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AN EXPERIMENTAL ANALYSIS OF MEMORY PROCESSING

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Rhesus monkeys were trained and tested in visual and auditory list-memory tasks with sequences of four travel pictures or four natural/environmental sounds followed by single test items. Acquisitions of the visual list-memory task are presented. Visual recency (last item) memory diminished with retention delay, and primacy (first item) memory strengthened. Capuchin monkeys, pigeons, and humans showed similar visual-memory changes. Rhesus learned an auditory memory task and showed octave generalization for some lists of notes—tonal, but not atonal, musical passages. In contrast with visual list memory, auditory primacy memory diminished with delay and auditory recency memory strengthened. Manipulations of interitem intervals, list length, and item presentation frequency revealed proactive and retroactive inhibition among items of individual auditory lists. Repeating visual items from prior lists produced interference (on nonmatching tests) revealing how far back memory extended. The possibility of using the interference function to separate familiarity vs. recollective memory processing is discussed.

Key words: memory, inhibition, interference, serial position functions, familiarity, pigeons, humans, monkeys

Animal memory traditionally has been studied with single items. The result is typically a forgetting function showing accuracy decreasing with retention delay. Examples of single-item forgetting functions are shown in Figure 1 for monkeys and pigeons performing a delayed-matching-to-sample (DMTS) task with two stimuli (the minimum number of stimuli for this task). Performance declines with the delay between the sample and the two choice stimuli and approaches chance performance after about 1 minute. One can ask whether one minute is the limit to their memory, or whether it has any simple relation to memory limits. If so, how could these species have survived? If not, then what do such single-item forgetting functions tell us about memory? These questions will be addressed later in this article after discussing training and testing of animals in visual and auditory list-memory tasks. (The shortened form, animals, will be used for nonhuman animals.)

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Traditional single-item tests of animal memory perhaps miss the most important aspect of memory. Events in the real world are virtually never encountered in isolation. Any single event is part of an ongoing stream of events. Memory for any particular event is influenced by the events that surround it, which in turn can radically alter memory for any single event. Serial-list memory studies were among the first studies of memory (Ebbinghaus, 1902; Nipher, 1876). Many well-known memory phenomena such as primacy and recency effects, proactive and retroactive interference or inhibition, distinctiveness, long-term recency, repetition, and suffix effects require tests of list memory. Results from serial list memory studies are displayed as a serial position function (SPF) which is typically bow or U shaped with better memory for the first list items—the primacy effect—and better memory for the last list items—the recency effect. The serial list memory task is considered to be the "test bed" of memory theories (e.g., Glenberg, Bradley, Kraus, & Renzaglia, 1983), underscoring its prominent position in shaping thinking on how memory works.

Armed with this background information, we began our animal memory studies. We were determined to explore the possibility that animals could be trained in list-memory tasks so that we could make more direct comparisons to human memory than were previously possible with single-item memory tasks. At the

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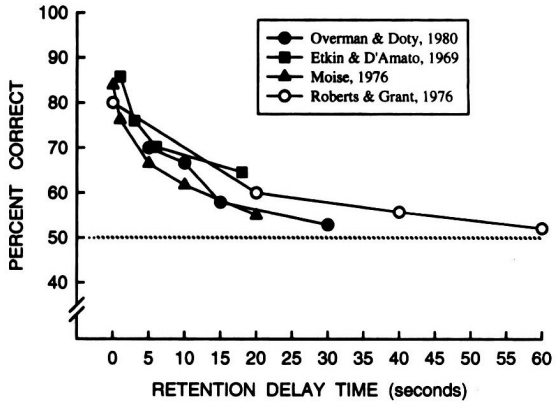

Fig. 1. Single-item memory functions from three delayed matching-to-sample experiments with monkeys (filled symbols) and one delayed matching-to-sample experiment with pigeons (open symbols). The dotted line represents chance performance.

time we began our animal memory studies, there was some evidence with humans indicating that memories of items of a list might interact and change over time. We wanted to explore these possibilities with several animal species. Of course, any success in determining how memory works for different species would depend upon being able to train these animals in list-memory tasks.

This article presents a program of animal memory research that I and my collaborators have been pursuing for some time. Among the aims in writing this article were to communicate a sense of the difficulties in training animals in list-memory tasks, the issues of why one would want to conduct such experiments in the first place, and what their results might mean in terms of how memory works. Any discussion of how memory works will necessarily involve some discussion of alternative views and, therefore, reference to memory theories—often a focus of human memory studies.

Some readers may not be as favorably disposed to cognitive research as we are, but I hope to dispel at least some of these reservations. Our approach is perhaps more data driven than many memory research programs. Indeed, I have been accused, more than once, of not having a theory of memory. In discussing evidence that I think implicates processes critical to how memory works (e.g., retroactive and proactive retrieval inhibition that occurs among items of a memory list), I have been accused of simply restating the results. (Interesting isn't it—the different perspectives on theory.) In any case, what I mean by how memory works are the functional relationships that critically affect memory performance. On one level of functional relationships, parameters of the list-memory task such as retention delay are manipulated, showing substantial changes in which list items are remembered. On another level of functional relationships, list length and item separations are manipulated, showing converging evidence that inhibition among items of a to-be-remembered list is responsible for the form of the SPF, and the nature of this inhibition changes with retention delay producing changes in the SPF. On yet another level of functional relationships, proactive interference is manipulated and is used to determine how far back in time previous list items can confuse memory judgments when they appear later as test items and do not match any current list item.

The first section of this article focuses on visual list-memory processing—primarily in animals. Individual memory results are presented for several species—including the gradual acquisition of the list-memory task. The second section focuses on auditory list memory of rhesus monkeys and includes experiments that manipulate inhibition among items of individual memory lists to test the role of inhibition in producing changes of the SPF when retention delay is varied. The third section focuses on proactive interference from previous list items that appear on later trials as test items. Proactive interference will be shown to have powerful and pervasive effects making list-memory tasks difficult to learn, and may eventually be shown to affect whether familiarity or recollection is instrumental in animals remembering lists of items.

VISUAL LIST MEMORY

Training Animals in a List-Memory Task

Our first attempt to train accurate list-memory performance was with a rhesus monkey (Sands & Wright, 1980a, b). We used picture stimuli with objects, scenes, or animals and have referred to them as travel slides. In this task, the monkey pushed down on a three-position lever ("T" pattern) to start trials. Initially, pairs of pictures were presented with Carousel slide projectors and the monkey

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moved the lever right or left to indicate that the two pictures were either the *same* (right movement) or *different* (left movement). The monkey mastered this *same/different* task in about 3 months of training. The procedure was then changed and the first picture was removed from the upper screen before the second picture was presented in the lower screen. The upper list item was then gradually expanded into a 10-item list. Each item of the 10-item list was presented for 1 s, with a 0.8-s interstimulus interval (ISI) and a 1-s retention interval. If the test item (in the lower screen) matched any one of the list items shown in the upper screen, then a *same* response (right lever movement) was correct. If it matched no list item, then a *different* response (left lever movement) was correct. These changes from a simultaneous *same/different* task to a 10-item list-memory task caused only slight disruption of performance. We conducted over 16,000 trials with each of the 211 items tested in each of the 10 serial positions. Performance was 86% correct with these 10-item lists. Performance was even a respectable 81% correct with 20-item lists.

Shown in Figure 2 are this monkey's SPFs from these two experiments. These SPFs show primacy and recency effects and were the first evidence of both these characteristic signatures of human list memory. These signatures of serial list memory have been replicated many times since with a variety of species including: apes (Buchanan, Gill, & Braggio, 1981), rhesus monkeys (Castro, 1995, 1997; Castro & Larsen, 1992; Sands & Wright 1980a, b; Wright, Santiago, & Sands, 1984; Wright, Santiago, Sands, Kendrick, & Cook, 1985), squirrel monkeys (Roberts & Kraemer, 1981), capuchin monkeys (Wright, 1999b), rats (Bolhuis & van Kampen, 1988; Harper, McLean, & Dalrymple-Alford, 1993; Kesner & Novak, 1982; Reed, Croft, & Yeomans, 1996), and pigeons (Santiago & Wright, 1984; Wright et al., 1985). Thus, a variety of animals show at least some of the important characteristics of list memory as humans do.

At the time, we had no way of knowing whether animals like monkeys would show primacy effects in their SPFs. The most popular human memory model had primacy effects resulting from rehearsal of the first list items during presentation of the list including the interstimulus interval or ISI (Atkinson &

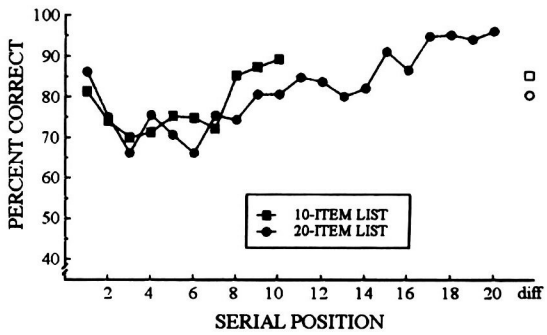

Fig. 2. SPFs for a rhesus monkey with 10- and 20-item lists of pictures. Performance on *different* trials, where the test item did not match any list item, is shown on the right of the graph (open symbols). Serial position is the order in which pictures were presented.

Shiffrin, 1968; Waugh & Norman, 1965). We were skeptical about whether this monkey (or any animal subject) would actively rehearse the pictures. Rehearsal is a memory process that is very difficult to test objectively with human participants, let alone animals. Nevertheless, an objective procedure to test human rehearsal was developed and thoroughly tested shortly after we had conducted the 10- and 20-item list memory experiments shown in Figure 2 (Intraub, 1980). This objective procedure was based on the ISI or "blank" time between list items to be remembered. Experimental results from several laboratories have converged on the conclusion that humans used this blank time to rehearse the items already seen (e.g., Graefe & Watkins, 1980; Intraub, 1980; Proctor, 1983; Watkins & Graefe, 1981).

Intraub in her landmark 1980 experiment presented humans with 16-item lists. Each item was briefly presented (110 ms). When the ISI was long (890 ms) performance was equivalent to when the items were presented for 5 s with no ISI. The ISI was shown to be critical because as the ISI was systematically decreased, performance fell precipitously and was only slightly above chance performance when it was 0 s. We used a similar blank-time procedure to test monkeys (and humans) with our travel-slide pictures. The humans were, of course, the control group and they showed the characteristic blank-time or ISI effect (improved performance with longer ISIs) verifying that our procedure with a short list of six travel slides did work. But as Figure 3 shows,

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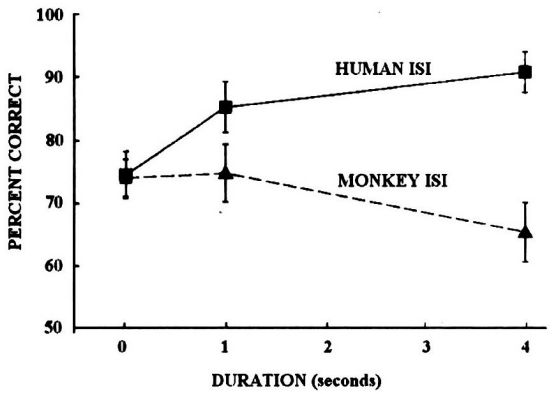

Fig. 3. Memory performance as a function of the interstimulus interval (ISI) for monkeys (triangles) and humans (squares) tested with lists of six pictures.

the monkeys showed no evidence of such an ISI effect (Cook, Wright, & Sands, 1991). The monkeys' ISI function was even slightly decreasing. Thus, the monkeys were not taking advantage of time between list items to rehearse them. From these results we can conclude that the primacy effects of the SPFs shown in Figure 2 were not a product of rehearsal. The monkeys' primacy effect does not always appear immediately like in the SPFs shown in Figure 2. The next section shows that it takes some time for the monkey's primacy effect to develop, which in itself points to processes different from rehearsal.

