

Research Article

AUDITORY LIST MEMORY IN RHESUS MONKEYS

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Abstract—Auditory memory of 2 rhesus monkeys was tested in a serial probe recognition task. Lists of four environmental or natural sounds were followed by a retention interval and a test. The test matched one of the list items on half of the trials. The retention interval was varied across sessions. Six experiments showed similar results and changes in the serial position function. At short retention intervals, there was good memory for first list items (primacy effect) and poor memory for last list items. At intermediate retention intervals, memory improved for last list items (recency effect). At long retention intervals (20 s and 30 s), the recency effect was strong, and the primacy effect had dissipated. These auditory primacy and recency effects and their changes with retention interval were opposite to those for visual memory. Implications for processes and mechanisms of memory are discussed.

The U-shaped serial position function has been a test bed for theories of memory virtually since the study of memory began (Ebbinghaus, 1902). The serial position function typically shows good memory for items at the beginning of lists, a primacy effect; good memory for items at the end of lists, a recency effect; and poorer memory for items in the middle of lists. More than a half century after Ebbinghaus's memory experiments, the recency effect was shown to be separable from the remainder of the function (e.g., Gardiner, Thompson, & Maskarinec, 1974; Glanzer & Cunitz, 1966; Postman & Phillips, 1965; Roediger & Crowder, 1975). Recency memory dissipated with retention and virtually disappeared after about 30 s. During the delay, subjects engaged in distractor activity (e.g., counting backwards from 100) to prevent memory rehearsal. This finding spawned proposals about underlying memory processes, including the proposal that the recency effect reflected short-term memory (STM), the primacy effect (i.e., prerecency) reflected long-term memory (LTM), and rehearsal moved memory from STM to LTM (Atkinson & Shiffrin, 1968; Waugh & Norman, 1965).

Our studies of monkeys' visual list memory were originally motivated by a desire to test animals for similar or related memory processes (Sands & Wright, 1980a, 1980b). To train rhesus monkeys, we used a large collection of "travel" slides, unlike the small collection of geometrical shapes and colors other researchers had used. In this serial probe recognition task, monkeys pushed down on a three-position lever that moved in a T pattern to start memory lists. List items were presented on an upper rear-projection screen. A single test item, on a lower screen, followed each list. On half the trials, the test matched one of the list items. On the other half of the trials, it matched no list item. The correct response was a lever movement to the right when it matched, and to the left when it did not match. Good performance depended on our using a large number of different memory items in these experiments and thereby minimizing proactive interference from

item repetitions. The monkeys performed accurately with 10- and 20-item lists and revealed primacy and recency effects, similar to those shown for humans.

The rhesus monkeys were then tested with four-item lists and retention manipulations to determine whether or not recency memory (and STM) would dissipate as it did for humans. We tested four-item lists in randomized 20-trial blocks with each of six delays (Wright, Santiago, Sands, Kendrick, & Cook, 1985). Two 20-trial blocks were tested daily. The duration of item presentation and interitem interval were both 1 s. As for humans, the recency effect dissipated and eventually disappeared as the retention delay was lengthened to 30 s. Another change, and one that was unanticipated, occurred at short delays. On the immediate test, there was no primacy effect, only a recency effect. The primacy effect appeared after a short delay. This appearance of a primacy effect was an absolute (as well as relative) increase in memory performance. Similar changes in the primacy effect (and the recency effect) have since been shown for other species: pigeons (Wright et al., 1985) and capuchin monkeys (Wright, 1998), both tested with travel slides, and humans, tested with kaleidoscope patterns (Wright et al., 1985), snowflake patterns (Neath, 1993; Neath & Knodler, 1994), and antique-car drawings (Korsnes, 1995; Korsnes & Gilinsky, 1993).

One issue raised by these results is whether the observed form of the serial position function and its changes with retention are representative of memory processing generally, or are particular to visual memory. The purpose of the experiments reported in this article was to address this issue by conducting similar experiments on the auditory memory of rhesus monkeys.

EXPERIMENT 1

Monkeys' auditory list memory cannot be tested until they are trained in an auditory same/different task. Monkeys generally have difficulty learning auditory tasks, and the same/different and list memory tasks are among the more difficult to learn. In our first attempt to train rhesus monkeys on the auditory same/different task, my collaborators and I duplicated the visual memory task but with natural sounds instead of pictures. There was no learning after the better part of a year of training. In our second attempt, a monkey was trained with a visual-auditory compound and then the visual component was faded. Again, the monkey did not demonstrate learning with auditory stimuli. Finally, 2 monkeys, B.W. and F.D., were able to learn the task illustrated in Figure 1, demonstrating good performance with novel sounds (Wright, Shyan, & Jitsumori, 1990). In addition to using a large collection of different sounds, having the monkeys touch the speakers, the sound sources, proved critical (cf. Harrison, Iversen, & Pratt, 1977).

In preparation for Experiment 1, B.W. and F.D. were trained and tested with progressively longer lists of 4, 6, 8, and 10 sounds (Wright & Rivera, 1997). Their serial position functions showed primacy and recency effects with these different list lengths. The monkeys were then returned to training and testing with 4-item lists, and Experiment 1 presents the results of manipulation of the retention interval.

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Methods

The subjects were two 15-year-old male rhesus monkeys (*Macaca mulatta*). They were maintained in state- and federal-approved facilities. They were fed and given water approximately 2 hr after experimental sessions, which were conducted 5 or 6 days per week.

