

ceptible, whereas those produced from homocaryotic mycelium have properties dependent on their nuclear constitution. The nuclear and cytoplasmic constitution of the mycelium from which spores are formed presumably determines the nature of the wall and surface of the spores. It is reasonable to assume that the nature of the wall or surface of the spores of *C. lagenarium* may play a significant role in determining susceptibility or resistance to ingestion by myxamoebas of *A. rosea*. Since the spores of *C. lagenarium* are uninucleate, it is possible that the susceptibility of spores from heterocaryotic mycelium may have been determined by the mixed cytoplasm of the heterocaryon (4).

E. D. GARBER
S. K. DUTTA

Department of Botany,
University of Chicago,
Chicago, Illinois

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Retention as a Function of Degree of Overlearning

Abstract. The effects of overlearning on retention were investigated with serial lists of words of high and low frequency of linguistic usage. For both types of materials, amount recalled showed a positively accelerated increase with degree of overlearning. These increases in recall resulted from improved retention of relatively difficult parts of the lists. Speed of relearning to complete mastery was a direct function of degree of overlearning.

This study reexamines the effects of overlearning, that is, practice past the point of complete mastery, on the retention of verbal materials. A classical experiment by Krueger (1) led to the conclusion that overlearning favors retention but yields diminishing returns when it is carried beyond a moderate level. With lists of 12 nouns as learning materials and retention intervals from 1 to 28 days, Krueger found that recall and saving scores increased sharply at first, and then much more slowly, as degree of overlearning was varied from 0 through 50 to 100 percent.

In the light of recent analyses of the conditions of retention, the generality of these results is open to question. Krueger used well-practiced subjects who served in several conditions of the experiment. It is now known that the amount recalled by practiced subjects is drastically depressed by the cumulative effects of proactive interference from prior lists learned in the laboratory (2). As a case in point, Krueger's subjects retained less than 2 percent of a list 7 days after learning to criterion. When interference is massive, practically all items must be overlearned in order to be recalled. A moderate amount of overlearning will be sufficient for the easiest items in the list, whereas more difficult items will require extensive additional practice. Hence, retention will increase with overlearning at a negatively accelerated rate. In the absence of heavy proactive interference, on the other hand, only relatively difficult items will require overlearning. The beneficial effects of overlearning on retention may then be expected to develop gradually and to show initial positive acceleration. To test this prediction, naive subjects who learned and recalled a single list were used in the present study.

The experimental lists consisted of 12 two-syllable nouns. The word frequency of the items was varied in order to assess the interaction between pre-experimental language habits and the effects of overlearning. There were two types of lists drawn from the extremes of the frequency range in the Thorndike-Lorge word count (3). For the words in the high-frequency lists the number of occurrences in the "L" count was between 1000 and 3300 in 4.5 million; for the low-frequency lists the range was between 1 and 3 in 4.5 million. At each level of frequency there were two lists and two different serial orders of each list. The lists were presented on a Hull-type memory drum at a 2-second rate, with a 6-second interval between trials. Learning was by the method of serial anticipation. There were three degrees of overlearning: 0 percent, 50 percent, and 100 percent. For 0-percent overlearning, practice was terminated at a criterion of one perfect recitation. For 50-percent overlearning, practice was continued beyond the point of mastery for half as many trials as had been required to reach criterion; for 100-percent overlearning the number of trials was doubled. The lists were re-

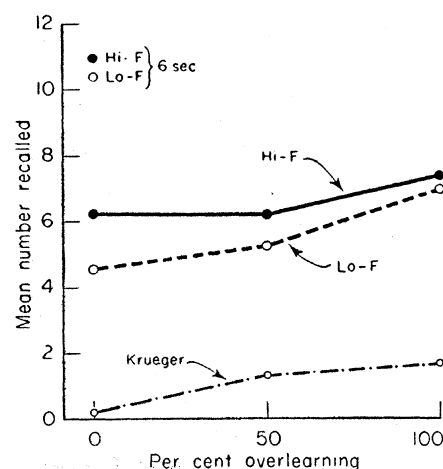


Fig. 1. Mean numbers of items recalled 7 days after the end of original learning as a function of word frequency and degree of overlearning. Points marked "6 sec" show amounts recalled on the first trial after criterion was reached. Krueger's data for the same retention interval are also shown.

learned to criterion 7 days after the end of original learning.

There were no significant differences in speed of learning to criterion among the groups tested with a given type of list. The mean number of trials to criterion was 19.25 for the high-frequency lists, and 25.48 for the low-frequency lists. This difference is significant ($t = 3.42$, $df = 94$, $P < .01$). Figure 1 shows the mean numbers of items recalled on the first trial of relearning. (Krueger's data for a 7-day retention interval are included for comparison.) Since associative strength at criterion varies di-

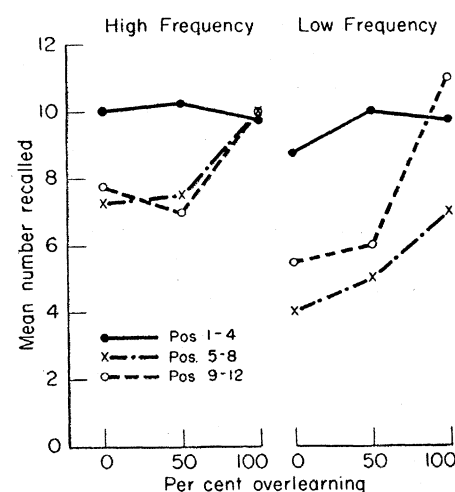


Fig. 2. Mean numbers recalled from the initial, middle, and terminal sections of the serial lists after different degrees of overlearning. The numbers of subjects giving correct responses are averaged over the four serial positions in each section.

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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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.