

repertoire. For example, some chimpanzees suck their thumb, which is similar to the "drink" sign. On the other hand, the "look" sign—touching the index finger near the eye—might not only be absent from the chimpanzee's behavioral repertoire, but might also be an aversive experience because of the natural response to protect the eyes when something is poked in or even near them. These results are consistent with a hypothesis of Hayes and Hayes (8) that ability to show imitative behavior depends on the prior existence of that behavior in the chimpanzee's repertoire.

All of the signs were acquired by all of the chimpanzees, and some of the signs were acquired in remarkably short time. Thus it does not appear that Washoe is exceptional in her ability to acquire signs in ASL. Individual chimpanzees differ in their ability to acquire these signs. Some of the errors during the double-blind box tests were possibly influenced by being conceptually related, which is consistent with Washoe's errors in testing (1). Also, the gestural similarity between signs

and preferences for a sign or signs were noted as possible sources for errors.

ROGER S. FOUTS

*Institute for Primate Studies,
Department of Psychology, University
of Oklahoma, Norman 73069*

References and Notes

1. R. A. Gardner and B. T. Gardner, *Science* **165**, 664 (1969); B. T. Gardner and R. A. Gardner, in *Behavior of Nonhuman Primates*, A. M. Schrier and F. Stollnitz, Eds. (Academic Press, New York, 1971), pp. 117–184.
2. W. C. Stokoe, D. Casterline, C. G. Croneberg, *A Dictionary of American Sign Language* (Gallaudet College Press, Washington, D.C., 1965).
3. The chimpanzees were exclusively trained with fruit to acquire the "more" sign, but outside of the training situation they spontaneously combined the "more" sign with the "drink" sign to obtain more to drink.
4. More than 30 volunteers were used; the chimpanzees' acquisition of sign was thus not attributable to a unique trainer.
5. R. S. Fouts, *J. Comp. Physiol. Psychol.* **80**, 515 (1972).
6. O. I. Lovaas, J. F. Berberich, B. F. Perloff, B. Schaeffer, *Science* **155**, 705 (1966).
7. R. A. Gardner and B. T. Gardner, paper presented at the meeting of the Psychonomic Society, St. Louis, November 1971.
8. K. J. Hayes and C. Hayes, *J. Comp. Physiol. Psychol.* **45**, 450 (1952).
9. I thank W. B. Lemmon, director of the Institute for Primate Studies, for his most valuable assistance, and I thank the student volunteers who assisted in training and testing.

20 November 1972

Visual Free Recall

Abstract. *Lists of complex pictures, not easily encoded verbally, were presented to subjects who recalled them by writing brief descriptions. The lists were 10, 20, and 40 pictures in length. Recall failed to show the primacy and recency effects seen with verbal materials, but was lower for pictures in longer lists. This argues for serial-position effects based in short-term memory and independent list-length effects arising during retrieval from long-term memory.*

In recent years, the study of memory and forgetting has relied heavily on the paradigm of free recall. In this paradigm, a series of items, usually words, are presented one at a time. Then the subject is asked to recall as many items as he can, in any order he wishes. Three basic effects are found in graphs giving the probability of recall as a function of serial presentation position. These serial-position curves show a pronounced recency effect, a smaller primacy effect, and a flat central region which is lower for longer lists. Typical sets of curves are shown in Fig. 1, A and B (1).

The recency effect has commonly been attributed to the operation of short-term memory. It is assumed that the items near the end of the list are still in short-term memory when the recall period begins. These are output at once, giving rise to the recency

effect, and all additional recall results from retrieval from long-term memory. There is considerable evidence supporting this view. To give just a few examples, a period of arithmetic following presentation and preceding recall eliminates the recency effect, presumably by causing forgetting of the list words from short-term memory (2); an additional free-recall test at the end of the session for all lists in the session shows no recency effect, presumably since such a test precludes any short-term retrieval (3); and the elimination from recall scores of those items undergoing overt rehearsal at list termination tends to eliminate the recency effect, presumably since the rehearsed items represent the major part of the contents of short-term memory at that moment (4).

The primacy effect is usually thought to result from additional rehearsal given the first few items of a list. The extra

rehearsal presumably results in more long-term storage for these items. Support for this hypothesis comes from the fact that controlling rehearsal so that all items receive equal amounts can eliminate the primacy effect (5).

The list-length effect is one of the strongest seen in memory research. When arithmetic between presentation and recall is used to eliminate retrieval from short-term store, the probability of recall for a given word can range from near 1.0 for lists of only a few items to near 0.0 for lists of many hundreds of items. I have previously suggested how a failure of retrieval from long-term store can account for the list-length effect (6, 7).