Acquisition of the Visual List-Memory Task and Delay Manipulations

The classic example of changes in the SPF with retention delay is the dissipation of the human recency effect (e.g., Glanzer & Cunitz, 1966; Postman & Phillips, 1965). Originally, these results were claimed to support the hypothesis that the recency effect was a result of limited capacity short-term store (Atkinson & Shiffrin, 1968; Waugh & Norman, 1965). We wanted to explore similar memory changes in animal memory and what such changes might say about how animal memory works.

Training animals in the list-memory task is not easily accomplished, we have discovered. In our current list-memory tasks, the color picture items are digitized and electronically presented on video monitors instead of with Carrousel projectors. A schematic of a four-item list memory task is shown in Figure 4. Subjects respond to the pictures by touching them instead of moving a lever, and responses are recorded with touch screens (see Wright, 1999b for details). Training begins with two pictures (one list item and the test item) plus a white rectangle like that shown in Figure 4, but with the three stimuli presented simultaneously as a *same/different* task. A touch to the lower picture indicated that the two pictures were *same,* and a touch to the white rectangle indicated that they were *different.* Correct responses were reinforced with either a banana pellet or small squirt (3-5 ml) of Tang orange drink. Incorrect responses were followed by a correction procedure (trial repetition with ITI until the correct response), but was employed primarily during the initial stage of *same/different* training. The correction procedure was rarely used after this initial training stage and only when a response bias adversely affected overall performance. Following learning this simultaneous *same/different* task, delays were introduced between the upper and lower items. Subjects in our studies had learned the *same/different* abstract concept which we consider a necessary prerequisite for accurate list memory performance.

The shortest delays of 0, 1, and 2 s were typically first introduced, with the longer delays of 10, 20, and 30 s gradually added as memory performance improved. Delays were tested in blocks of 32 trials with one shorter and one longer delay (quasirandomly) tested daily. Blocked-delay testing produced more accurate performance than variable delays until the subjects became very proficient in the task. Typically, the chamber light was turned off during the delay period so that the delay would be distinct from the intertrial interval (ITI), during which the houselight was on. Following accurate performance with single items at the different delays, the top item was then gradually expanded to a list of items.

Monkeys gradually improve their list memory performance over the better portion of a year of training. Figures 5 and 6 show typical acquisitions for two rhesus monkeys of the four-item visual list-memory task. The results for each acquisition stage were from 30 sessions during the early, intermediate, or late portions of a total of roughly 200 training sessions. Figure 5 shows that monkey BF early in training was most accurate with the last list items (i.e., recency effects) at 1-s, 10-s, and 20-s

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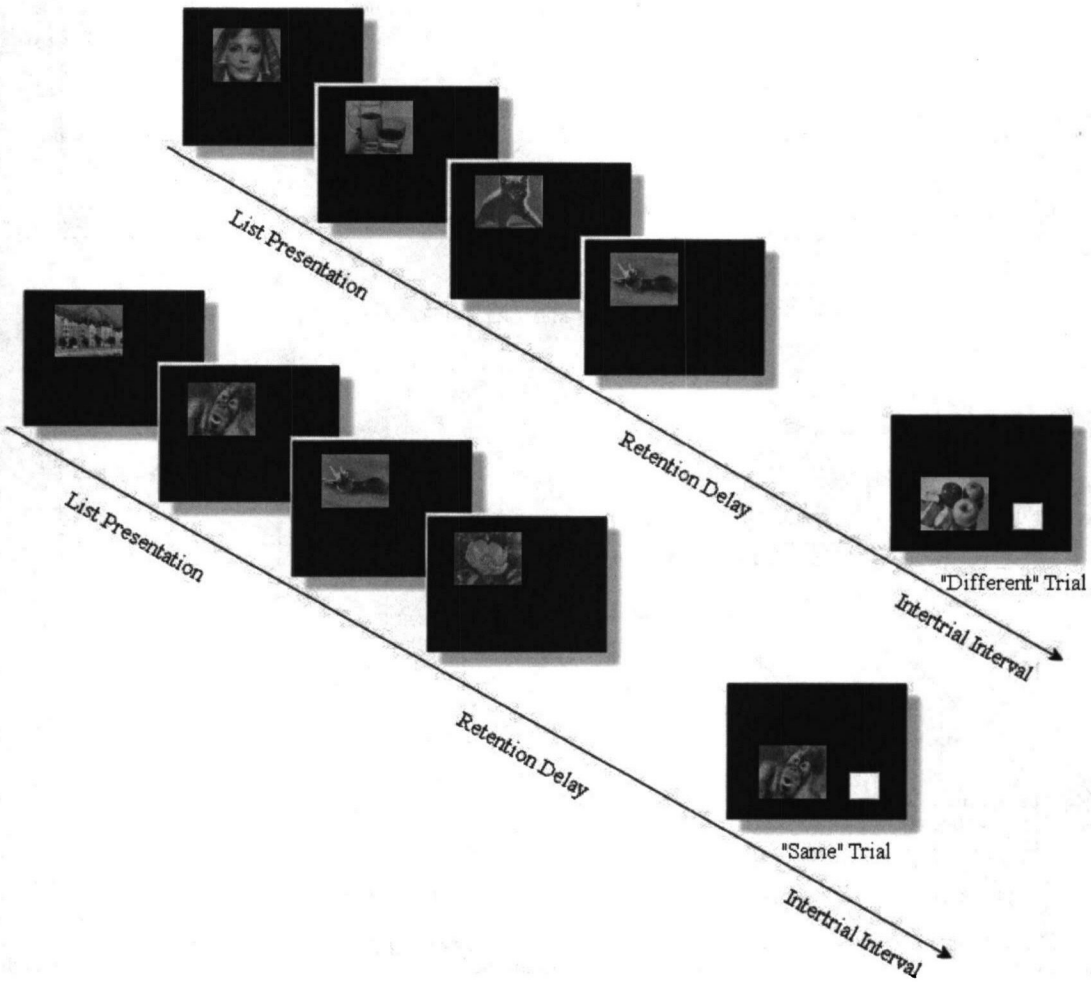

Fig. 4. Schematic examples of a *same* and a *different* trial showing the appearance of the displays during the four-item list presentation, retention delay, test presentation, and intertrial interval.

delays. As training progressed these recency effects gradually diminished at longer delays (e.g., 10 s, 20 s) and primacy effects for the first list items appeared. This development of list memory performance was likely the result of attending to all the list items as shown by overall performance (mean of *same* and *different* trial performance) improving from 66% correct for the early test, to 70% correct for the intermediate test, and to 77% for the later test. Similar trends are shown in Figure 6 for monkey GR. Monkey GR, however, does show a fairly strong primacy effect at the 30-s delay even early in training. Overall accuracy for the 30-s delay SPF was low (58% correct) but that was primarily due to this monkey's *different* bias (91% correct). As overall performance improved for this monkey (from 56% correct for the early test, to 69% correct for the intermediate test, and to 78% for the later test), there was a strengthening of the first-item primacy effect at the longest delays (100% correct for the 10-s delay, 83% correct for the 20-s delay, and 80% correct for the 30-s delay). These trends and improved accuracy are typical of those we have observed in the list memory task.

Comparing the Visual List Memory of Four Species

The mean results of two groups of rhesus monkeys trained and tested with different procedures are shown in the top panel of

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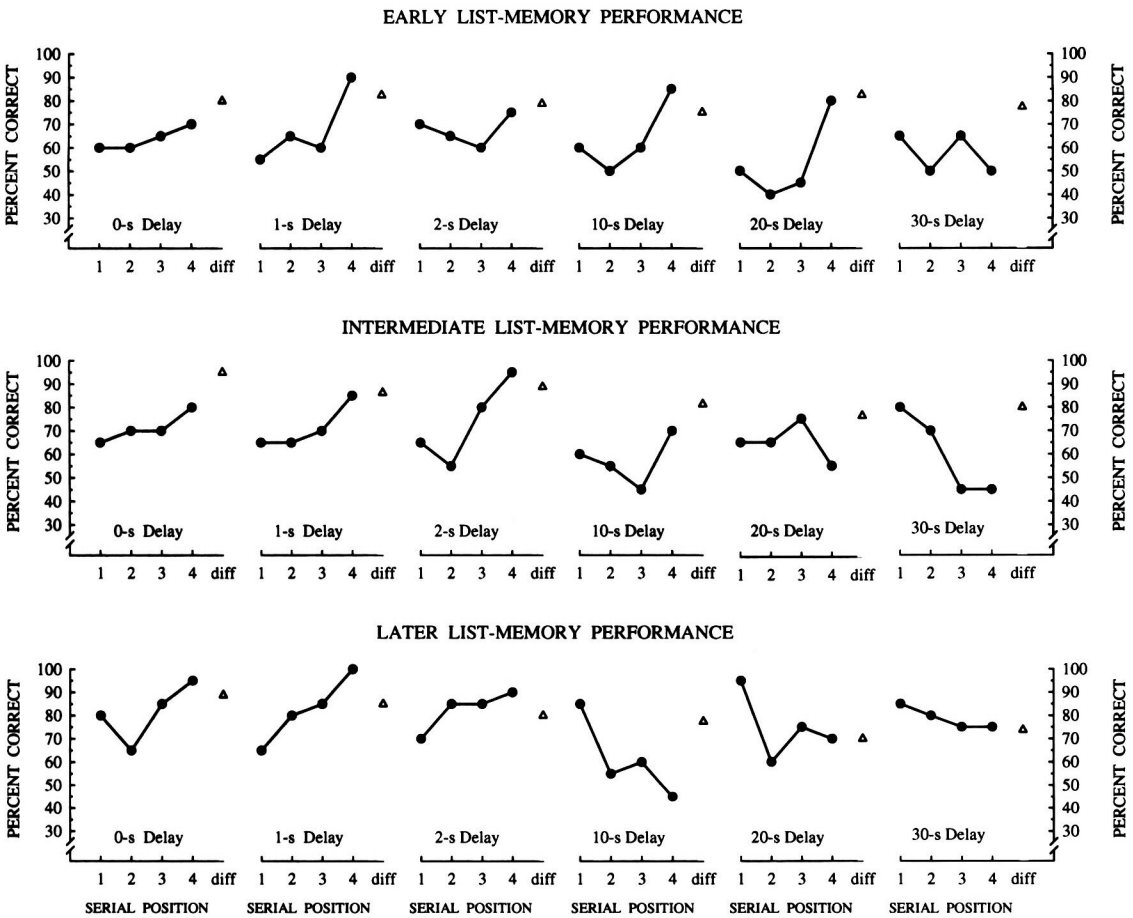

Fig. 5. Development of stable SPFs for monkey BF during an early (top panel), intermediate (middle panel), and later (bottom panel) stage of training. Open triangles (diff) show performance on trials (*different*) where the test item did not match any of the list items.

Figure 7. One group (squares) was trained like the monkey shown in Figure 2 with Carousel projectors and lever. Another group (circles) was trained with digitized pictures, video monitors, and touch screens like monkeys BF and GR. The item presentation times, inter-item intervals, and retention intervals were the same for these two groups. The results from these two groups were similar. When the test appeared immediately following the list (0-s delay) there were strong recency effects and no primacy effects. Primacy effects appeared after short delays of 1 s or 2 s and remained strong with further increases in delay. Recency effects dissipated after a 10-s delay. These similar results by different groups of rhesus monkeys tested with different methods of picture presentations (35-mm slides versus digitized pictures on a video monitor) and different responses (lever versus touch screen), show the reproducibility of the SPFs for visual memory.

