noradrenaline elicited eating (*8*). The remaining 6 percent of the responses covers five different response types and are grouped into a single "other" category (response types five through nine). In most instances, however, eating is related to adrenergic, and drinking to cholinergic, stimulation. It should be noted that combined dual response and noradrenaline single response type percentages (response types three and four) indicate that only 21 percent of the loci tested may be positive to noradrenaline stimulation. Salmoiraghi and Bloom (*9*) suggest that noradrenaline and acetylcholine may function as neurotransmitters at mammalian central nervous system synapses. Therefore, the behavioral effects reported here may normally be mediated by noradrenaline and acetylcholine functioning as neurotransmitters within the central nervous system.

As indicated in Table 3, however, exceptions to complete differentiation do occur; there are mixed effects at 6 percent of the loci tested. Most of this variability may be attributed to the fact that carbachol occasionally elicits eating. This has been observed at the lateral hypothalamus (*5*). The elicitation of drinking by noradrenaline stimulation, however, is extremely rare. This chemical elicited drinking at only one of the 184 loci tested. The "mixed response" variability falls within two brain regions, hypothalamus and cingulate gyrus. Thus, the two regions may share a common function.

The loci, represented by the first four response types, may be classified as negative, dual response, or single response types. However, only 15 percent of the loci tested were of the dual response type. It is likely, then, that the negative and single response loci type indicate the presence of functional systems, other than those related to eating or drinking.

Table 3 shows one other important relationship: the total percentage distribution between the first four categories of response seem proportional to each other. Thus, the twofold significance of the existence of categories of loci that have a possible quantitative relationship between them becomes clear. First, it indicates that there are shifts in chemical receptor densities across a range of neural tissue, and that this shift is in the form of a density gradient. Second, it indicates that these shifts in receptor densities are the basis of a distribution of overlapped neurobehavioral systems within "Nauta circuit" brain areas. Citing the hippocampus as an example, a careful lamina and pyramidal field analysis should reveal zones of chemically receptive neurons whose organization would reflect structural and functional characteristics specific to the various motivational and emotional states. Findings within this limbic structure may be generalized, on neuroanatomical grounds, to other "Nauta circuit" areas.

It seems unlikely that neurobehavioral systems could have widespread limbic, diencephalic, and midbrain representation without involvement of neocortical areas. In fact, frontal cortical areas may be involved in the control of food and water intake (*10*). There may be a continuity between "Nauta circuit" brain areas and neocortex, and an integrated structural and functional characterization of neurobehavioral systems may be possible.

John N. Coury
*Department of Anatomy,
Northwestern University Medical
School, Chicago, Illinois 60611*

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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-

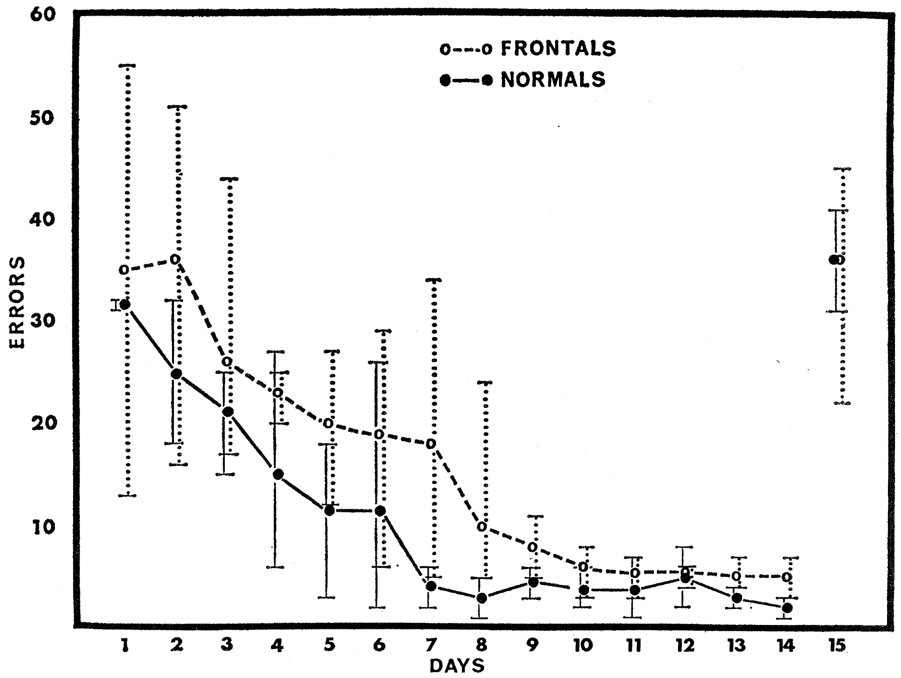

Fig. 1. Graph of the average number of errors made by monkeys having ablations of the frontal cortex and by their controls. Bars indicate ranges of errors made. For day 15 are shown records of the number of errors made on return to the classical 5-second alternation task.