The test chamber was a modified primate cage located inside a custom-built sound-deadening cubicle. Three bars were removed from the

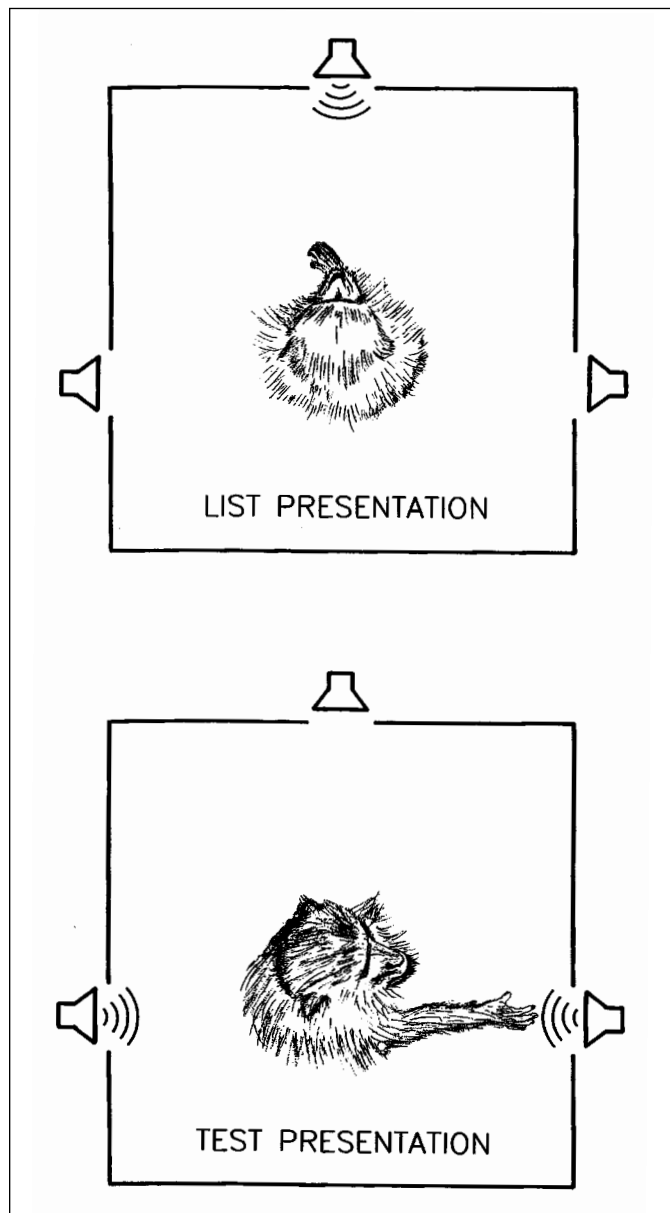


Fig. 1. Schematic of the testing procedure. The upper panel shows a top view of a monkey with list sounds being presented from a center speaker. The lower panel shows a top view of a monkey touching a right-side speaker while a test sound is being presented from both side speakers. A touch to the right-side speaker was correct when the test sound matched a list sound, and a touch to the left-side speaker was correct when the test sound matched no list sound.

test cage so that the monkeys could touch copper screens in front of speakers positioned outside the cage. Touches and other aspects of the experiment were electrically monitored and computer controlled.

A flashing light-emitting diode (LED) behind the center-speaker copper screen cued monkeys that a trial could begin. A touch produced a banana pellet and a list of four different sounds. Each sound was presented for a 2-s duration, with a 1-s interval between sounds. A retention interval (although in one condition it was 0 s) followed each list. A test sound was then played simultaneously from both side speakers for 2 s to 6 s. The same sound always came from both side speakers. Responses were accepted after 2 s of test, and the choice response terminated the test sound. If the test sound matched one of the list sounds (*same* trial), a touch to the right-side speaker produced 3.5 cc of Tang orange drink. If the test sound matched none of the list sounds (*different* trial), a touch to the left-side speaker produced a similar reward. Juice rewards were dispensed adjacent to the side speakers. Incorrect choices or aborts (not responding within the 2- to 6-s response interval) were not rewarded and were followed by 30-s time-outs. Intertrial intervals (ITIs) were 12 s. Each daily session lasted for 32 trials, 16 *same* trials and 16 *different* trials, with a fixed retention delay. The four delays (0 s, 1 s, 10 s, and 20 s) were tested in a random order within each of 10 blocks, so that there were 40 tests at each serial position at each delay.

The studies reported here used 520 environmental sounds (e.g., Morse code, stagecoach yells, dog howling, footsteps, seagulls, tea kettle, angry cat, riveting, crickets chirping, dentist drill, sheep baaing, steamboat whistle, dinner triangle, carpet sweeper, children playing, water pouring, cable car, woman laughing, horse whinnying, air-raid glissando, wood chopping, pig grunting, buoy bell, turkey gobbling, cuckoo clock, water-well pump, frog calls), plus additional novel sounds used in Experiment 4. Most sounds were taken from 13 sound-effect records (Elektra Records, New York, New York). List compositions and sequences varied daily, and the sounds were unique to each trial within a daily session.