We also tested visual list memory of capuchin monkeys and pigeons in similar four-item list memory tasks. Capuchins and pigeons were trained similar to the rhesus shown above but required somewhat more training than rhesus as the list length and delays were expanded. Although capuchins (*Cebus apella*) are not the standard human model like rhesus, they are new-world monkeys and therefore have a different evolutionary history from rhesus which are old-world monkeys. When this research began, capuchins were thought to be among the most intelligent nonhuman primate species (Chevalier-Skolnikoff, 1989; Parker &

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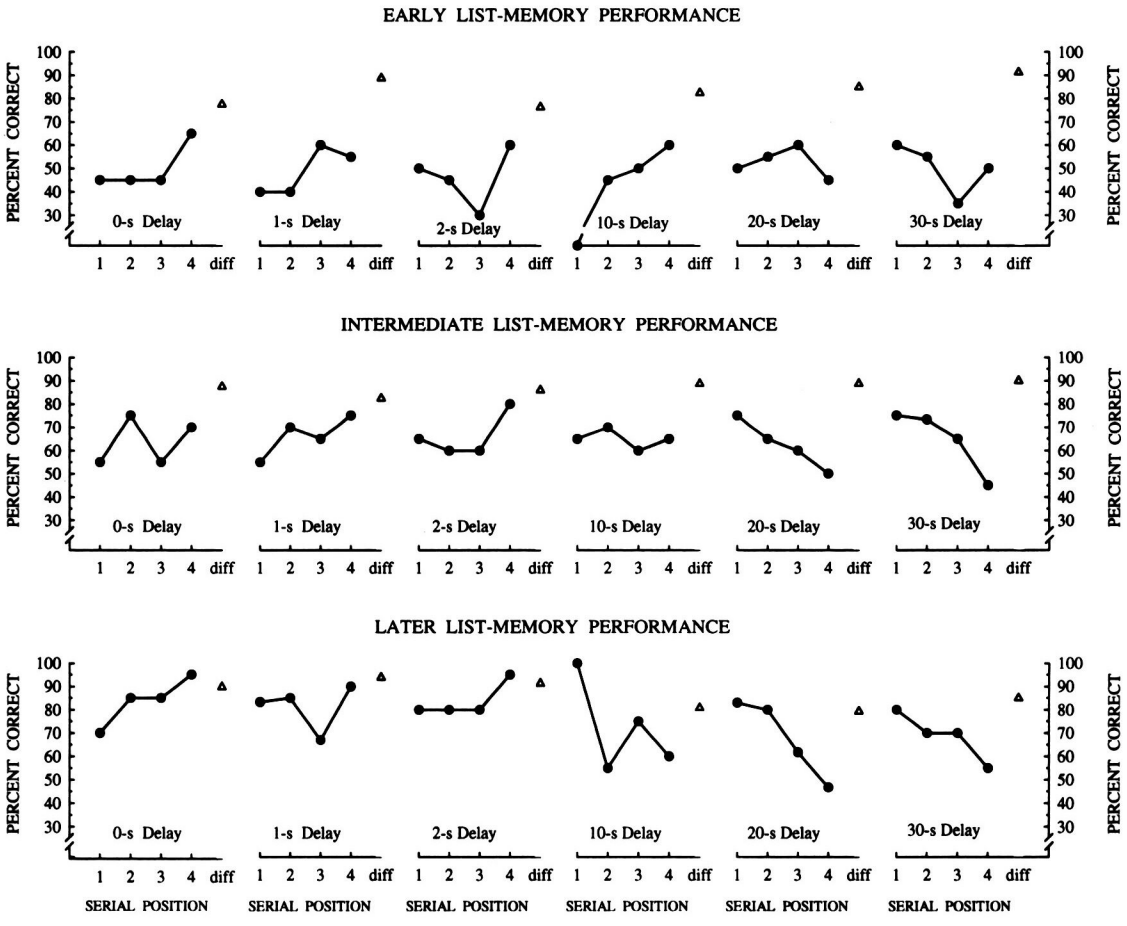

Fig. 6. Development of stable SPFs for monkey GR during an early (top panel), intermediate (middle panel), and later (bottom panel) stage of training. Open triangles (diff) show performance on trials (*different*) where the test item did not match any of the list items.

Gibson, 1977). Pigeons (*Columba livia)* provide an avian comparison and have a vastly different evolutionary history and neural architecture from either monkey species.

Capuchin monkeys were tested with digitized pictures, video monitors, touch screens, and orange-drink reinforcers like the procedure schematic shown in Figure 4 (Wright, 1999b). Pigeons were tested in a custom-built pigeon chamber with the stimuli projected via Carousel projectors. Pigeons viewed the stimuli through a transparent window at one end of the chamber. They pecked side keys (red/green circles) located on either side of the window to indicate whether the test item was or was not in the list (Santiago & Wright, 1984).

We also tested humans with four-item lists. To avoid ceiling effects, we tested the humans with lists of four kaleidoscope pictures. Kaleidoscope pictures are attractive and distinctive, but since humans do not verbally code or rehearse them, language likely played a diminished role in their performance and provided a more direct comparison to the animals.

The SPFs for the different species are shown in Figure 7. The form of the SPF changed systematically with retention interval. At the shortest delay, the SPFs were upward sloping, showing virtually pure recency performance. As the delay was increased, primacy effects appeared, giving the function its characteristic U-shape. At the longest delays, the recency

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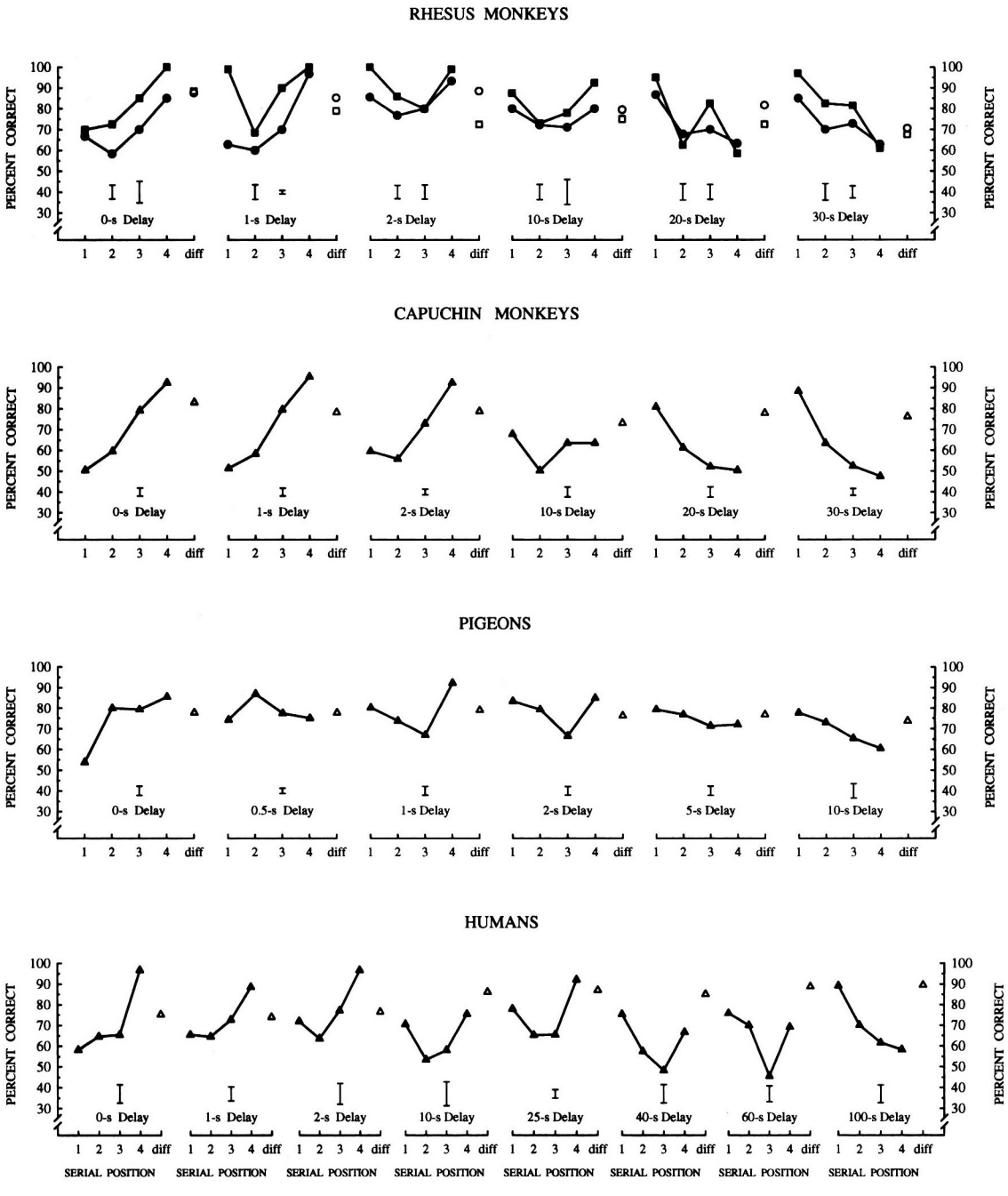

Fig. 7. Mean SPFs for rhesus monkeys, capuchin monkeys, pigeons, and humans on four-item visual list-memory tests. One group of rhesus monkeys (squares, right error bars) was trained and tested with Carousel projectors and a lever response, and another rhesus group (circles, left error bars) was trained with digitized pictures, video monitors, and touch screens. Serial position 1 was the first list item. Open triangles (diff) show performance on trials (*different*) where the test item did not match any of the list items. Delay was the retention interval (in s) between the last list item (position 4) and the test. Error bars are the average standard error of the mean for the four serial positions of each function.

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effect dropped out, and the SPFs were downward sloping showing virtually pure primacy performance. The same qualitative pattern of changes in the SPFs occurred for all species, but there was a time course difference for different species. With regard to dissipation of the recency effect, it was complete within 30 s for monkeys, 10 s for pigeons, and 100 s for humans. The primacy effect began to appear in only one or two seconds after the end of the list presentation and was somewhat more rapid for rhesus monkeys and pigeons than it was for capuchin monkeys and humans. These different time courses for the different species are quantitative differences. The similar pattern of SPF changes for the different species, in contrast, is a qualitative similarity showing similar visual memory processing for these species.

Taken together, these systematic SPF changes constrain possible explanations for these observed changes in visual memory with retention delay. Consider the consistent result that memory for the first list item improves with retention delay. This finding is opposite to the typical notion that memory is supposed to decay with time. Moreover, this finding shows that poor first-item list memory at short delays cannot be due to encoding failure because at long delays, memory for these items suddenly appears. This result severely constrains some of the possible explanations of these memory changes over time.

