

rectly with speed of learning (4), the appropriate base line for measuring forgetting of the two types of material after 0-percent overlearning is the amount recalled immediately (6 sec) after attainment of the criterion. These base-line measures were obtained from the protocols of the 50-percent and 100-percent groups. The interaction, time  $\times$  word frequency, is not significant ( $F = 1.80$ ,  $df = 1/92$ ), that is, retention loss does not vary as a function of word frequency when associative strength at criterion is taken into account (5).

There was no change in the amount of recall for the high-frequency lists, and only a small increase for the low-frequency lists, after 50-percent overlearning. There were clear increases in the retention of both types of material after 100-percent overlearning. Degree of overlearning is a significant source of variance ( $F = 4.15$ ,  $df = 2/90$ ,  $.02 < P < .05$ ) but does not interact with word frequency ( $F < 1$ ). As Fig. 2 shows, the gains in retention are almost entirely a function of positively accelerated increases in the recall of the relatively difficult middle and terminal sections of the serial lists.

The mean numbers of trials to relearn the high-frequency lists to criterion were 6.12, 4.69, and 3.69 after 0-, 50-, and 100-percent overlearning, respectively. The corresponding means for the low-frequency lists were 7.31, 5.44, and 3.75. The numbers of trials in relearning decrease steadily with the degree of overlearning. The decreases are significant ( $F = 11.71$ ,  $df = 2/90$ ,  $P < .01$ ) but do not interact with word frequency ( $F < 1$ ). Comparison between the two measures of retention indicates that speed of relearning is more sensitive than amount of recall to increases in associative strength produced by moderate amounts of overlearning.

While progressive increases in degree of overlearning must eventually yield diminishing returns, this point will be reached slowly when the beneficial effects of continuing practice are measured by the amount of recall for relatively difficult items. This conclusion applies to verbal series composed of items of high as well as low frequency of linguistic usage (6).

LEO POSTMAN

Department of Psychology and  
Center for Human Learning,  
University of California, Berkeley

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6. This research was supported by a grant from the National Science Foundation.

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## Proprioceptive and Positional Cues in Solving Delayed-Response Problems

**Abstract.** Delayed-response performance of monkeys was unaffected by combined labyrinthectomy and section of the dorsal columns at C3. Superimposed frontal resections impaired performance and the ultimate recovery was attributed to a positioning cue.

Analysis of the delayed response in requirements for solution has led to the view that there are a multiplicity of solutions which monkeys can adopt in order to succeed on these problems (1). Remembering which cup was baited, that is, carrying the solution centrally, is only one way of solving the delayed response. Another way would be to depend upon self-generated differential cues which span the time gap and guide the response. For example, the animal may derive cues from his posture, the direction of his gaze, or his position in space. In fact, monkeys occasionally position themselves in front of the positive food cup to wait until choice is permitted. After frontal lobe removals, they have even been observed to circle differentially according to which food well was baited (1). Accordingly, an understanding of the nature of the delayed-response impairment, whether in the realm of immediate memory or not, depends upon a prior determination of

the solution that monkeys ordinarily adopt in solving the problem. Since postural mnemonic devices are clearly available to the monkey, and since a proprioceptive projection area has been identified in dorsolateral frontal cortex (2), I decided to explore the effects of peripheral proprioceptive deprivation on delayed-response performance.

Seven immature rhesus monkeys, *Macaca mulatta*, five males and two females, were studied. All learned to succeed on the delayed response. Scores are shown in Table 1. Four of these monkeys, 0, 2, 3, and S, first underwent bilateral labyrinthectomy via an extracranial approach (in two stages with a week intervening between stages). The mastoid bone was rongeured away until the cochlea could be seen. A dental drill was used to destroy the vestibular apparatus. No special effort was made to spare nonvestibular portions of the inner ear or adjacent sympathetic and cranial innervations. After the first stage, the following ipsilateral disturbances were noted: head listing, absence of lid reflex, ptosis, facial drop, nystagmus with fast-phase contralateral, and constricted pupil. After the second stage, a marked head bobbing was seen, the monkeys sat with broad base, showed locomotor ataxia and a frog-like stance, had difficulty righting, and were deaf. Despite these disturbances, all monkeys showed perfect or near perfect retention of delayed response when tested 2 weeks after the operations (Table 1).

Each of the four monkeys then underwent section of the dorsal columns of the spinal cord at C3. The monkeys were temporarily unable to use their limbs, except as props. Again, despite this marked physical handicap involving a lack, or imbalance, of input from muscles as well as inner ear, all monkeys showed perfect retention of the delayed response (Table 1). There was no manual response, to be sure, but the

Table 1. Delayed-response up to 5-second delay. Trials and errors to 90-percent correct responses in 30 trials.

Animal	Pre-operative		Post-labyrinthectomy		Post-spinal transection		Post-frontal lesion	
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors
3	147	31	0	0	0	0	1334	440
0	0	0	0	0	0	0	1211	362
S	30	5	0	0	0	0		
2	19	2	40	6	0	0	643	226
B	165	48					1120	341
M	172	54					30*	8*
4	30	8					60*	11*

\* Scores following multiple transection of frontal granular cortex.

monkeys indicated their preferences by falling or rolling in the direction of the correct food well. The reward was then placed in the monkeys' mouths by the experimenter.