Results

Figure 2 shows results for the 2 individual subjects. The serial position functions show performance for trials on which the test matched one of the list items. Unfilled points show performance when the test did not match any list item (*different* trials). The 2 subjects' serial position functions show similar trends. The 0-s (immediate) test shows prominent primacy effects, but no recency effects. Recency effects grow and primacy effects dissipate as delay is extended. Analysis of variance (ANOVA) showed a significant interaction between delay and serial position, $F(9, 16) = 3.10, p < .05$.

The form of these functions and their changes over time are opposite to previous findings for visual memory. A series of follow-up experiments and replications was conducted to verify this surprising difference. The results from these five additional, independent experiments are presented because I feel that they work together to promote at least some confidence in the basic form of these results.

EXPERIMENT 2

Experiment 2 was similar to Experiment 1 except that the inter-stimulus interval (ISI) was 0.5 s instead of 1.0 s, and 12 tests were conducted at each serial position of each function.

Figure 3 shows that the form of the functions is similar to the form of the functions obtained in Experiment 1. Primacy effects were prominent

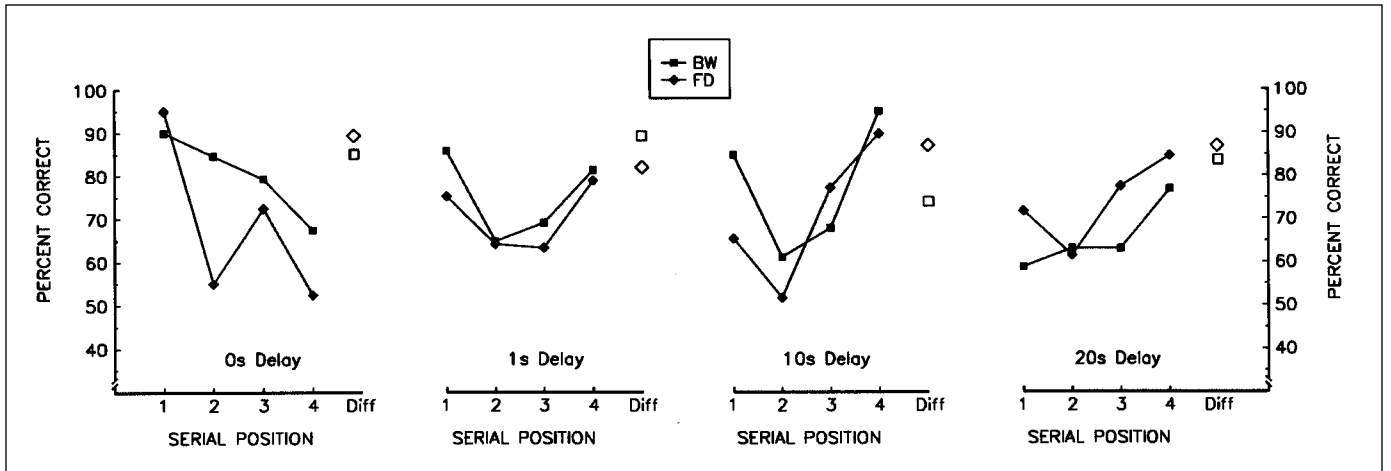


Fig. 2. Serial position functions for 2 monkeys (B.W. and F.D.) from Experiment 1 for trials in which the test sound matched one of the list sounds. (Serial Position 1 is the first item in the list.) Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval between list and test.

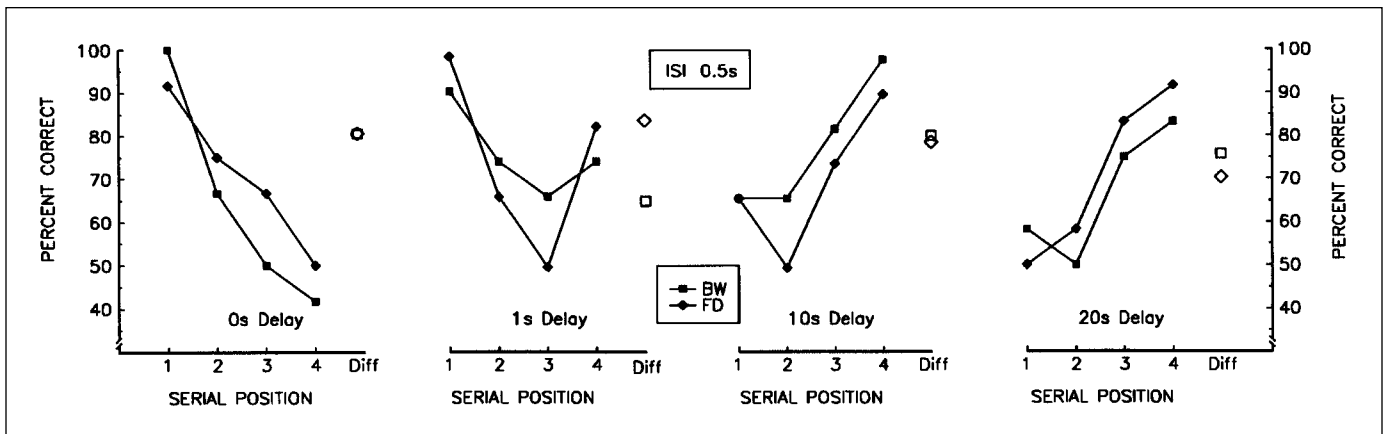


Fig. 3. Serial position functions for 2 monkeys (B.W. and F.D.) from Experiment 2, in which the interstimulus interval (ISI) was 0.5 s, instead of 1.0 s, as in Figure 2. Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval between list and test.

initially, but gave way to recency effects as retention delay increased. Recency effects were prominent at longer delays (10 s and 20 s). An ANOVA showed a highly significant interaction between delay and serial position, $F(9, 16) = 13.7, p < .0001$. Serial position functions at 0-, 10-, and 20-s delays showed significant linear (monotonically increasing or decreasing) trends, $F(1, 6) = 47.1, 11.1, \text{ and } 27.0$, respectively, all $ps < .02$.