What the Delay Changes Might Reveal about How Memory Works

The increase in primacy memory with retention delay is difficult for most memory theories to handle. Memory according to most theories is supposed to decay with time—a so-called law of disuse—otherwise known as forgetting. Such forgetting is often portrayed as a passive decay process, like the recency effect. The waning of the recency effect, like all forgetting, is a hallmark of most memory theories. Indeed, the passive decay of the recency effect in human memory contributed to the rising popularity of the study of short-term memory and the so-called cognitive revolution (Peterson & Peterson, 1959). The time course of the recency effect was supposed to be a measure of the short-term memory buffer. But even this (theoretical) concept has not survived the test of time. Recency effects have been shown for greatly extended time scales (where decay should have long since run its course) such as recall of United States Presidents (Roediger & Crowder, 1976), and rugby scores by pub patrons (Baddeley & Hitch, 1977). Indeed, these were some of the results that prompted Robert Crowder to question the whole endeavor of studying short-term memory (Crowder, 1993). Notwithstanding any lingering debate over whether dissipation of the recency effect is brought about by passive decay, the same cannot be said about the primacy effect. After all, the primacy effect increases with delay. Such increases with delay point to inhibitory processes that change with delay. Indeed, it appears that changes in the recency effect also may be accounted for by inhibitory processes.

Two Time-Dependent Inhibitory Processes

These visual memory results are perhaps best conceptualized by two interacting memory processes such as inhibition or interference that change with time. Two different types of inhibition, or interference, have a long history of study in experimental psychology. The traditional term has been *interference*. Nevertheless, recent developments (including some reviewed in the next section) indicate that interactions among items within lists are different from interference which is used to describe confusions over whether some item was present in the current trial or some previous trial (Gorfein & Macleod, 2007). Therefore the term *inhibition* will be used for interactions among items of a memory list.

The dynamically changing SPFs of Figure 7 appear to be the result of a shifting balance of proactive inhibition (memory for recent items inhibited by past items) and retroactive inhibition (memory for past items inhibited by recent items) over time. According to this scheme, an initial strong recency effect, like that shown in Figure 7, would mean that the last list items retroactively inhibited the subject's memory of the first items. Dissipation of retroactive inhibition would allow the primacy effect to appear, producing a U-shaped SPF. As retroactive inhibition continued to dissipate, the primacy effect would strengthen and produce proactive inhibition that would diminish memory for the recency items. Similar changing patterns of serial position effects with delay have been shown by other research-

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ers of human memory (e.g., Knoedler, Hellwig, & Neath, 1999; Korsnes, 1995; Korsnes & Gilinsky, 1993; Neath, 1993a, b; Neath & Knoedler, 1994; Wheeler, 1995). We are not the first to propose that inhibition processes might account for the shape of the SPF (Foucault, 1928; Hull, 1935). We are, however, the first to test inhibition, and these tests were conducted on the rhesus monkey's auditory memory.

TESTING THE RHESUS MONKEY'S AUDITORY MEMORY

The results of Figure 7, showing a similar changing pattern of SPFs for different species, raised the issue as to whether all memory works this same way. We wondered, for example, whether auditory memory would show similar SPF changes. We thought, for example, that auditory recency possibly might be somewhat extended (e.g., modality effect), but that basically similar SPF changes would be found (i.e., qualitative similarity). We were determined to use rhesus monkeys in these tests, but no one at that time had been able to adequately train rhesus monkeys in auditory memory tasks.

Undaunted, we tried training rhesus monkeys in an analog of our visual list-memory task. We thought that by using a large number of auditory training stimuli we could eliminate proactive interference (as we did in the visual list memory task) and the monkeys then would learn. Sounds were played by upper and lower pairs of speakers, and the monkeys moved a lever to indicate *same* or *different* as other monkeys had in the first-described visual *same/different* task. Unfortunately, there was no learning, not even after two years of training. We even tried combining the visual and auditory tasks and then fading the visual part of the task. Still, there was no auditory learning. It was not until we conjoined response location with the sources of the auditory stimuli that our monkeys began to learn the auditory memory task (cf. Harrison, Iversen, & Pratt, 1977).

In our successful procedure, there were three speakers (see Figure 8). Monkeys were required to touch copper screens in front of the speakers enclosed in wood cabinets. Initially, the monkeys touched the center speaker, which produced a sample sound,

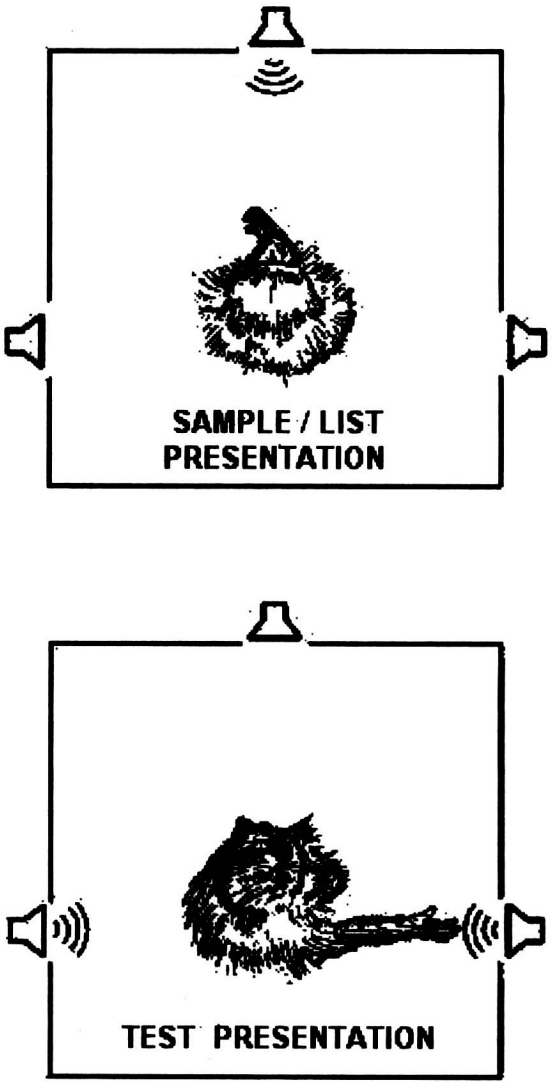

Fig. 8. Schematic of the auditory testing apparatus. Upper panel: Top view of a monkey with an individual sound or a list of four sounds presented from a center speaker. Lower panel: Top view of the monkey touching a right-side speaker with a test sound presented simultaneously from both side speakers following the list presentation. A touch to the right-side speaker was correct when the test matched one of the list sounds, otherwise a left touch was correct.

and then they touched one of two side speakers. If the test sound matched the sample, then the correct response was to touch the right-side speaker (*same* response), otherwise the correct response was to touch the left-side speaker (*different* response). The test sound was always the same sound played at

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the same time from both side speakers. Sounds were selected from a 520-item set of natural/environmental sounds (e.g., wood chopping, pig grunts, bongo drums, water gurgling, cash-register bell, toy train whistle, girls giggling, coins dropping, ducks quacking, xylophone, yodeling, geese, lion roar, electric drill, squeaky door, sneezing, frogs, Big-Ben chimes, glass breaking, horse whinny, etc.; see Wright, 1998a, b; Wright, 1999a; Wright & Rivera, 1997, for other sounds).

This auditory memory procedure has features that proved useful in the initial training of the auditory memory task. Early in training, the test sound came only from the correct side speaker. The monkeys readily learned to go the side from where the sound was coming. Sound from the incorrect side speaker was gradually increased, and by titrating the intensity, we observed that the monkeys quite readily learned (several weeks) the task. The monkeys showed abstract-concept learning with novel sounds (Wright, Shyan, & Jitsumori, 1990), a feat that some others had considered beyond the cognitive capabilities of monkeys (e.g., D'Amato, Salmon, & Colombo, 1985).

Testing the Rhesus' Auditory Memory for Musical Passages

The monkeys' accurate auditory *same/different* concept learning provided an opportunity to test the monkey's music perception for lists of notes, that is, musical passages (Wright, Rivera, Hulse, Shyan, & Neiworth, 2000). In these experiments the delay was 1 s. Typically, there were 24 training trials with natural/environmental sounds, like those previously described, and four to six music trials in daily sessions. The musical passages were six notes. Some music trials were training trials (identical matches or mismatches in both note sequence and frequency range). Others were test trials where either the note sequence ("tune") or frequency did not match. (On these test trials, either response was reinforced with a probability equivalent to the subject's accuracy during its previous session.) These and other musical passages were matched in terms of the number of different instruments that played them (10) and the number of different octaves in which they were played (4).

The test trials of greatest interest were those that were transposed (0.5 – 2.0) octaves (up or down). An initial test from randomly selected notes yielded no significant generalization (52% correct responses) for one-octave transpositions as shown in Figure 9. However, when we tested 12 childhood songs (e.g., "Camptown Races," "Happy Birthday", "London Bridge," "Oh Susanna," "Old MacDonald," "Yankee Doodle", etc.), one-octave generalization was 79%, and even improved to 85% generalization for two-octave transpositions. Other tests showed little or no transfer for half-octave transpositions (0.5, 1.5 octaves) or pitch transpositions (the same note repeated six times and transposed by 0.5, 1.0, 1.5, or 2.0 octaves) and added to the overall picture of the monkey's music perception. Half-octave transpositions tend to alter the human's perception of a tune, as apparently they also do for monkeys. Pitch transpositions produced decreasing transfer as a function of transposition distance. This last finding makes perfect sense from the standpoint of music perception because a single note has no melody. It is the melody that is critical in octave generalization and music perception. Figure 9 shows the critical role of melody by using a tonality algorithm (Maximum Key Profile Correlation, Takeuchi, 1994) to generate tonal and atonal passages. The two monkeys' mean octave generalization was 81% for tonal and 48% for atonal tunes.

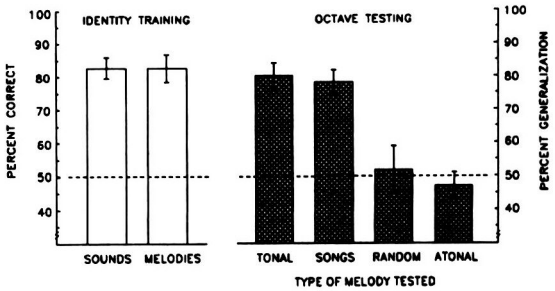

Fig. 9. Mean performance of two rhesus monkeys on training with natural/environmental sounds or six-note musical passages (left panel) and testing with one-octave transposed musical passages (right panel). Transpositions were conducted with childhood songs, random/synthetic musical passages, and tonal or atonal passages synthesized using a tonality algorithm. Error bars represent ±1 standard error of the mean.

Taken together, these results show that the critical variable for octave generalization is a high degree of tonality (shared by childhood songs and tonal passages). These results make

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perfect sense from the standpoint of memory. Tonal musical passages have signature melodies that are well remembered (e.g., sometimes so much so that we cannot get the tune "out of our heads"). Tonal passages can be characterized graphically as distance measures on a circle of fifths (Bartlett, 1993). For example, a melody in the key of C major forms a point of departure and arrival. The note G, a perfect fifth, will be judged musically stable, likely to occur, and highly anticipated. Atonal passages, in contrast, will contain unlikely and unanticipated note transitions (e.g., the note $F^{\#}$ which is 6 semitones or half an octave removed from the note C) and therefore will not have memorable melodies. Without a memorable melody there will be little if anything to be generalized when the passage is transposed an octave or two. These experiments show that rhesus monkeys perceive music in much the same way that people do. Moreover, if music perception depends upon so-called critical cognitive modules, then rhesus monkeys apparently share them as well.

