT IIIb

Method

Subjects. In order to see if the frontal group's performance could be improved by using an ostensibly more "compelling" cue the (same) Ss were run again. Since the control group had already reached criterion it was not feasible to use them and it was deemed unnecessary to break in a new unoperated group just for this last test, until (and unless) a definite change in frontal group performance was discerned.

Apparatus. Exactly the same $WGTA$ and experimental environment was used as in Experiment IIIa, but the red light was replaced by a loud buzzer activated by a switch convenient to E.

Pretraining. Because Ss were familiar with the mechanics of being transported, uncovering the foodwells, and so on, no pretraining was necessary; one brief run of a random series of trials was given to make sure they tested actively. The same mild deprivation diet as before was followed.

Training. As in Experiment IIIa, 40 R-L trials were given per day, beginning with the first day.
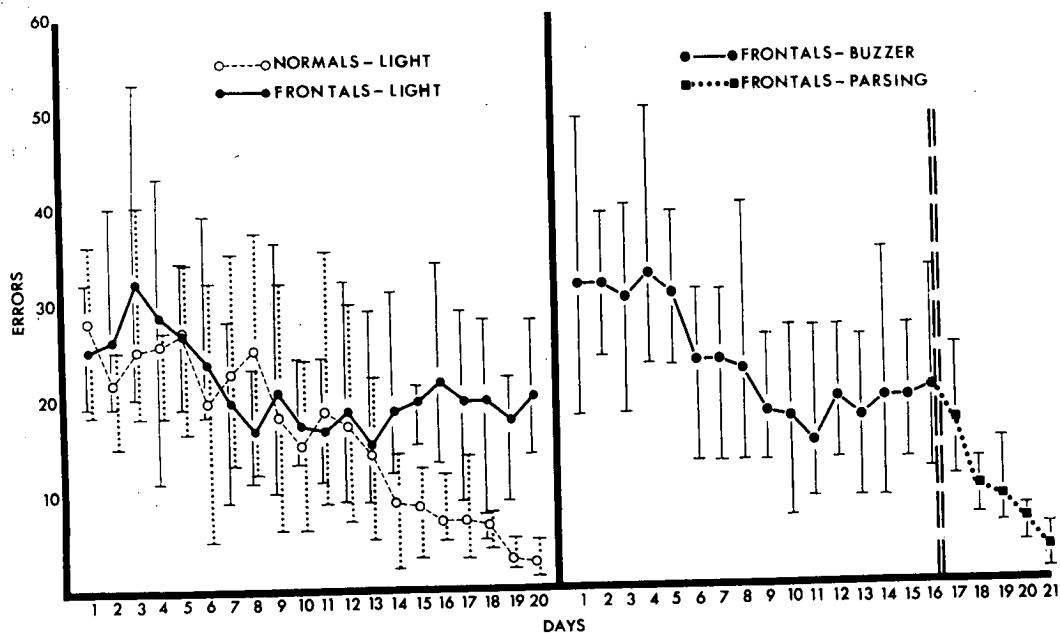

FIG. 3. (Left): Graph of the average number of errors made by monkeys having ablations of the frontal cortex and by their controls in the "light parsing" situation. Bars indicate ranges of errors made. Note that the frontally lesioned subjects showed no basic improvement in performance over the standard alternation task (Figure 2) and even the controls took longer to learn in this situation. (Right): Graph of the average number of errors made by the same frontal group in the "auditory parsing" situation. Bars indicate range of errors made. Note that the frontally lesioned subjects did no better in this than in the "light parsing" situation; but returning to "temporal parsing", indicated by broken vertical line, resulted in immediate improvement.

Procedure. The procedure was exactly the same as in Experiment IIIa, with this modification: on every other trial E depressed the buzzer switch for 3 seconds. This auditory cue was stopped as the screen was raised to expose the two feeding wells, thus: R-L-buzzer-R-L-buzzer .... The same reinitiation procedure as before was used in case of an error to the Right foodwell. Daily sessions were run until 40 trials had been accomplished. On completion of this run, the Ss were again tested using the temporal parsing procedures as in Experiment II.

Results

Figure 3 shows that the frontally-lesioned Ss did no better on the task with the compelling auditory cue than they had with the visual. As can be seen, even after 800 trials the frontal Ss showed no improvement. Note, however, that returning to the temporally structured task immediately resulted in a dramatic improvement—that is, criterion (90 percent correct)—within a very few days.

DISCUSSION OF EXPERIMENT III

The finding that neither the light nor the buzzer served as a "prosthetic" device as did temporal parsing in helping frontally-lesioned Ss to perform the alternation task is interesting in and of itself. As already noted, cue-response proximity is a variable that determines difficulty in the successive discrimination task. Neither the light nor buzzer was placed physically close to the response cup in the present experiment because, of course, a temporal interval could not be so placed. When far away, the visual and auditory cues were in fact more of a hindrance—even a distraction to the normal as well as to the operated group—than a help, as shown by the excessively long time (see Fig. 3) it took them to master a task easily learned by unoperated Ss.