EXPERIMENT 3

Performance changes were somewhat more robust in Experiment 2 than Experiment 1, resulting in steeper serial position functions. In Experiment 3, the ISI was changed back to 1 s to test whether the shorter ISI in Experiment 2 enhanced the effects shown in Experiment 1 or the subjects were just more experienced in the task and more adapted to daily changes in retention interval. Twelve tests were con-

ducted at each serial position at each delay. Other experimental conditions were unchanged.

The results are shown in Figure 4. Form of the functions, similarity between individual subjects’ results, and magnitude of the effects were similar to the results for Experiment 2. An ANOVA showed a significant interaction between delay and serial position, $F(9, 16) = 11.4, p < .001$. Serial position functions at 0-, 10-, and 20-s delays showed significant linear (monotonically increasing or decreasing) trends, $F(1, 6) = 43.4, 11.9, \text{ and } 27.1$, respectively, all $ps < .02$.

In conclusion, the form of the functions and the magnitude of the effects were the same whether the ISI was 0.5 s or 1.0 s.

EXPERIMENT 4

The monkeys had heard the sounds many times. It was unclear whether or not familiarity had played a role in these results. By

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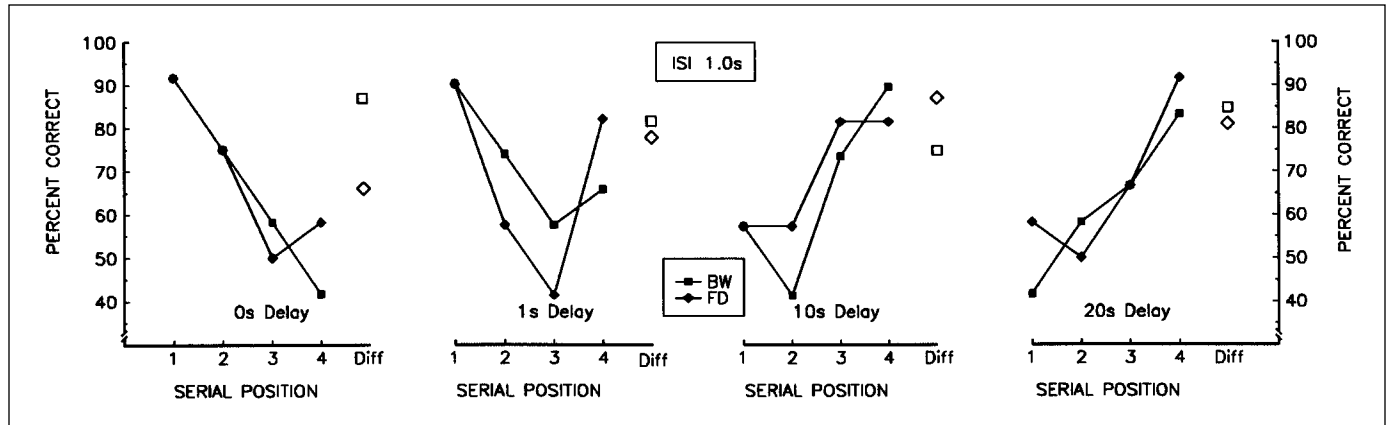


Fig. 4. Serial position functions for 2 monkeys (B.W. and F.D.) from Experiment 3. Testing conditions, including the interstimulus interval (ISI) of 1.0 s, were similar to those used in the study providing the data for Figure 2. Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval.

intermixing novel-stimulus trials with familiar-stimulus trials, Experiment 4 tested this possibility. For the sake of efficiency, only the shortest (0-s) and longest (20-s) retention intervals were tested.

There were 8 novel-stimulus trials, composed entirely of never-before-heard sounds, mixed pseudorandomly with 24 familiar-stimulus trials. The ISI was 0.5 s. Other procedures were unchanged. The 24 daily sessions alternated between the two retention delays. There were 864 novel sounds used in this study, plus the 520 familiar sounds.

Results are shown in Figure 5. The serial position functions for novel and familiar stimuli were similar to each other and similar to previous functions at these same delays. An ANOVA showed a highly significant interaction between delay and serial position, $F(9, 16) = 16.4, p < .0001$. The serial position functions showed significant linear (monotonically increasing or decreasing) trends: $F(1, 6) = 25.8$ and 24.6 at 0-s delays for familiar and novel stimuli, respectively, and $F(1, 6) = 24.4$ and 14.7 at 20-s delays for familiar and novel stimuli, respectively, all $ps < .01$. This study shows that familiarity or novelty of the stimuli does not affect the serial position functions.