Testing the Rhesus' Auditory Memory for Lists of Sounds

The auditory list-memory procedure was similar to the auditory *same/different* procedure except that a list of four natural/environmental sounds (selected quasi-randomly from the set of 520 natural/environmental sounds) was played from the center speaker and the retention delay was manipulated (Wright, 1998a). In the first test, sounds were presented for 2 s with 1 s between sounds. The retention delays (0, 1, 10, or 20 s) were tested in blocks. As in the auditory *same/different* task, a single test sound followed the delay. The test was played simultaneously from both side speakers. If it matched one of the list sounds, then a touch to the right-side speaker produced 3.5 cc of Tang orange drink, and if it did not match any list sounds, then a touch to the left-side speaker produced a similar outcome. Incorrect choices or aborts (not responding within a 2- to 6-s response interval) were not rewarded and were followed by 30-s timeouts. Intertrial intervals were 12 s. One 32-trial block was tested daily at one of the four delays with the order of delay testing varying quasirandomly for 40 consecutive sessions.

The results from this first auditory-memory test are shown in the top panel of Figure 10. We were so astonished by these results that we doubled the number of trials that we usually conduct. The auditory SPFs were opposite and changed in opposite ways compared to the visual SPFs (cf. Figure 7). Auditory memory showed an initial strong primacy effect and no recency effect. As the delay was increased, the recency effect appeared and the primacy effect began to dissipate. At long delays, there was a strong recency effect and no primacy effect.

These auditory list-memory results were followed by a series of five additional experiments to convince us (and an Editor) of their reliability. We reduced the ISI from 1 s to 0.5 s, conducted the experiment (middle panel), and then changed the ISI back to 1 s and reconducted that experiment again (bottom panel). Figure 10 shows that the auditory SPFs became somewhat more robust as training and testing continued (top vs. bottom panels in Figure 10), possibly similar to the acquisition of the visual list-memory task shown in Figures 5 and 6. The next test (results not shown) ruled out familiarity/novelty as being responsible for the auditory SPFs. Other tests ruled out center-speaker touches and other cues (e.g., flashing LED light and food-pellet delivery for center-speaker touches) or a fixed time between trials as being instrumental in producing the primacy effect as some theorists had hypothesized (Gaffan, 1983; Gaffan, 1992). The testing delays were expanded to include all the same delays used to test visual memory. The results for the individual monkeys are shown in Figure 11. Both monkeys showed similar SPFs and changes with delay.

Figure 12 shows the opposite pattern of changes for the mean auditory and visual memory SPFs. Immediately following the list presentation (i.e., 0-s delay), the auditory SPF shows a pure primacy effect. As the retention interval was increased, the primacy effect begins to wane and a recency effect appears. Eventually, for example at 20-s and 30-s retention delays, the SPFs become pure recency functions with worst performance to the first item and best performance to the last list item. There was more than a 45% change in accuracy for both the primacy and recency items over the retention delays tested. This finding of poor recognition memory for the last list item on the immediate test shows the powerful effects of proactive inhibition from

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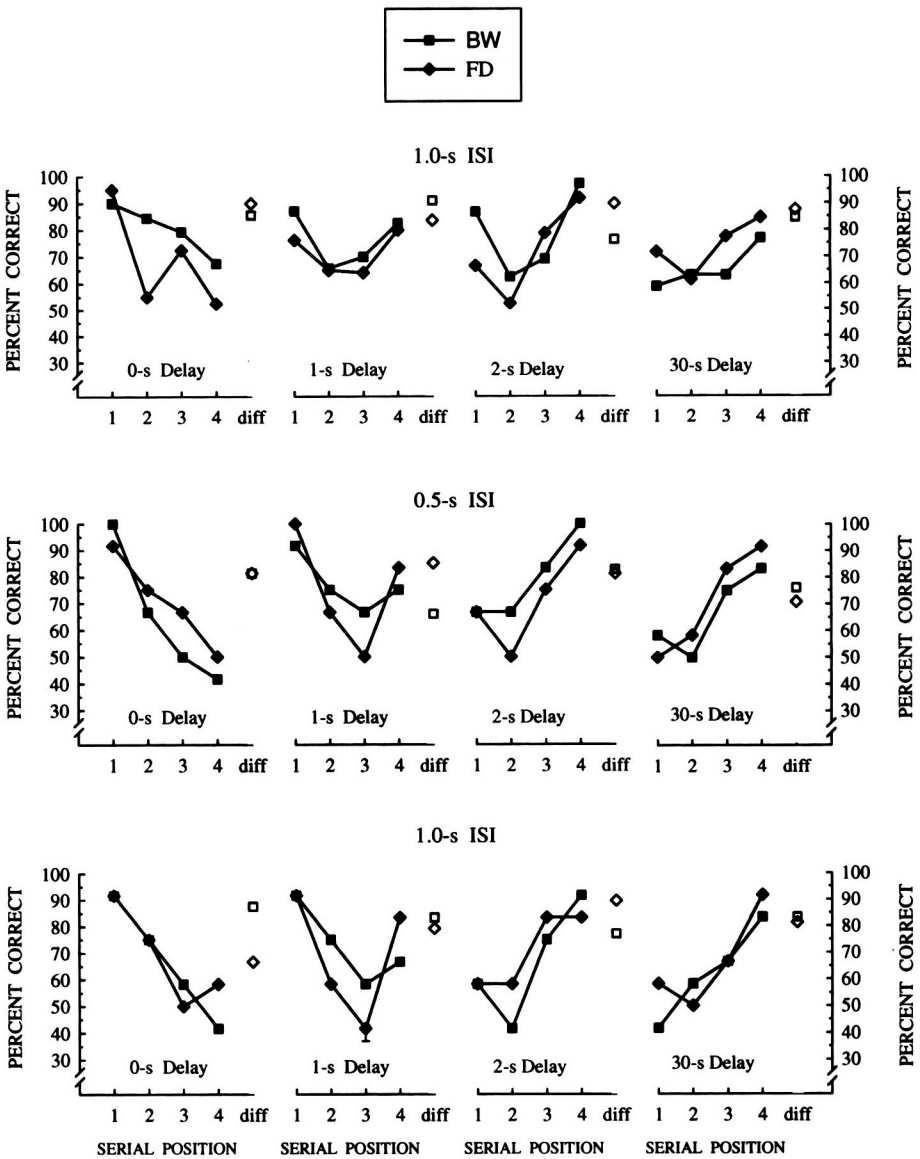

Fig. 10. Three tests of four-item auditory list memory with 2 rhesus monkeys BW and FD. Upper panels show their first test results. Middle panels show their second test results with the interstimulus interval changed from 1 s to 0.5 s. Lower panels show their third test results with the interstimulus interval changed back to 1 s. Open symbols (diff) show performance on *different* trials where the test item did not match any list item. Delay is the retention interval between the last list item (position 4) and the test.

the first list items on the last list items. These auditory SPFs and their changes with retention delay have been replicated in more than 13 independent experiments (Wright, 1998a, 1999a, 2002; Wright & Roediger, 2003).

The auditory list memory of one monkey was retested 4 years later and these results are shown in Figure 13 (Wright, 2002). The procedure was similar except that there were 16 rather than 32 trials tested daily. The sounds were from the same auditory pool (but different random selections) with retention delays tested in blocks as was done previously. Each retention delay was tested for 20 blocks for a total of 120 daily test sessions. The results from these two tests were very similar with

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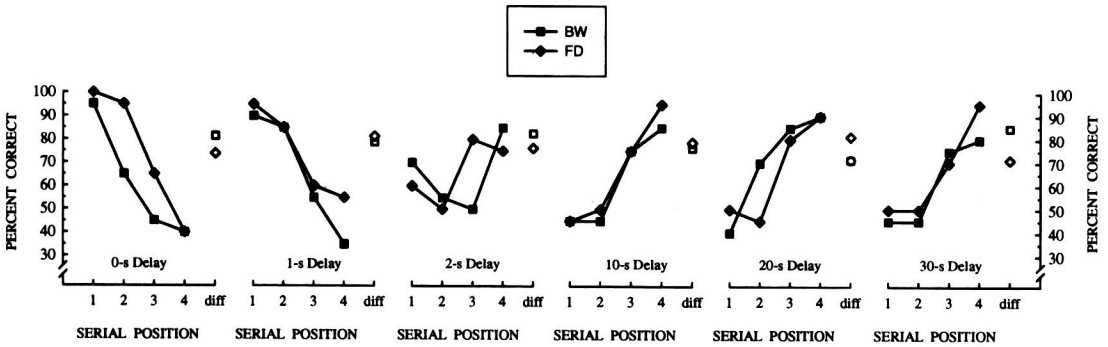

Fig. 11. Auditory SPFs for 2 monkeys at six delays between the last list item and the test. Open symbols (diff) are *different*-trial performance where the test item did not match any list item.

regard to level of performance, SPF shapes, and changes with retention interval. The primacy effect at the shortest delay (0 s) shows a very high level of accuracy of 95% correct or better. Performance for the last list item at 0-s delay is below chance, 45% correct or less. Similar results are shown for the 1-s retention interval delay. At 2 s, the serial position function changes markedly. At this retention delay, a prominent recency effect emerges. Along with this emergence of the recency effect, the primacy effect falls to 70% correct. With further increases in delay, the recency effect strengthens to better than 80% correct and the primacy effect falls further to the 40–45% correct range. Thus, the SPFs and their changes with retention interval have remained very stable over the 4 years between the two tests.

Another experiment with this monkey showed that random vs. blocked delays produced nearly identical results (Wright, 2002).

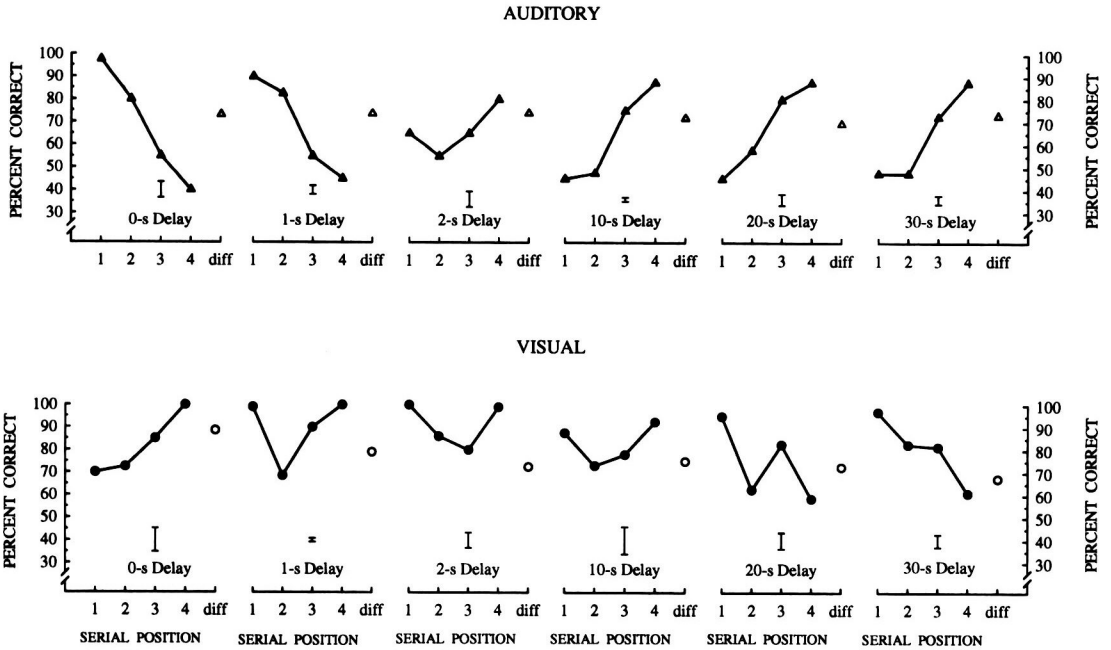

Fig. 12. Mean rhesus monkey SPFs for four-item auditory memory lists (upper panels) compared to the rhesus monkey SPFs for visual four-item lists (bottom panels). The open symbols (diff) show performance on *different* trials. Delay is the retention interval, and error bars are the SEM average for the fourserial positions at each delay.