Finally, three of the four monkeys underwent amputation of frontal poles and resection of dorsolateral frontal granular cortex back to the two limbs of the arcuate sulcus. There were no apparent additional neurological signs and the expected pacing was delayed 1 to 5 months in appearing. This time there was a pronounced retardation in relearning the delayed response. Nevertheless, every monkey eventually succeeded in returning to the preoperative level of efficiency (Table 1). Careful observation of the mode of solution revealed that positioning in front of the baited food well was used in every case.

As a control, the fifth monkey, B, underwent bilateral resection of frontal granular cortex uncomplicated by peripheral lesions. His relearning scores on the delayed response were quite comparable to those of the three monkeys with peripheral deprivations, certainly no worse. An attenuated disturbance might have been expected in those monkeys receiving repeated tests. This suggests that overtraining on the delayed response did not protect the monkeys from the effects of frontal resections. In contrast, earlier work had indicated that overtraining on visual discriminations protected monkeys from the effects of infero-temporal neocortical resections (3).

The remaining two monkeys, M and 4, derived from another experiment and reported here for comparative purposes, underwent multiple transection of frontal granular cortex. The knife cuts were about 2 mm apart and arranged in the form of a grid. Sperry's surgical technique was employed (4). The purpose was to determine whether horizontal intracortical interconnections are those responsible for successful performance of delayed response. In the context of the present experiment, this represented another attempt to mimic the effects of frontal resection. Both monkeys showed almost perfect retention of delayed response, and there was no evidence of the hyperactivity so characteristic of the frontal lobectomized monkey. This lack of effects should be contrasted with those following multiple transection of infero-temporal neocortex (5).

Delayed alternation has been used interchangeably with delayed response

as a test of immediate memory. There is some evidence that certain non-delay features distinguish the two tests in requirements for solution (6). We offer the following additional suggestive evidence. The four monkeys with frontal resections were unable to acquire the delayed-alternation habit within the limits of testing (2000 trials), whereas they did succeed in relearning the delayed response. Though the delay feature is common to both tests, delayed alternation alone seemed to be beyond the scope of the frontal operates.

To complete the evidence, the two monkeys with multiple frontal transections succeeded in acquiring the delayed-alternation habit within normal limits. And all seven monkeys acquired a simple color discrimination in 90 trials or less, within normal limits.

These results, taken together, suggest that proprioception may be more critically involved in the solution of delayed alternation than in delayed response, and that the frontal operate may depend upon positioning in order to succeed on the delayed response. In the broadest sense, the various sense modalities probably contribute to the solution of the delayed response, and no unimodality deprivation mimics the effects of frontal resections, though both visual and auditory discrimination may be impaired (1, 7). Unimodality deprivations are ineffective because of the multiplicity of solutions available to monkeys. As in the maze-learning experiments on rats (8), combined sensory deprivations will probably prove to have a more deleterious effect than unimodality deprivations (9).

J. ORBACH

*Institute for Psychosomatic and  
Psychiatric Research and Training,  
Michael Reese Hospital,  
Chicago, Illinois*

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## Relative Reinforcement Values of Food and Intracranial Stimulation

**Abstract.** Rats trained in a discrimination-reversal situation with either food pellets or intracranial stimulation as the reinforcing stimulus were not appreciably different in their first-task performance, but reversal training was slower if the first discrimination was learned with brain stimulation.

When utilized as a positive reinforcing stimulus, intracranial stimulation (ICS) has proved capable of maintaining high rates of responding in free operant situations under continuous reinforcement (1). Animals also perform satisfactorily in trial-by-trial maze and obstruction situations where intracranial stimulation is the reinforcer (2). Although it is now clear that intracranial stimulation is similar to other known reinforcers in many respects—for example, reinforcement schedule effects (3, 4)—there persists the opinion among many workers that ICS-reinforced behavior is less permanent than behavior conditioned with, say, food as the reinforcer.

The actual evidence for this assumption is scanty. Many investigators have informally reported difficulties in establishing and maintaining free operant responding when intermittent reinforcement is employed. Indeed, only short variable interval and fixed-ratio values appear to have been used with any degree of success in cats and rats (3), although success in getting some monkeys to work under extended values of fixed-ratio schedules has been reported (5). In the straight alley situation, extinction of ICS-reinforced running appears to be extremely rapid (6); and in mazes, there appears to be more overnight retention loss by ICS-reinforced than by food-reinforced rats (2).

The present experiment represents an attempt at a direct comparison of the relative permanence of behaviors conditioned with food and with ICS reinforcement. Male rats of the Sprague-Dawley strain were stereotaxically implanted with bipolar electrodes aimed at the posterior hypothalamus. The effectiveness of intracranial stimulation was then tested in a bar-pressing situation, and animals were discarded if they failed to respond consistently under continuous reinforcement conditions within 30 minutes. All animals, in all phases of the experiment, received the same stimulation: 0.5-second train of biphasic rectangular waves, at a frequency of 100 per second, and having