EXPERIMENT 5

In the previous studies, the monkeys initiated lists by touching the center speaker, and other cues were also associated with the beginning of lists (e.g., a flashing LED and a banana pellet). Other researchers had hypothesized that list-initiation responses were responsible for primacy effects shown in animal list memory experiments (D. Gaffan, 1983; E.A. Gaffan, 1992). Although this possibility seemed unlikely in the present case because the primacy effect had varied with retention despite constant conditions of list initiation (Wright, 1994; Wright, Santiago, & Sands, 1983), this hypothesis was tested in Experiment 5. If list-initiation responses (and associated cues) were eliminated, then, according to the hypothesis, primacy would disappear at all retention delays. Thus, the purpose of this study was to eliminate list-initiation responses and associated cues to test the list-initiation hypothesis and determine if any other aspects of the serial position functions would be altered.

Lists were presented without a list-initiation response, and there was no flashing LED cue light or banana pellet marking the start of a trial. So that (reinforcing) conditions would be as close as possible to

conditions in the previous studies, banana pellets were delivered following juice rewards on correct trials. Neither monkey was observed touching the center speaker (i.e., making noncontingent responses) in this or the subsequent experiment. The monkeys typically sat facing the center speaker during list presentation, and then turned, during the test, and touched one of the two side speakers. Other conditions were unchanged relative to Experiment 1: The ISI was 1 s, there were 40 tests at each serial position of each function, and the ITI was 12 s.

Figure 6 shows the serial position functions, which are similar in form to those of the previous experiments. Primacy effects dominate initially, but dissipate and give way to recency effects at long delays. If list-initiation responses or other cues associated with the start of lists had been critical in producing the primacy effects, then primacy effects should have disappeared at all retention delays when these responses and cues were eliminated. But primacy effects did not disappear. The serial position functions were essentially unchanged.

An ANOVA showed a highly significant interaction between delay and serial position, $F(9, 16) = 24.0, p < .0001$. Serial position functions at 0-, 1-, 10-, and 20-s delays showed significant linear (monotonically increasing or decreasing) trends, $F(1, 6) = 61.6, 27.5, 34.2,$ and 158.2 , respectively, all $ps < .01$.

EXPERIMENT 6

This study expanded several aspects of the previous study. Another possible cue for the beginning of lists was the fixed time of 12 s between trials. Conceivably, subjects could have anticipated the beginning of the next trial by timing the 12-s ITI. This possibility was tested by varying the ITI quasi-randomly from 12 s to 27 s in 1-s steps. Each of the 16 ITIs was used twice in each 32-trial session in a pseudorandom sequence that varied from session to session. The other cues (flashing light, initiation response, and banana-pellet reward for list-initiation response), which had been eliminated in Experiment 5, were also absent in this experiment.

Experiment 6 was made more comparable to the visual memory experiment discussed in the introduction by testing all of the six delays (0, 1, 2, 10, 20, 30 s) tested in that experiment (Wright et al., 1985). The six delays were tested in a randomized block design for five

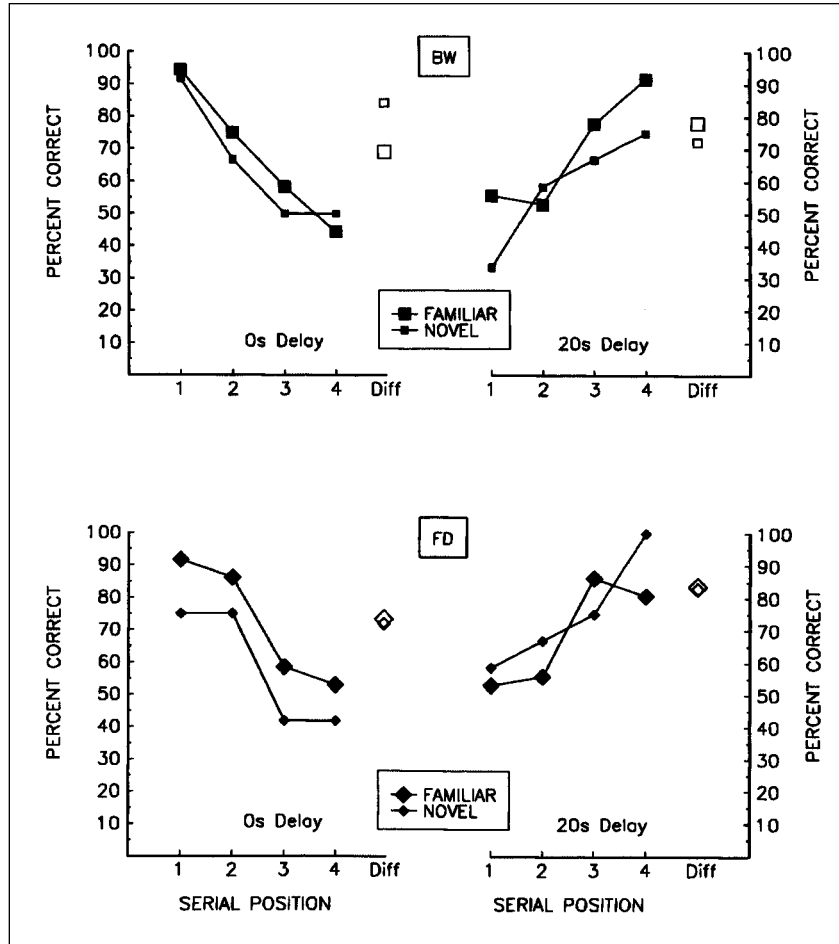


Fig. 5. Serial position functions from Experiment 4, which tested novel (small points) and familiar (large points) stimuli at the shortest (0-s) and longest (20-s) delays previously tested. Data from the 2 monkeys (B.W. and F.D.) are presented separately in the upper and lower panels. Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval.