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 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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Erratic Display as a Device against Predators

Abstract. *Prey animals in many different taxonomic groups behave erratically when attacked by predators. This reaction is not accidental, but acts as a specific antipredator device. Observational data and theoretical considerations indicate that such protean displays function to confuse and disorient the predator and to increase its reaction time. Thus the survival of the prey is assisted, and the selective advantage whereby such erratic patterns of the prey animals may have evolved is created.*

When attacked by predators, many prey animals do not flee in a straight line; their behavior is highly erratic and unpredictable, taking the form of zigzagging, looping, spinning, or wild bouncing. This phenomenon is often briefly noted in the literature, but with no explanation of its significance; it has been recorded separately in several taxonomic groups including many mammals and birds (*1, 2*), noctuid and geometrid moths (*3*), grasshoppers (*4*), and the marine copepod *Calanus* (*5*). It occurs in many other types of animals including dipterous insects, cladoceran crustaceans, voles, the stickleback *Gasterosteus*, shore hoppers, and fleas. We now propose a unifying theory.

The audiogenic seizures of small mammals provide the first clue. It has been suggested (*6*) that the phase of intense erratic activity at the beginning of such seizures might have survival value if it were to occur in the wild during predatory attack. On the basis of this suggestion Chance and Russell (*7*) coined the term protean behavior, and proposed that patterns of erratic behavior may exist having the function of confusing predators. Here we point out that such patterns are in fact very common (see the foregoing list), and that they pose some interesting and important theoretical problems. We shall show that the basis for understanding their confusing effect upon predators is provided by modern psychological conflict theory.

We define protean behavior as behavior that is sufficiently unsystematic to prevent a reactor from predicting in detail the position or actions (or both) of the actor. It includes many reactions that are released only when the animal is in immediate and obvious danger. For example, if small insects resting on tree bark are disturbed, they usually take to the wing in a characteristically erratic spinning and looping action; there is no known aerodynamic or physiological reason for such flight. The flight path is much more direct and simple when the insect leaves its resting place of its own accord. Similarly, noctuid and geometrid moths show a bewildering variety of unoriented maneuvers when exposed to the ultrasonics of hunting bats; their behavior has been shown to have a selective advantage of about 40 percent (*8*).

The protean nature of such single erratic displays may be enhanced by changes in color; Huxley (*4*) notes that flash coloration and zigzag fleeing are associated in some grasshoppers. Swift changes in color also occur in the squid *Sepioteuthis* when zigzagging during escape (*9*), and in the reef fishes *Haemulon flavolineatus* and *Epinephalus striatus* (*10*). In the latter example the display is further complicated by a series of percussive sounds (*11*).

In many species of birds, including waders, gulls, ducks, and starlings, the erratic pattern is shown by whole flocks and may then be termed a united erratic display; it acts as a deterrent (*1*) against the attacks of aerial predators like the peregrine falcon. On appearance of the predator the birds draw together into a tight group, which zigzags unpredictably in swift flight, sometimes splitting into subgroups, with the individuals continually shuffling their relative positions.

Certain animals move very erratically even when undisturbed, especially insects that spend considerable periods on the wing, for dispersal or feeding movements, during daylight hours; they are highly vulnerable to predation by birds that feed on aerial plankton, and their erratic flight may well be a form of protean insurance against sudden attack.

In all the foregoing examples the function of the erratic displays appears to be to disorient the predator's attack. Some protean displays, however, seem to be designed to switch the predator's motivation from attack to escape, having in this respect the same function as certain systematic responses like eyespot displays in Lepidoptera (*4, 12*). Erratic, convulsive movements, combined with intermittent flashing of colored surfaces, occur in several species of butterflies and moths when disturbed while in a cryptic posture. Swift and complete changes in color, associated with darting movements, occur in the cuttlefish *Sepia officinalis* (*13*). The luminescent "berserking" display of sea pansies, although static, seems to be a similar phenomenon. Such displays have an effect of startling and may arouse escape tendencies because of the sudden unexpected changes in the predator's visual field (*13*). Sudden movements are known to evoke escape reactions in many vertebrates (*14*).

We propose that the essential feature of all protean displays is that they are likely to arouse mutually incompatible tendencies in the reactor. These tendencies may be of simple orienting components or of fundamental behavioral categories like escape or defense. The theories of Berlyne (*15*) on arousal and conflict are highly relevant to an understanding of the effect on the