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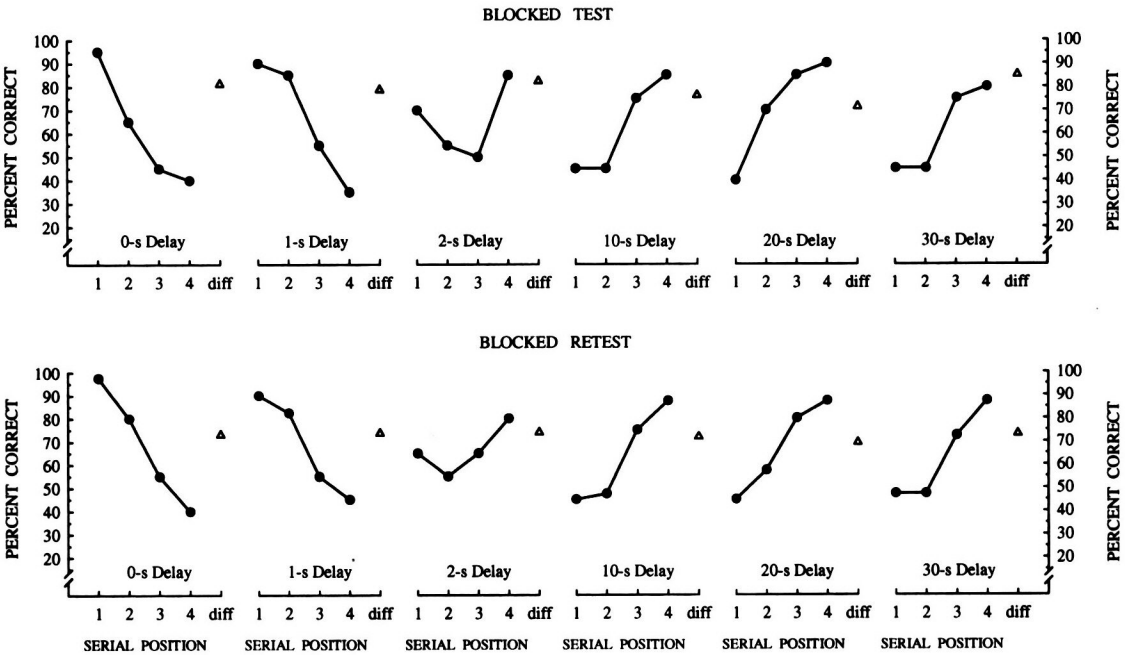

Fig. 13. Auditory SPFs for a rhesus monkey with retention delays tested in blocks of trials. Lower panels show a retest of this monkey under the same test conditions 4 years later. Triangles (diff) show performance on *different* trials where the test item did not match any list item.

Random delays make the time between tests unpredictable so that list separations with long delays (e.g., 30 s) are not uniformly greater than with short delays (e.g., 1 s). Random delays also prevent any possibility of delay-specific memory strategies because the subject cannot predict the delay when being presented with the list of items to remember. Each serial position at each delay was tested 12 times. Figure 14 shows nearly identical results for random (filled symbols) versus blocked (open symbols) tests and demonstrate that both blocked and random delays produce valid and stable auditory memory results.

Significance of Opposite Shaped SPFs

I have frequently been asked what possible benefit could there be for opposite-shaped SPFs. Since I have given this issue some thought and have not wanted to plead total ignorance, I offer a possibility grounded on principles of associative learning. Associative learning studies with pigeons have shown that visual stimuli are more easily associated with

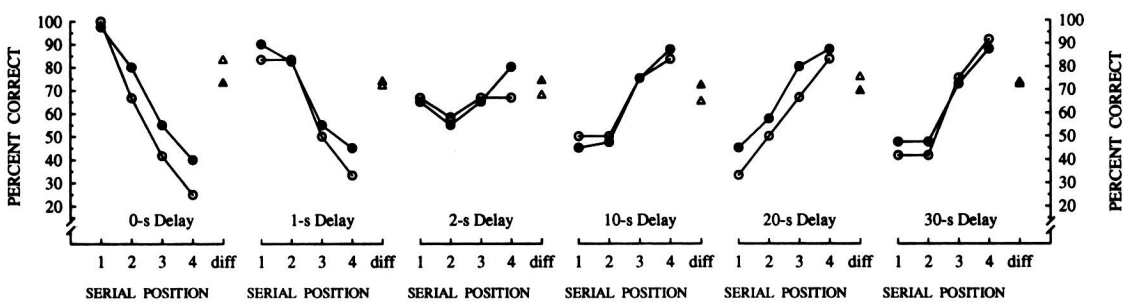

Fig. 14. Auditory SPFs from a test with random retention delays (filled symbols) superimposed on this monkey's blocked-delay functions that were tested at a similar time (Figure 13 lower functions, shown by open symbols). Triangles (diff) show performance on *different* trials where the test item did not match any list item.

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food, and auditory stimuli are more easily associated with danger (e.g., Shapiro, Jacobs, & LoLordo, 1980). If such learning differences were generally shared across species, then one could entertain the following scenario for visual memory. If, in one case, an animal were to have good luck foraging for food in one patch (e.g., under a pine tree), then it would need to remember (visual recency, short delay) to go to a similar patch (e.g., another pine tree) to continue feeding. If, on the other hand, an animal fed in a diurnally depleting patch (e.g., berries that ripen in the morning), then it would need to remember (visual primacy, long delay) to go to this same patch first thing the next morning. Although the time scales in this hypothetical example differ from those of the laboratory studies, human studies have shown that time scales expand proportionally to the intervals between visual events (e.g., Brown, Neath, & Chater, 2007; Glenberg et al., 1983) and auditory events, with perhaps an added effect of the absolute auditory delay (Cowan, Saults, & Nugent, 1997).

Now consider auditory memory for dangerous situations. If, on the one hand, an animal hears a danger sound, then it would need to remember (auditory primacy, short delay) the starting point of the sound to determine whether the sound (e.g., made by a predator) is coming toward it or going away from it. If, on the other hand, an animal hears a danger sound that stops, then it would need to remember (auditory recency, long delay) where the sound had stopped in order to avoid the spot where a predator might be hiding. From this scenario it seems possible that the rhesus monkey's auditory and visual memory systems may have adaptively specialized due to the different type of selective pressure. On the other hand, the selection pressures early in the monkey's evolution may have been different than they are today, and the evolved memory systems (i.e., cognitive modules) may have adapted effectively (i.e., exaptations) in dealing with food getting and danger avoidance.

Testing the Rhesus' Auditory Memory for Inhibition Among Items of a List

The change from a primacy-dominated function to a recency-dominated function for monkey auditory memory is rapid, and the ability to recognize the fourth (last) item in the list dramatically increases in just a few seconds. Such recovery of information strongly implicates the presence of inhibition coupled with spontaneous recovery or release from inhibition. If such inhibitory processes were instrumental, then proactive inhibition on memory (e.g., memory retrieval) of the last list items would have to be strong initially. As the delay increased, proactive inhibition would have to dissipate allowing memory for the last items to recover. Recovering memories of the last list items would then have to retroactively inhibit memory retrieval of the first list items as the delay was extended further.

In this section, a summary of five experiments is presented dealing with parameters that would be expected to manipulate inhibition if inhibition were instrumental in determining the shape of these auditory SPFs (Wright, 1999a; Wright & Roediger, 2003). In one experiment, the list items were separated by increasing the ISI from 1 s to 2.5 s. The rationale was that by separating further the list items, they should interact less with one another. The increased separation greatly reduced the short-delay primacy effects from 92% to 63% as shown in Figure 15. This decrease in primacy was accompanied by an increase in recency (i.e., from 50% to 79% at the 0-s delay). In another experiment (not shown), adding 2 s to just the middle ISI of the list produced similar results. We also made the memory items more difficult to remember by repeating the items in different memory lists during each of the daily sessions (as opposed to having the items being trial-unique during daily sessions). The reason that a high frequency of presentation makes the items more difficult to remember is discussed in a later section on repeated-item interference. Progressively higher frequencies of presentation were tested by reducing the training set from 144 items (trial-unique items each session) to 8 items (each repeated 64 times a session). Figure 16 shows that higher frequencies of presentation lower overall accuracy because the items are more difficult to remember. By making the items more difficult to remember the strong primacy effect at short delays was eliminated. Most important for the purposes of this experiment was that with the elimination of the primacy effect at short delays, the recency effect improved. Despite the fact that

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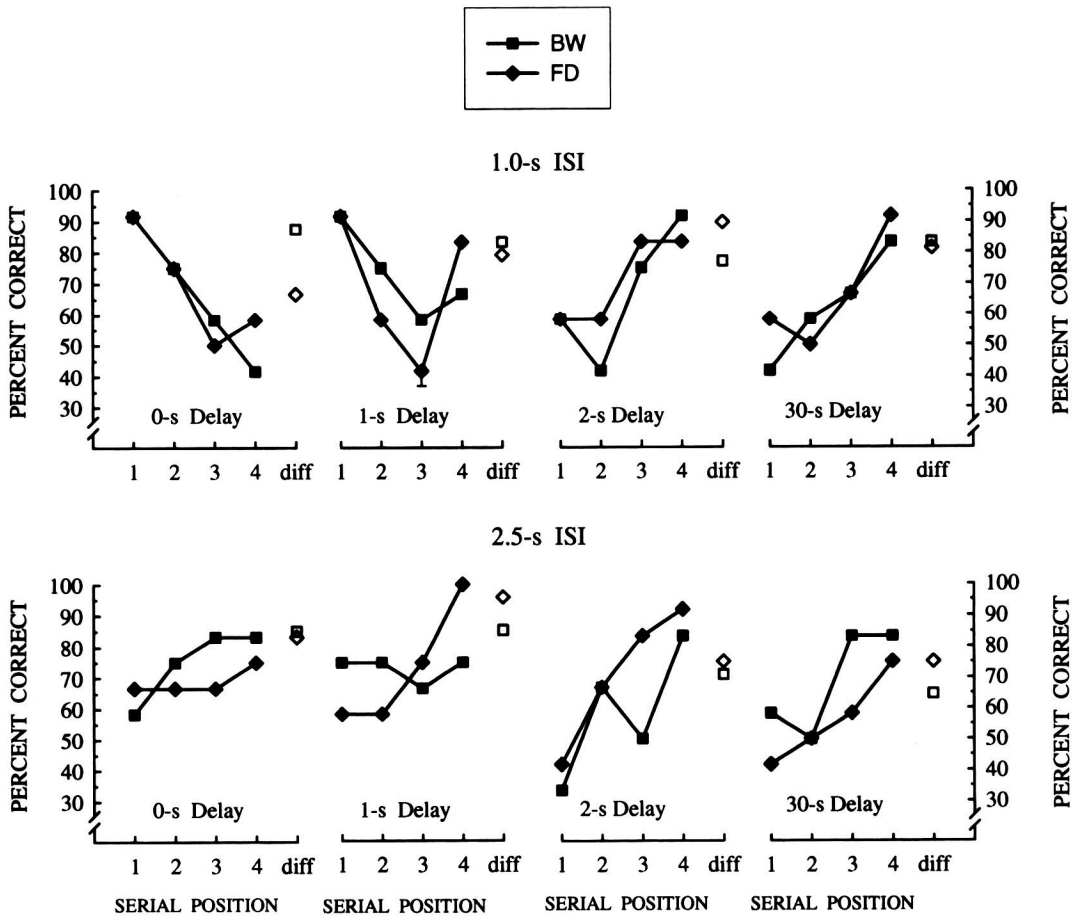

Fig. 15. Auditory SPFs for 2 monkeys tested with a 2.5-s interstimulus interval (bottom panels) with the retest of the 1.0-s ISI functions from Figure 10 shown at the top of this figure for comparison.

the items were more difficult to remember, the recency effect showed a remarkable 37% accuracy improvement (46% to 83%).