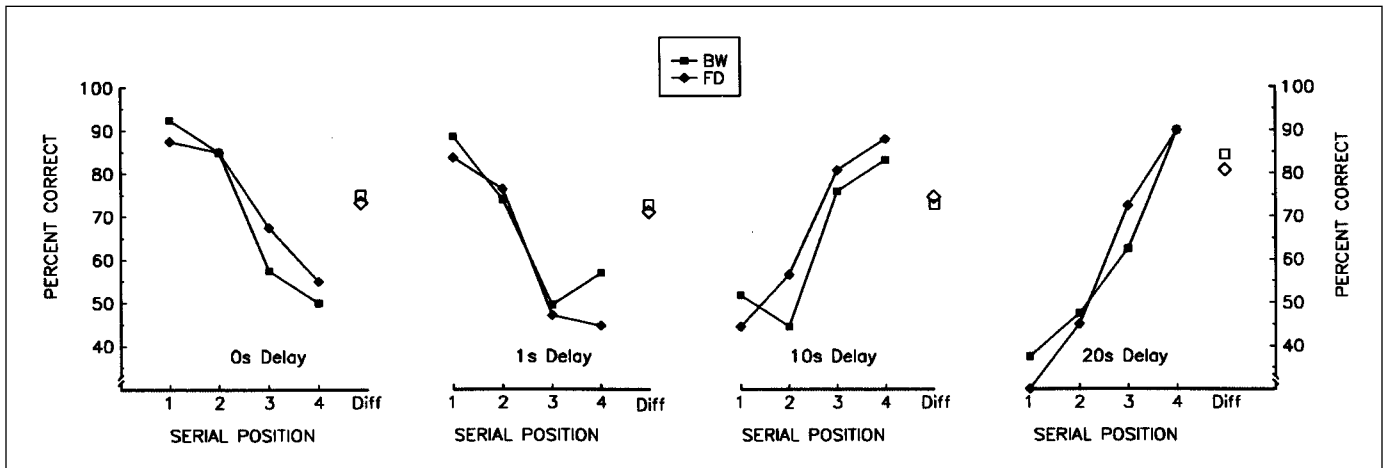


Fig. 6. Serial position functions for 2 monkeys (B.W. and F.D.) from Experiment 5, which was similar to Experiments 1 and 3 (cf. Figs. 2 and 4), except that lists were presented without list-initiation responses or cues (light and reward) for the beginning of lists. Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval.

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blocks. Thus, each delay was tested in five daily sessions, for a total of 30 days of testing. Each of the four serial positions was tested four times per session for a total of 20 times at each delay. The ISI was 1 s. Other conditions were unchanged from the previous study.

Individual results are shown in Figure 7. The serial position functions for the 2 subjects were similar, and the form of these functions was similar to that from previous studies at the same delays. There were no systematic differences as a function of length of the ITI.

An ANOVA showed a highly significant interaction between delay and serial position, $F(15, 24) = 11.7, p < .0001$. Serial position functions

at 0-, 1-, 10-, 20-, and 30-s delays showed significant linear (monotonically increasing or decreasing) trends, $F(1, 6) = 33.7, 48.2, 56.3, 32.2,$ and $32.8,$ respectively, all $ps < .01$.

One conclusion is that fixed ITIs, list-initiation responses, and other cues associated with the start of lists (e.g., light, reward) are not responsible for producing the primacy effects or other features of the functions.

The average (mean) results are presented in Figure 8, along with results from a similar visual memory experiment (Wright et al., 1985). The two experiments were similar: 2 rhesus monkeys, four-item lists,

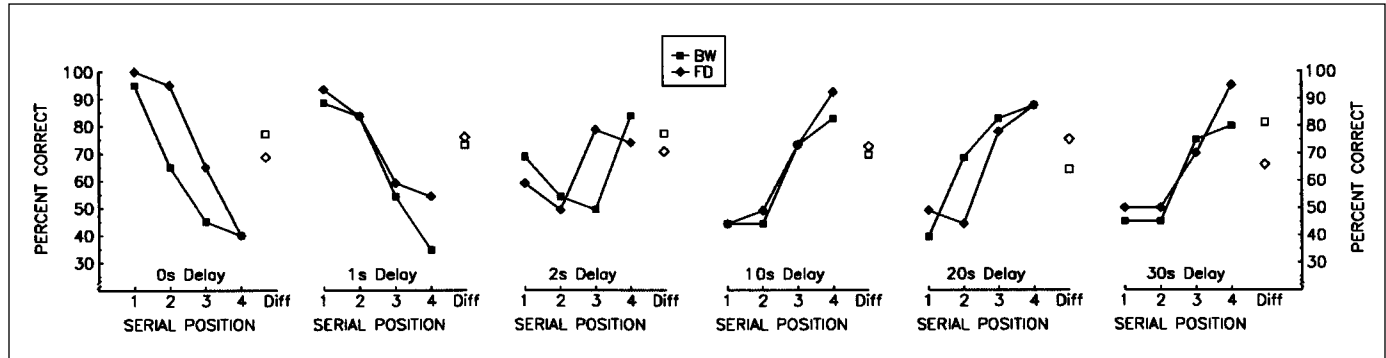


Fig. 7. Serial position functions for 2 monkeys (B.W. and F.D.) from Experiment 6, which was similar to Experiment 5 (cf. Fig. 6), but with two additional retention delays and a variable intertrial interval. Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval.