These various results in free recall have been perhaps the strongest evidence in favor of a memory system divided into an active limited short-term store and a passive unlimited long-term store. It should be noted, however, that some other models have been proposed, with at least partial success, which do not follow the general theoretical outline proposed above. Bernbach (8) and Postman and Phillips (2) have proposed "single" memory theories, and Norman and Rumelhart (9) have proposed a decay theory to explain both serial-position and list-length effects in free recall and related tasks. We cannot go into such theories in this report, but the three mentioned have the common property that the serial-position effects and list-length effects are integrally related. On the other hand, theories postulating separate short- and long-term stores propose that these effects are relatively independent. The present study is, therefore, designed to demonstrate considerable independence of the list-length effects from serial-position effects. We will demonstrate this by describing a free-recall task in which serial-position effects are absent but in which list-length effects are present and unattenuated.

The clue to the type of paradigm needed arose from a study in which we presented complex pictures to be remembered for a later recognition test (10). Both the presentation times of individual pictures and the times between pictures were varied. It was found that presentation time affected recognition but the time following a picture did not affect its recognition. Furthermore, recency effects were not seen. We concluded that complex pictures were not being given effective rehearsal during periods when they were not

physically present, and that retention of these pictures in the short-term store was quite brief. These results and conclusions suggest the use of complex pictures in a free-recall task. The lack of rehearsal and short-term persistence might be expected to eliminate serial-position effects in such a task. At the same time, the number of pictures presented in a list can be varied and list-length effects tested.

A brief survey of the literature reveals that free recall has been tried with visual materials (11), but with pictures which have a clear and unambiguous single-word verbal label. In fact, the subject recalled the verbal labels. We are instead interested in using complex pictures in a task in which verbal encoding by a brief label at the time of storage is minimized. How, then, does one test recall? We adopted a procedure in which subjects wrote brief descriptions of all the pictures they could recall, and then they matched these descriptions to the actual pictures.

Complex pictures which were difficult to encode in a brief verbal fashion were taken from the collection of slides used in an earlier experiment (10). The slides were presented via a random access slide projector controlled by an IBM 1800 computer. Each subject received five lists of slides, in a random order: 10 slides at 1 second per slide, 10 slides at 2 seconds per slide, 20 slides at 1 second per slide, 20 slides at 2 seconds per slide, and 40 slides at 1 second per slide. In all conditions, in addition to the times listed, there was always 1 second between slides.

At the conclusion of each list the subject wrote down brief descriptions of as many slides from that list as he could recall, in any order. When the subject was unable to recall any additional slides, he was then shown all of the slides from that list, in a new random order. For each slide the subject responded with one of six keys numbered 0 to 5. He responded 0 if the slide was one for which a description was not written. If a slide appeared which had been recalled, the subject first noted next to his description the number of the slide being presented. Secondly he responded with keys 1 to 5 on a scale representing the vividness with which he had remembered the slide in question when he had written its description (5 representing most vivid recall). The next slide was presented when the subject had finished responding to the previous slide. One hundred and

ten subjects were run in all, in groups from one to four in size.

The subjects had little difficulty in carrying out the ratings or description tasks. Seldom were descriptions written which the subject did not match against some slide from the preceding list, and these may have been intrusions from previous lists. Thus all the results to follow are based on the rating responses and not on the content of the written descriptions.

Figure 1, C and D, shows the probability of recall, that is, the probability of giving a written description (or, equivalently, the probability of a non-zero vividness response), as a function of serial position for each of the five list types (12). Also given in the legend is the mean probability of recall averaged across each list.

The results are quite clear. (i) Serial-position effects, that is, primacy and recency, are minimal. While there are some indications of a trend toward both primacy and recency, the magnitudes of these effects are at most very small compared to those seen in verbal free recall (1). (ii) Slides presented for longer durations are recalled better,

when list length is held constant. (iii) Slides in longer lists are recalled more poorly. This list-length effect is quite large, comparable to or greater than that usually found in verbal free recall (6).

The fact that additional presentation time leads to a small amount of additional recall is not surprising—the same effect occurred in recognition tests (10), and all theories would predict this. The relative lack of serial-position effects is also expected on the basis of the previous study (13). A slight decrease in recency is often seen when verbal materials are presented visually rather than auditorially (14), but the magnitude of the decrease is too small to explain the loss of recency seen in the present case.