Yet, a return to the temporal parsing task—even after considerable time—resulted in immediate and dramatic improvement in each case. In other words, it is difficult not to conclude that the interposition of a light or buzzer provides an entirely different structuring of input—and thus a different representation of the task—than does temporal parsing. Or to put it another way: if instructions presented to the organism are not properly coded they cannot be retrieved; continued presentation of the same instructions is therefore meaningless and "useless" to the organism.

It has thus been shown that the dramatic improvement observed as a result of temporal parsing is not due to changing the problem into a successive discrimination. The latter experiments reported here—interposing a red light or a loud buzzer as a "flag" or marker for every other trial—failed to produce any such dramatic improvement in performance, and in fact seemed only to confuse the Ss. And meanwhile, any return to the temporal interposition was immediately—and dramatically—effective in restoring adequate performance.

GENERAL DISCUSSION

The results of the temporal parsing experiments were fairly straightforward even as originally described, but are perhaps especially so in the light of these subsequent experiments. It seems clear that, at the behavioral level, an attempt can fruitfully be made to compensate for the deficiency produced by frontal lesions by providing the organism with a kind of "syntactical" prosthesis. Using this external substitute for his frontal cortex a lesioned S is able to perform as well as his unoperated control in the delayed alternation situation.

These results lead to the suggestion that for the frontally-lesioned primate the alternation task, and perhaps many other situations, appear much as would this printed page if there were no parsing—no spaces between words, no punctuation at the ends of phrases, sentences and paragraphs. The following example of this provided by McCulloch (Pribram, personal communication) provides a graphic illustration:

INMUDEELSARE
INCLAYNONEARE
INPINETARIS
INOAKNONEIS

IN MUD EELS ARE
IN CLAY NONE ARE
IN PINE TAR IS
IN OAK NONE IS

Spaces, by organizing, coding input, provide one extremely effective way to give temporal structure to the organism's event space.

Another cogent suggestion is provided by turning to the ever-fruitful analogy of the hardware brains which mimic so effectively many of the functions ordinarily carried on by the wetware in our heads. Mechanical as well as biological thinking machines continually face the simultaneous demands of a variety of inputs and outcomes. These could easily interfere with one another and with any of the central operations being carried on at the moment by the computer. To prevent this, some "noticing order" must govern the acceptance of first this, then that, product of the input-output devices. In its simplest form, each of these devices is fitted with a "flag" which in essence decrees that while "busy" with one set of productions, the computer temporarily shuts off the paths to and from other devices. In more complicated forms, only part of the computer might thus be preempted, or a program can be used to regulate the flow of information. Simple "flexible noticing order" programs have been used for years for this purpose; more recently these have burgeoned into full-scale executive routines which effect the time sharing of large multiple-user machines.

The functions of the frontal cortex have already been compared to that of a "flexible noticing order" (Pribram, et al., 1964) construed as a primitive executive program. Thus, by building into the *task* a simple parsing routine which "chunks" the stream of input (Miller, 1956), problems previously failed could now be solved by the lesioned monkeys. The finding that, in a test of a detailed experimentally derived model, frontally-lesioned primates can perform so readily the task that has been their nemesis for three decades, makes it very likely that here in fact is the key to the solution of the enigma of frontal lobe function (Luria and Pribram, in press). The temporal structuring of behavior—within *this particular* context at least—is apparently a difference that makes a difference.

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The philosopher must go further than the scientist. Making a clean sweep of everything that is only an imaginative symbol, he will see the material world melt back into a simple flux, a continuity of flowing, a becoming. And he will thus be prepared to discover real duration there where it is still more useful to find it, in the realm of life and of consciousness. For, so far as inert matter is concerned, we may neglect the flowing without committing serious error: matter, we have said, is weighted with geometry; and matter, the reality which *descends*, endures only by its connection with that which *ascends*. But life and consciousness are this very ascension. When once we have grasped them in their essence by adopting their movement, we understand how the rest of reality is derived from them. Evolution appears and, within this evolution, the progressive determination of materiality and intellectuality by the gradual consolidation of the one and of the other. But, then, it is within the evolutionary movement that we place ourselves, in order to follow it to its present results, instead of recomposing these results artificially with fragments of themselves. Such seems to us to be the true function of philosophy. So understood, philosophy is not only the turning of the mind homeward, the coincidence of human consciousness with the living principle whence it emanates, a contact with the creative effort: it is the study of becoming in general, it is true evolutionism and consequently the true continuation of science.

HENRI BERGSON, *Creative Evolution*