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Short-Term Memory, Parsing, and the Primate Frontal Cortex

Abstract. *Removal of the frontal cortex of primates resulted earlier 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. We report an experiment in which the classical 5-second-delay right-left-right-left (R-L-R-L) alternation task was modified by placing a 15-second interval between each R-L couplet: R-L . . . R-L . . . R-L . . . . This modification made it possible for monkeys with frontal lesions, which had failed the classical task, to perform with very few errors. The result suggests that proper division, parsing of the stream of stimuli to which the organism is subjected, is a more important variable in the mechanism of short-term memory than is the maintenance of a neural trace per se.*

Interest in the problem of short-term memory has recently revived. Psychologists have become adept at manipulating verbal learning (*1*), and biologists have used intracerebral injection of drugs to good advantage (*2*). 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 (*3*). 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.

Our experiment was 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 the subject's attention to the cue (*4*), and that a variety of cue manipulations were more effective in ameliorating the deficit than were manipulations of the response contingencies (*5, 6*). Later experiments extended these results to show that the relative ambiguity of the cue was an important parameter in the situation (*7*), and that the defective performance of primates with lesions of the frontal cortex (both subhuman and human) concerned reinforcing as well as cuing stimuli (*8*).

Electrophysiological data support the neurobehavioral ones. Yoshii (*9*) showed that normal subjects display a characteristic electroencephalogram (EEG) at the time of cue presentation in the delay task, and that subjects 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 (*10*); 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 (*11*).

All these experimental results point to the suggestion that normally the frontal cortex contributes to an organism's

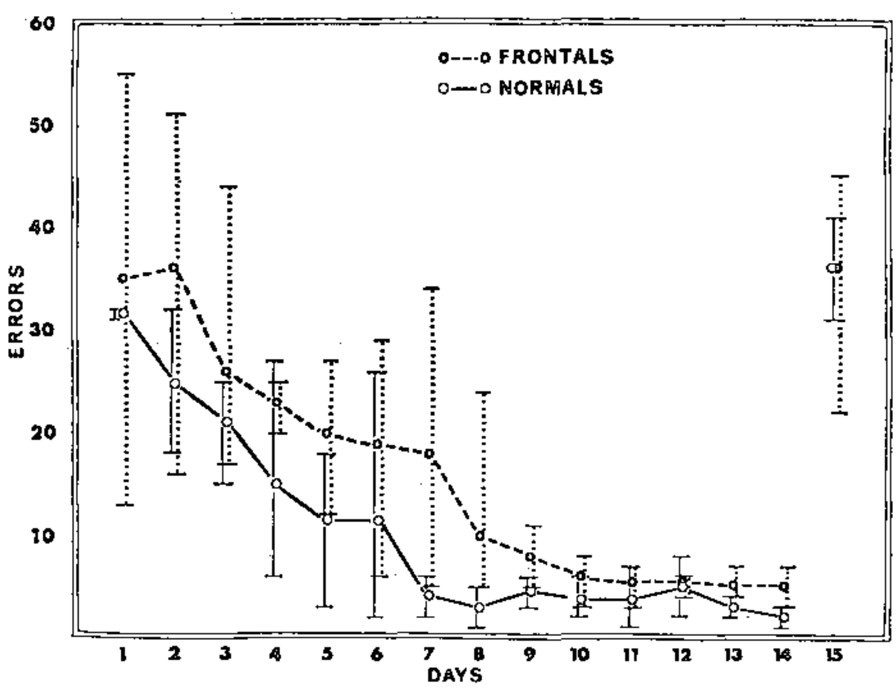

Fig. 1. Graph of the average number of errors made by monkeys having ablations of the frontal cortex and by their controls. Bars indicate ranges of errors made. For day 15 are shown records of the number of errors made on return to the classical 5-second alternation task.

ability to make some kind of effective division—some kind of effective organizational separation in the stream of stimuli with which it is faced—much as a sentence takes on meaning when properly parsed.

In the following experiment we attempted to test this hypothesis. Five monkeys with dorsolateral frontal lesions ("frontal" monkeys), made about 2.5 years earlier, and four controls were trained (by use of the correction technique) in a standard 5-second-delayed alternation situation in a modified Yerkes training apparatus (*5*). The control group learned the task in 440 trials on average; the frontal group failed to learn in 1000 trials. The frontal group were then given the identical alternation task except that a 15-second delay was interposed between each couplet (R, right; L, left): R-L . . . R-L . . . R-L . . . and so on; also, if an error was made to the right cup, the 15-second delay was repeated, in essence reinitiating the couplet trial. Daily sessions were run until 40 rewarded trials had been accomplished.

A second unoperated control group were given the same task; in background of laboratory experience they were similar to the other group tested but had not been given the classical alternation task. (Obviously, the initial control subjects had already achieved criterion performance in alternation and so could not serve as controls for the "parsing" experiment.)

The results for the frontal and the second control group were comparable. Error scores began with an average of 35 per subject on the initial day and gradually fell within 2 weeks (40 trials per day) to five errors per subject (see Fig. 1).

The monkeys did not maintain positions or show any other evidence of development of new external modes of response during this period: some continued to circle in either direction, others somersaulted, still others sat in the rear of the cage and dashed up to the test cup when the screen was raised—sometimes to the wrong cup, only to correct themselves at the last moment—a not unusual occurrence. When the monkeys were returned to the classical alternation task, the performance of both groups broke and an average of 36 errors was again scored per subject. The monkeys are still alive, being used in other experiments.

The marked improvement in performance of the frontal group suggests that a critical factor in short-term memory is the proper division, or "chunking," of the stream of stimulation to which the organism is subjected. The fact that the introduction of a 15-second interval in a structured fashion improved performance suggests, furthermore, that memory decay per se is not involved.

The results of our study thus support and extend, by recourse to a tried and simple technique, those of other experiments performed with more sophisticated, automated (DADTA) apparatus and more complex sequential tasks in our laboratory (*12*).

Taken together, the evidence suggests that the frontal lobe of primates is critically involved in the proper programming—the parsing 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 (*3, 13*), processes which in the "animal literature" are referred to as the development of hierarchies of sets (*14*).

K. H. PRIBRAM
W. E. TUBBS

Neuropsychology Laboratories, Stanford University School of Medicine, Palo Alto, California 94304

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