Taking the lead from the considerable accuracy changes resulting from high-frequency presentations of the previous experiment, these same items were employed either as the first two items of a list or as the last two items (the MIXTURE conditions in Figure 17). By making the first two list items difficult to remember, we tested whether the initial strong proactive inhibition from the first two list items would be reduced. The easy-to-remember items were from a 144-item set. In another condition, the last two list items were the difficult-to-remember items. There were also two other conditions tested and these were extreme conditions from the previous experiment retested in this experiment as controls: LO PI, where all four items were easy to remember (the 144-item set), and HI PI, where all four items were difficult to remember (the eight-item set). All four conditions were randomly tested in sessions with delays of either 0 s or 20 s. Individual results are shown in Figure 17. When the first two items were from the difficult-to-remember eight-item set (third row, left panel), memory for these items decreased as expected. The important result was that memory of the last two list items increased, and this was a large absolute memory increase relative to the easy condition (LO PI; top row, left panel) with the same memory items tested in both conditions. This shows that by making the first two items difficult to remember, these items generate little or no proactive (retrieval) inhibition on memory for the last two items. Similarly, when

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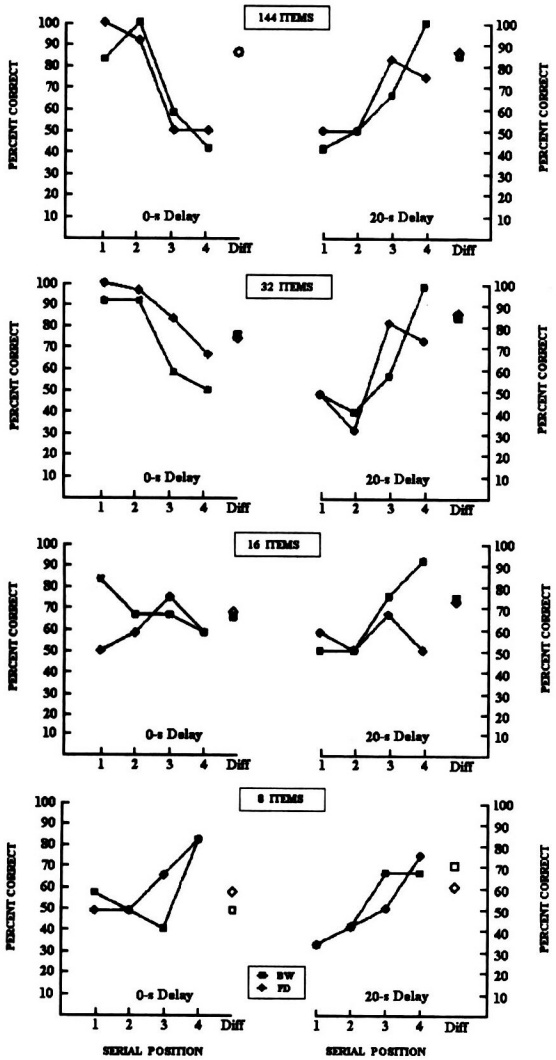

Fig. 16. Auditory SPFs for 2 monkeys tested at two retention delays (0 s, left column, and 20 s, right column) with a progressively decreasing training set size (144 to 8) and increasing proactive interference from list-item repetitions (0 to 16) on each 32-trial session.

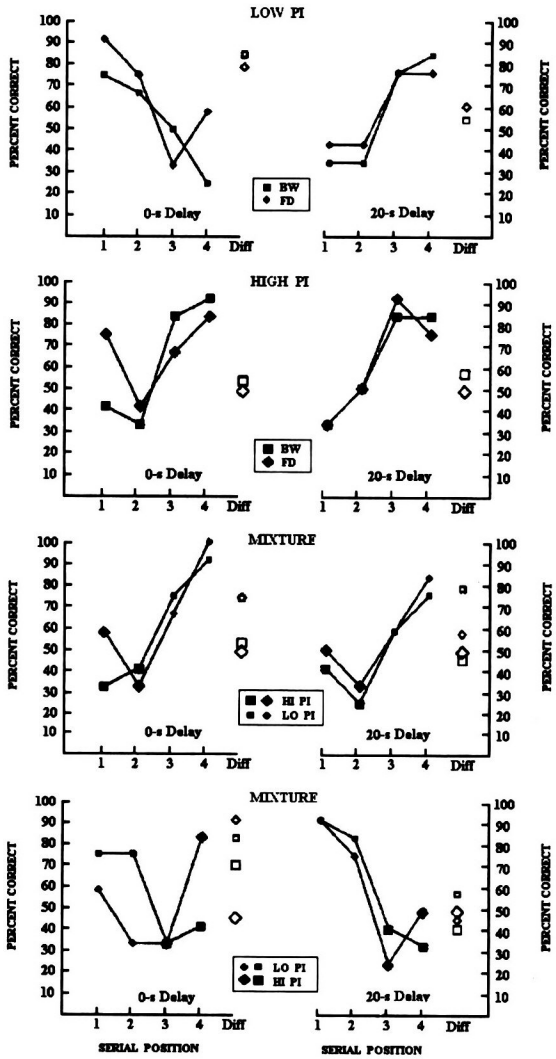

Fig. 17. Auditory SPFs for 2 rhesus monkeys tested at 0-s (left column) and 20-s (right column) delays with four types of lists: Low interference (LO-PI) with items from a 144-item pool, high interference (HI-PI) with items from an eight-item pool, mixtures where either the first two list items were high interference or the last two list items were high interference. Open symbols (diff) show performance on *different* trials where the test item did not match any list item.

the last two items were made difficult to remember and memory was tested at the 20-s delay (fourth row, right panel), memory of the first two list items increased relative to the easier (LO PI; top row, right panel) condition. This shows the powerful retroactive inhibitory effects of the last items on the subjects' retrieval of memory for the first list items at these comparatively long retention delays. These effects cannot be due to encoding differences because the subjects have no way of knowing whether the last two items will be easy or difficult to remember. Thus, retroactive inhibition is the major mechanism controlling memory performance at long retention delays, like proactive inhibition at short retention delays.

In a final experiment on inhibitory effects, the rationale was that if proactive inhibition

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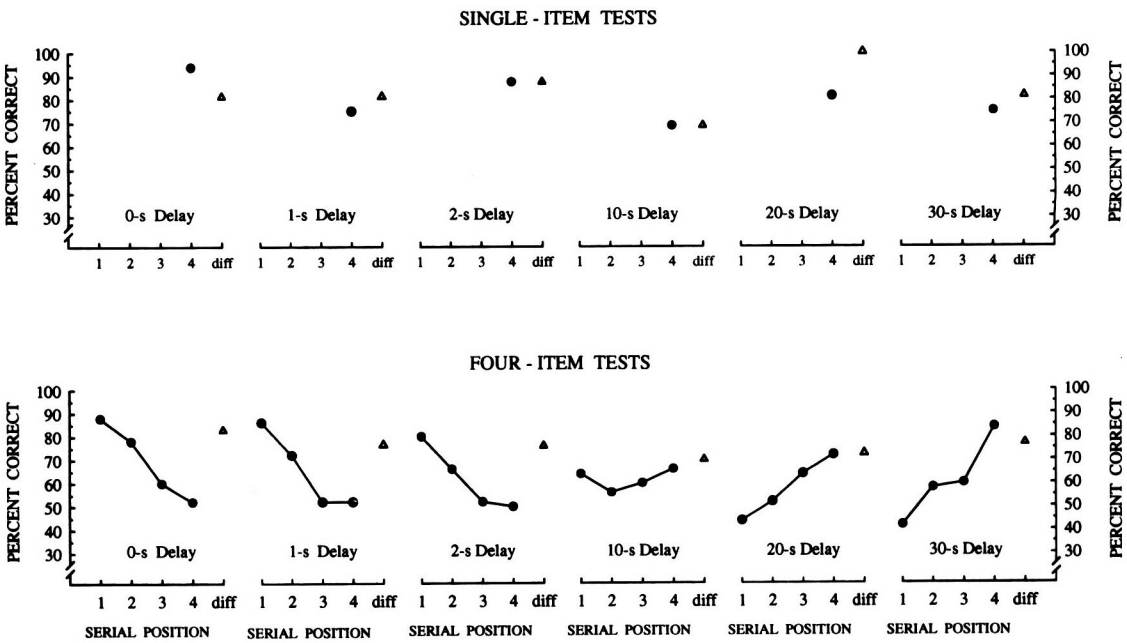

Fig. 18. Upper panel: Memory performance of a rhesus monkey for single sounds. Lower panel: Memory performance for lists of four sounds. Triangles show performance on trials (diff) where the test item did not match any list sound. Delay is the retention delay in seconds.

was responsible for the lack of an initial recency effect, then by eliminating the first three items, last-item performance should rise to the maximum performance level despite other aspects of the test (e.g., immediate test) remaining unchanged (Wright & Roediger, 2003). Single-item memory and four-item list memory were tested on alternating sessions, and these results are shown in Figure 18. The four-item list memory results were similar to those shown previously for this monkey (Figures 13 and 14). Memory performance with the fourth (last) list item is compared to overall single-item memory performance (mean of *same* and *different* performance) in the left panel of Figure 19. Single-item performance was much more accurate than fourth-item performance over the shortest (0 s, 1 s, 2 s) retention delays. This large performance difference demonstrates the considerable effect of proactive inhibition from the first three items on the monkey's fourth-item memory at these short delays. As delay increased, fourth-item performance increased becoming equivalent to single-item performance as one would expect if earlier proactive inhibition had dissipated. The right-hand panel of Figure 19 shows that retroactive inhibition adversely affected the monkey's memory for the first list items at long delays. First item performance was initially at a performance level equivalent to single-item performance showing that there was no retroactive inhibition at short delays. As the retention delay was increased, retroactive inhibition increased to the point that the monkeys could not remember the first list items. Thus, retroactive inhibition at long delays is the second process (along with

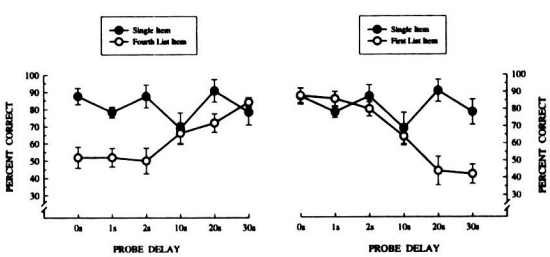

Fig. 19. Left panel: Single-item performance compared to last (fourth) list item performance. Right panel: Single-item performance compared to the first list item performance. Probe delays were the delays from Figure 18. Error bars are standard errors of the mean.

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proactive inhibition) explaining these shapes of the monkey's auditory SPFs.