The fact that a very strong list-length effect occurred in the absence of serial-position effects supports the argument that these effects can be quite independent of each other. Previous studies have shown that the recency effect and the list-length effect may be disassociated (2) but only when a period of interfering verbal activity is interpolated between presentation and test. The pres-

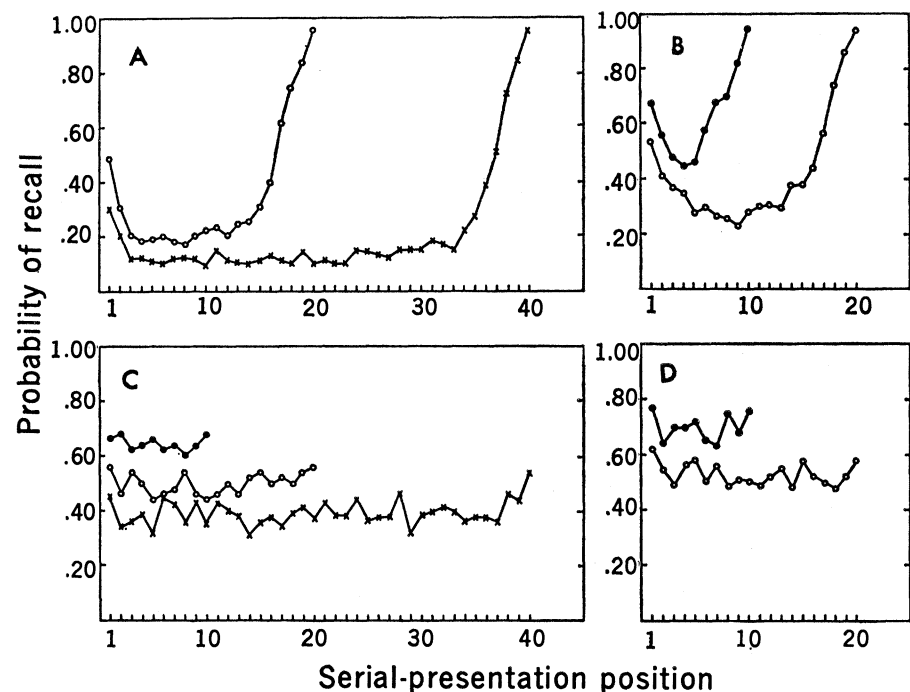


Fig. 1. Probability of recall as a function of serial-presentation position. (A and B) Typical functions for verbal free recall (1). Curves are shown for different list lengths and presentation rates. (A) Top curve: 20 words at 1 second per word; bottom curve: 40 words at 1 second per word. (B) Top curve: 10 words at 2 seconds per word; bottom curve: 20 words at 2 seconds per word. (C) Data for visual free recall for a presentation rate of 1 second per picture. Top curve: 10 pictures (mean recall, 0.64); middle curve: 20 pictures (mean recall, 0.48); bottom curve: 40 pictures (mean recall, 0.39). (D) Data for visual free recall for a presentation rate of 2 seconds per picture. Top curve: 10 pictures (mean recall, 0.70); bottom curve: 20 pictures (mean recall, 0.53).

ent results are consistent with theories of short- and long-term stores, in particular the models in (6) and (15). On the other hand, it is difficult for models like those in (2), (8), and (9) to accommodate them.

An interesting additional result is seen if we examine the average vividness rating of recalled slides for each list type (16). For the 10-1, 10-2, 20-1, 20-2, and 40-1 lists (referring to number of slides and seconds per slide) these ratings are, respectively, 4.2, 4.4, 4.2, 4.4, and 4.2. Thus average vividness was higher for recalled words which had been presented for longer durations, but average vividness did not depend on list length. To the degree that vividness ratings represent long-term trace strength we may conclude that strength varied with presentation time, but not list length. This conclusion is compatible with the theory proposed in (6) and (15).

One final note is worth emphasizing. Aside from the particular theoretical conclusions reached in the present study, the technique used to test recall for complex visual materials would appear to have quite general value. A similar technique could be used to examine recall in other free-recall tasks, in paired-associate tasks, in serial-learning tasks, or in any other recall tasks which have previously been investigated by using solely verbal materials. Such visual investigations may be contrasted with related verbal ones, and the comparisons can be expected to have considerable import for theories of memory.

RICHARD M. SHIFFRIN

Psychology Department,
Indiana University,
Bloomington 47401

References and Notes

1. See B. B. Murdock, Jr., *J. Exp. Psychol.* **64**, 482 (1962).
2. L. Postman and L. W. Phillips, *Quart. J. Exp. Psychol.* **17**, 132 (1965).
3. F. I. M. Craik, *J. Verb. Learn. Verb. Behav.* **9**, 143 (1970).
4. D. Rundus, *J. Exp. Psychol.* **89**, 63 (1971).
5. R. C. Atkinson and R. M. Shiffrin, *Sci. Amer.* **224**, 82 (1971).
6. R. M. Shiffrin, in *Models of Human Memory*, D. A. Norman, Ed. (Academic Press, New York, 1970), p. 375.
7. R. M. Shiffrin, *Science* **168**, 1601 (1970).
8. H. A. Bernbach, in *The Psychology of Learning and Motivation*, G. H. Bower and J. T. Spence, Eds. (Academic Press, New York, 1969), vol. 3, p. 201.
9. D. A. Norman and D. E. Rumelhart, in *Models of Human Memory*, D. A. Norman, Ed. (Academic Press, New York, 1970), p. 19.
10. W. O. Shaffer and R. M. Shiffrin, *J. Exp. Psychol.* **92**, 292 (1972).
11. W. Bevan and J. A. Steger, *Science* **172**, 597 (1971).
12. The data were also analyzed in terms of the ratings of vividness in many ways. For example, we graphed the probability of a vivid-

ness rating of 5 as a function of serial position. All these analyses looked qualitatively equivalent to the recall scores.