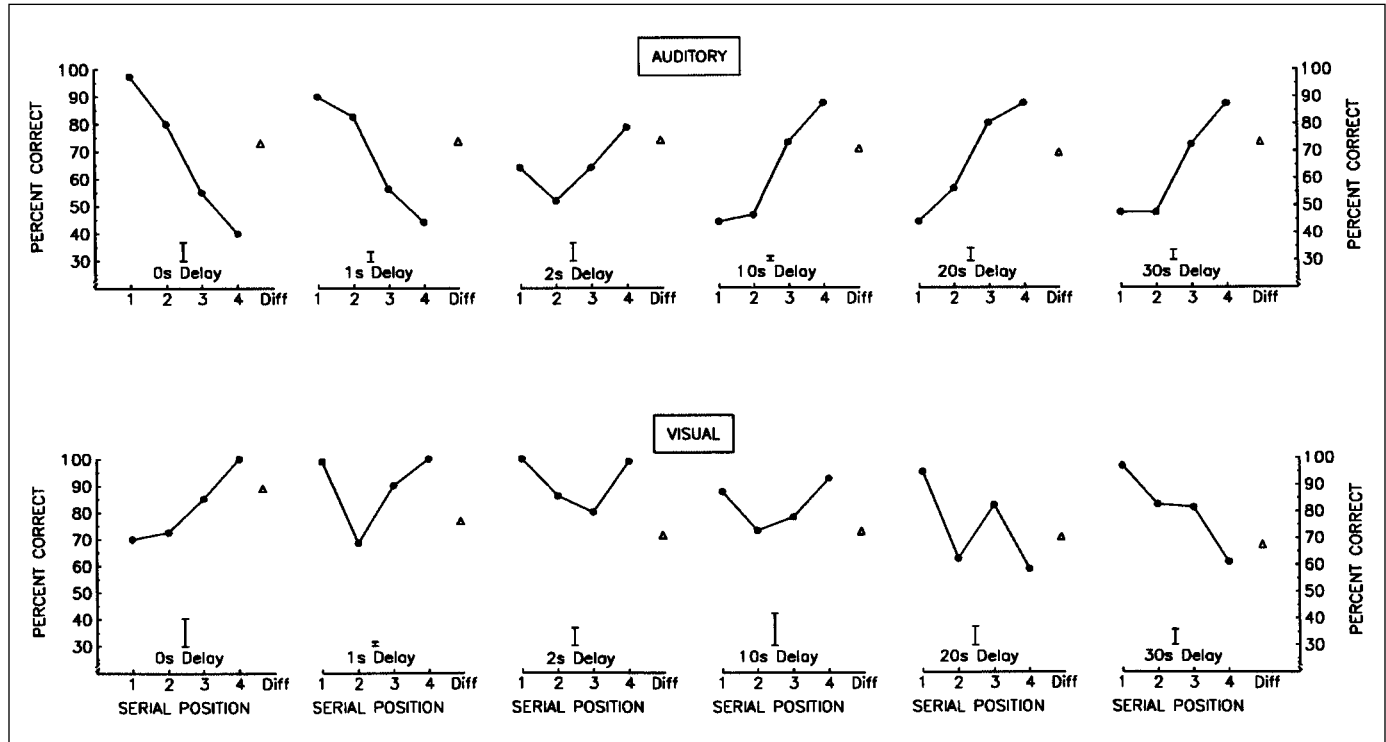


Fig. 8. Average performance for the results shown in Figure 7 (upper panels) and for 2 other monkeys in an otherwise similar study of visual list memory (lower panels; after Wright, Santiago, Sands, Kendrick, & Cook, 1985). Unfilled points (“Diff”) show performance on trials in which the test sound was different from all the list sounds. Delay is the retention interval. Error bars are the average standard error of the mean for the four serial positions of each function.

one test per trial, the same retention intervals presented in the same blocked design, and a large pool of memory items presented trial-unique within each session.

Perhaps the most striking comparison is the opposite shape of the serial position functions for auditory versus visual memory. On the immediate test (0-s delay), auditory memory shows a primacy effect but no recency effect, whereas visual memory shows a recency effect but no primacy effect. At a 2-s delay, functions from both modalities are U-shaped. If memory had been tested only at this delay, it might have been concluded that auditory and visual memory are similar. At longer retention intervals, the functions have reversed (in slope) and are opposite once again. Auditory memory shows a recency effect and no primacy effect, whereas visual memory shows a primacy effect and no recency effect.

GENERAL DISCUSSION

The monkeys' serial position function for auditory memory gradually evolved with retention delay. Initially, there was a strong primacy effect and no recency effect. The primacy effect gradually gave way to a recency effect. Eventually, the recency effect was strong and the primacy effect had disappeared. The results from the 2 monkeys were similar, and six experiments produced similar results across variations in several parameters: two different ISIs (Experiments 1 and 3 vs. Experiment 2), novel versus familiar sounds (Experiment 4), initiated lists (Experiments 1–4) versus noninitiated lists (Experiments 5 and 6), and different numbers of retention intervals tested (two in Experiment 4; four in Experiments 1, 2, 3, and 5; and six in Experiment 6). I have reported results from six experiments because combined they make a stronger case for these somewhat unusual results than any of the individual experiments alone. I now discuss briefly some of the more unusual aspects of these results.

The visual and auditory serial position functions for monkeys (Fig. 8) are of opposite shape. They combine to produce an interesting, if not artistically pleasing, balance to their overall pattern. The serial position functions change gradually as retention lengthens, and the performance changes in primacy and recency span virtually the entire performance range possible in these types of experiments. These large changes in memory, together with other aspects of the results, may provide new possibilities for investigating mechanisms of serial list memory.

An aspect of auditory memory that deserves some discussion is the unusually strong primacy effect at short delays. By contrast, in visual memory (e.g., of humans, monkeys, and pigeons), the recency effect is strong at short delays but dissipates with retention. Indeed, demonstrations of recency dissipation with retention (e.g., Glanzer & Cunitz, 1966) helped stimulate an era of research on STM that continues to this day. Implicit in this pursuit of STM was the hypothesis that all memory begins with a strong STM component, as evidenced by a strong recency effect, which then dissipates with retention. But apparently not all memory, at least not rhesus monkeys' auditory memory, operates in this manner. If recency represents STM in the rhesus monkey's auditory memory, then one would have to conclude that STM is not present initially but appears later. Such a conclusion would contradict the common conception of STM.

There have been other difficulties with the concept of STM (see Crowder, 1993, for a review). Notwithstanding problems and disagreement concerning STM, it would probably be fair to say that there is even less agreement regarding LTM. Perhaps the theory that has had the

greatest impact on the concept of LTM is the dual-store, or modal, model (e.g., Atkinson & Shiffrin, 1968; Waugh & Norman, 1965). According to this model, rehearsal of items maintained in an STM buffer moves them to LTM and thereby produces the primacy effect. But evidence showing long-term recency effects produced by delays between memory items (e.g., Glenberg, Bradley, Kraus, & Renzaglia, 1983), distractor activity between memory items (e.g., Bjork & Whitten, 1974), recall of presidents (Roediger & Crowder, 1976), and recall of rugby scores (Baddeley & Hitch, 1977) makes the concept of a limited-capacity STM rehearsal buffer untenable (Crowder, 1993; Greene, 1992). Other evidence shows that rehearsal (by humans) is not necessary to produce primacy effects (Wright et al., 1990). The present results regarding the monkey's auditory memory add to this evidence against a limited-capacity STM rehearsal buffer. These results show that initially there is a strong primacy effect and no recency effect, but how can there be LTM before STM if, as the modal model postulates, rehearsal of STM is supposed to produce LTM?

A somewhat unusual aspect of the results for both auditory and visual memory in monkeys is that within each modality there is a limb of the serial position function (auditory recency, visual primacy) that improves with delay. Memory that improves with delay is counterintuitive. More commonly, memory is thought to deteriorate (monotonically) with the passage of time. Such memory improvements with retention, coupled with decreasing memory for the other limb of the function, make it difficult for any single memory process (e.g., decay, displacement, unlearning) to account for these results (but see Crowder & Neath, 1991, and Neath, 1993, for distinctiveness accounts).

Another unusual aspect of these results is that auditory and visual memory initially have opposite-shaped serial position functions, and that the functions reverse during the course of retention and end up, once again, having opposite shape. The end result is a recency-dominated auditory serial position function and a primacy-dominated (absence of recency) visual serial position function. This recency advantage for auditory over visual memory is reminiscent of the modality effect in human memory. Perhaps similar trend differences in human serial position functions play a role in the modality effect, in addition to feature-processing (e.g., Nairne, 1990), temporal-distinctiveness (e.g., Glenberg & Swanson, 1986), and language (e.g., Shand & Klima, 1981) factors that have previously been proposed to account for this effect.

Human memory is undoubtedly influenced by many things that do not affect monkey memory. Humans come to the experimental setting with a lifetime of game-playing and school-study strategies (e.g., coding, rehearsal, associative network, and mnemonic strategies). Coding strategies frequently result in auditory-visual memory overlap. Written words are pronounced or mouthed silently (e.g., Crowder, 1983). Auditory items (environmental sounds, words) are visualized (e.g., Campbell & Dodd, 1980). There are advantages to cross-modality coding, advantages that are potentially greater than those of redundant, within-modality coding. Species that have serial position functions of opposite shape and that engage in cross-modality coding will have good auditory memory when their visual memory is poor and good visual memory when their auditory memory is poor. Contingencies of reinforcement operating in the everyday environment might, through learning, make such cross-modality coding automatic. Notwithstanding this potential advantage, cross-modality coding may become a disadvantage if it cannot be prevented when researchers need to separate auditory and visual memory for experimental study. Rhesus monkeys are reluctant to code items in experimental memory tasks unless

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explicitly trained to do so, and show no evidence of rehearsal, which should depend on coding (Cook, Wright, & Sands, 1991; Neiworth & Wright, 1994). Thus, some animals (e.g., rhesus monkeys) may eventually prove to be better suited than humans to help researchers explore some of the basic processes that underlie auditory and visual memory.

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