13. While the results in (10) lead one to expect minimal serial-position effects, it could also be argued that it is the act of writing descriptions that interferes with short-term memory and causes small recency effects.
14. B. B. Murdock, Jr., and K. D. Walker, *J. Verb. Learn. Verb. Behav.* **8**, 665 (1969).
15. R. C. Atkinson and R. M. Shiffrin, in *The*

Psychology of Learning and Motivation, K. W. Spence and J. T. Spence, Eds. (Academic Press, New York, 1968), vol. 2, p. 354.

16. Average vividness is the sum of the vividness ratings divided by the number of non-zero vividness ratings.
17. Supported by PHS grant MH 12717-05. I thank B. Shaffer and S. White for collecting and analyzing the data.

20 February 1973

Are Cell Membranes Fluid?

Singer and Nicolson (1) have suggested that the majority of cell membranes can be considered as a fluid mosaic structure, and that "the lipids of functional cell membranes are in a fluid rather than a crystalline state."

At present, however, there appears to be evidence accumulating in support of lipid heterogeneity, specifically, that some organisms actually contain crystalline or gel-state lipids in addition to the familiar "fluid" liquid crystalline domains that have been widely accepted as a central feature of many membrane models.

The techniques of differential scanning calorimetry, x-ray diffraction, nuclear magnetic resonance (NMR), electron spin resonance (ESR), and monolayer studies have yielded evidence that appears to be consistent with the notion that perhaps only a small fraction of the lipids of a cell membrane need be in this fluid condition for organism growth to occur, that is, large quantities of lipid may be quite rigid or crystalline. I consider, in particular, evidence pertaining to the plasma membrane of *Acholeplasma laidlawii* B and *Escherichia coli*.

The plasma membranes of both these organisms undergo reversible thermotropic gel-to-liquid crystal phase transitions of low cooperativity (2-4). With unsupplemented or stearate-supplemented cells of *A. laidlawii* B, the thermal transition encompasses the growth temperature, 37°C (2-4). Indeed, for stearate-supplemented membranes, the transition extends from about 35° to 73°C. This must indicate that the lipids are predominantly in a crystalline gel state at the growth temperature (37°C).

Similarly, with *E. coli* grown on "normal" media at 37°C, the membranes and their isolated lipids exist on a broad thermal transition (4), which extends from about 15° to 43°C. These broad thermal transitions are analogous to the melting of a highly impure crystal. Both crystalline gel ("solid") and

liquid crystalline ("liquid") phases, are present "on" the transition. This type of phase behavior has been well investigated in simple model systems (5) and is a result of heterogeneity of both lipid polar head groups and hydrocarbon chains.

This interpretation is supported by x-ray data for both membrane systems (6, 7). Engelman (6) has demonstrated that, in palmitate-supplemented membranes from *A. laidlawii* B, the thermal phase transition—as detected by x-rays (a sharp 4.15-Å band changing to a diffuse 4.6-Å band)—encompasses the growth temperature of 37°C, and has also shown that the crystalline 4.15-Å spacing disappears only at 44°C, that is, well above the growth temperature.

Similarly, Esfahani *et al.* (7) have demonstrated that both 4.2-Å and 4.6-Å spacings are obtained from *E. coli* K12, supplemented with elaidate and linolenate, at the growth temperature. Their results also indicate that some sort of "fluidity feedback" system may be in operation.

Organisms supplemented with linolenate or oleate, which would be expected to produce more fluid lipids (mainly phosphatidylethanolamines), were shown to incorporate large amounts of palmitate, a saturated acid. For example, linolenate-supplemented membranes contained 67 percent palmitate and only 23 percent linolenate. However, membranes supplemented with elaidate incorporated 75 percent elaidate and only 14 percent palmitate. This might be predicted on the basis of a model in which many lipids need to be quite rigid, since the physical properties of dielaidoylphosphatidylethanolamine are quite similar to those of dipalmitoylphosphatidylethanolamine (8). Esfahani *et al.* (7) demonstrated, with elaidate-supplemented membranes, that the x-ray detected thermal phase transition extended from 30° to 40°C for intact membranes (organisms grown at 37°C) and for linolenate- and myristoleate-