Alternative Accounts of the Serial Position Effects and Changes of the Function

Among the possible explanations for why the auditory SPFs might be different from the visual SPFs is that a lack of consolidation might account for the absence of a recency effect at short retention delays. Another is that the immediate test following the auditory list might function like a suffix-effect item (decreased recency effect from a prompt like "Okay" to human participants to begin recall). But the experiment where the first three list items were eliminated rules out these possible explanations (Wright & Roediger, 2003). In that experiment, the test followed the (last) list item just like it did when there were four list items, the only difference was that the first three list items were eliminated. Any effect due to lack of consolidation or to a suffix effect ought to be just as prominent on that sole list item as it was on the fourth item of the four-item list. But performance accuracy with only the one list item was improved greatly relative to the last item performance of the four-item list. Other attempts to explain the auditory SPFs by different encoding strategies for different delays due to blocked-delay testing, or by list-initiation responses causing the primacy effects, were ruled out by testing random delays and by eliminating list-initiation responses (Wright, 1998a, b; Wright, 2002).

In terms of general accounts of the serial position function, the venerable dual-store modal model claimed that the recency effect was a short-term memory (STM) component and decayed with time, whereas the primacy effect was a long-term memory component resulting from rehearsal (e.g., Atkinson & Shiffrin, 1968; Gillund & Shiffrin, 1984; Haarmann & Usher, 2001). Neither proposal makes any sense from the standpoint of the visual SPFs in Figure 7 or the rhesus monkey's auditory SPFs. More recent SPF proposals show that many of these same SPF changes could be the result of temporal distinctiveness (e.g., Brown et al., 2007; Murdock, 1960; Neath, 1993a) or feature distinctiveness (e.g., Nairne, 1990). Distinctiveness could, in principle, account for many of these SPF changes with retention delay. Increasing the separation between successive list items (i.e., longer ISIs), for example, could be argued to increase the distinctiveness of those separated items (e.g., Brown et al.). Likewise, eliminating the first three auditory list items could be argued to increase temporal distinctiveness of the last list item. Indeed, it is difficult to imagine how memory performance could improve without distinctiveness improving too. But I think the real issue is whether a change in inhibition produces a change in distinctiveness, or the other way around. Perhaps most damaging to distinctiveness being the root cause is that there is no obvious reason why distinctiveness should change from being most prominent at visual recency to most prominent at visual primacy, or from auditory primacy to auditory recency as the retention delay is increased. As Bjork (2001) has emphasized, temporal distinctiveness cannot account for absolute memory recovery (i.e., increase in percentage accuracy) shown by the visual primacy effect with retention delay. By contrast, two inhibitory processes (proactive and retroactive) with different time courses do make this case, particularly in light of converging evidence implicating inhibition.

Inhibition as the Root Cause of the Monkey's Changing Auditory SPFs

The results from our experiments suggest that retrieval failure results from inhibition among items of a list. Release from proactive inhibition caused an absolute increase in auditory recency performance as the retention delay was lengthened. This finding was counterintuitive because memory is commonly thought to decay with time. Inhibition is different from decay. Inhibition is a process which, on the one hand, can decrease memory performance and, on the other hand, can, when inhibition is released, increase memory performance. In the experiment where the list-item separation was increased (from 1 s to 2.5 s), inhibition from the first list items at short retention delays was reduced and produced as much as 44% improved recency. In the experiment where the first three items were removed, recency performance improved by 36%. In the experiment where frequently repeated eight items were tested, recency performance improved 37% at the 0-s delay. In the experiment where the first two list items were from the highly repeated eight-item set,

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recency performance improved 54% at the 0-s delay. As the auditory recency effect increases with retention delay, the resulting (retroactive) inhibition causes retrieval failure of the first items of the list. This effect was also shown in the previously mentioned experiment where the last two list items were from the highly repeated eight-item set and primacy performance improved by 54% at the 20-s delay (an improvement equal to the recency improvement at 0-s delay). These very substantial memory changes converge on the conclusion that inhibition is the root cause of the dynamically changing SPFs of the rhesus' auditory memory.

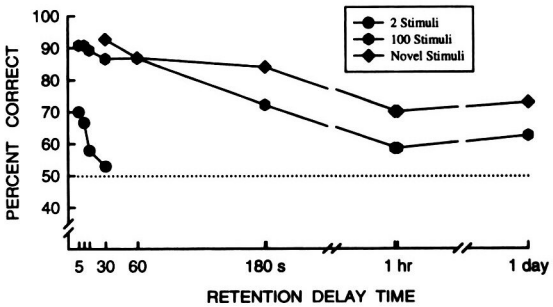

Fig. 20. Three delay functions from the Overman & Doty (1980) experiment. Results for the two-stimulus condition are from Figure 1 (but rescaled here). In the 100-stimulus condition, repetitions of the stimuli were separated by many trials. The novel stimuli had not been seen previously by the monkeys. The dotted line represents chance performance.

INTERFERENCE FROM THE MEMORY ITEMS OF PREVIOUS LISTS

Most of the list-memory experiments presented here used relatively large numbers of stimuli for training and testing, with the result that repeating items within sessions were minimized. Notable exceptions were the experiments with the difficult-to-remember eight auditory items. Item repetitions tend to interfere with the subject's being able to make accurate decisions as to whether a test item was or was not in the list being tested. When items are repeated—a necessary condition with small item sets—subjects become confused about whether some test item was in the list being tested or in the list of some previous trial. Such confusions are not the result of failures to remember. Indeed, memory is too good. Subjects may have experienced a test item so often—possibly in the previous trial—that the subject is confused as to which trial in which it saw the item. This repeated-item interference builds as the session progresses for humans (e.g., Keppel & Underwood, 1962; Underwood, 1957) and for animals (e.g., Olton, 1978; Roberts & Grant, 1976).

This repeated-item interference is different from the previously discussed inhibitory effects that occur among list items. Repeating items creates confusion and decision conflict. Therefore, the term *interference* is used to distinguish this effect from *inhibition* among list items (i.e., retrieval inhibition). Additional evidence that these two effects are different is that inhibition occurs among distinctly different auditory items and begins to dissipate in about 2 s in the auditory memory task. Repeated-item interference, by contrast, occurs across similar items, is most prominent with identical items, and persists for minutes, hours, and even days (e.g., Jitsumori, Wright, & Cook, 1988). Moreover, inhibitory effects among list items appear to be fairly automatic processes akin to what Jacoby (1998) refers to as "automatic" memory processes or Watkins (1989) refers to as "unwillful" processes. By contrast, the effect of repeating items and the resulting interference is less automatic and may be modifiable by how the subject performs memory tasks (e.g., familiarity vs. recollection).

The effects of repeated-item interference have been seen earlier with the single-item memory functions shown in Figure 1 because all these studies used very small training set sizes (e.g., two items). One of those studies shown in Figure 1 clearly demonstrated the effect of repeated-item interference. In the Overman and Doty (1980) study, the training set size was increased from 2 to 100 slide-picture items and the monkeys' memory performance greatly improved as shown in Figure 20. Even after a 24-hr delay, memory performance was better than it had been after only 30 s when tested with the two-item memory set. Also shown in Figure 20 are the results of an experiment where each trial contained novel items, and memory performance improved even further. These comparisons show how devastating interference can be to memory. One can conclude that the memory functions of Figure 1 say more about interference of memory and interference increasing with delay than anything about how

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long something can be remembered by these species (see also Gallistel, 1990, p. 545, but see Sargisson & White, 2003; White, Parkinson, Brown, & Wixted, 2004; White & Wixted, 1999, for mathematical descriptions of memory functions similar to those of Figure 1).

Repeated-Item Interference in List-Memory Experiments

Detrimental effects of repetitions on single-item memory are, if anything, greater on list-memory performance because there are more items to remember each trial. We tested the interfering effects of item repetitions on the monkey shown in Figure 2 in a three-item list memory task with a small set of six items (travel slides) that were repeated frequently. A control condition (low interference) used 211 items. Daily sessions alternated between these two conditions. Other procedures were similar to those previously discussed for this monkey (1-s presentations, 1-s ISIs, 1-s retention delays, and right/left lever movements to indicate list-item match or no match). List-memory performance was a very accurate 93% correct overall in the low-interference condition (mean of the three serial positions for *same* = 91.5%, and for *different* = 94.5%), but was only 70% correct overall in the high-interference condition (mean of the three serial positions for *same* = 60.8%, and *different* = 79.3%) as shown in Figure 21. Thus, repeating a small set of six items lowers three-item list-memory performance by a considerable 23 percent and explains why other investigators likely had trouble obtaining accurate list-memory performance from their monkeys (Devine & Jones, 1975; Eddy, 1973; Gaffan, 1977).

Discovering the locus of this repeated-item interference effect was of particular interest to us. Consider a monkey performing the three-item list-memory task of Figure 21. After just a few trials, all six items will have been seen, and by the middle of the session all items will have been seen many times. When this subject is then presented with a test on a *different* trial (where the test does not match any item from the current trial), the subject will be confused as to whether this item was in the current list or some previous list. Confusion and conflict will be greater the more recently the interfering item was seen (e.g., the preceding trial).

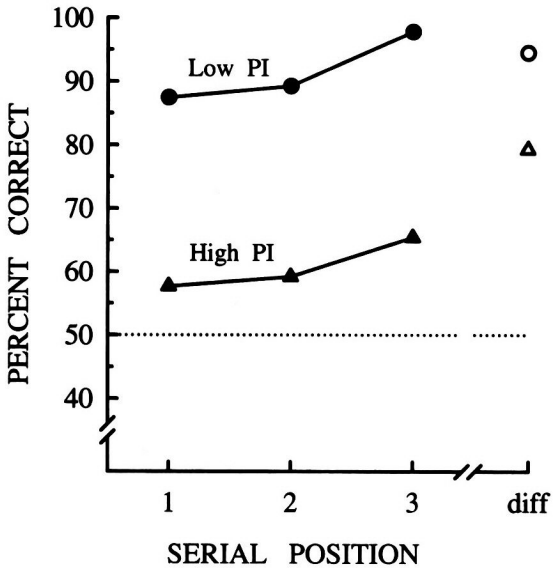

Fig. 21. Repeated-item interference on a rhesus monkey's three-item list memory results with memory items selected from a six-item set (High PI) compared to a low interference condition with items selected from a 211-item set (Low PI). Serial position 1 was the first list item. Open symbols (diff) show performance on trials (*different*) where the test item did not match any list item. The dotted line represents chance performance.

We conducted a test of this locus of the proactive interference effect by embedding potentially interfering items within previous lists and testing them later on *different* trials (Wright, Urcuioli, & Sands, 1986). Figure 22

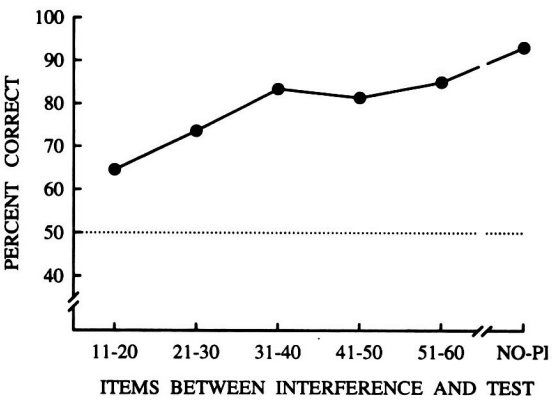

Fig. 22. Interference tests of a rhesus monkey's 10-item list memory performance as a function of the number of items occurring between a test item on a *different* trial and its previous presentation. The NO-PI condition is a no-interference condition. The dotted line represents chance performance.

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shows that when an interfering item was in the immediately preceding list, performance was comparatively poor—64% correct. This is nearly a 30% drop in accuracy from baseline (NO-PI) performance. As the trial separation increased, performance improved showing the graded effect of this interference. At the largest separation that was tested (six lists or as many as 60 items), performance had improved to 83% correct, but was still 10% less than the 93% correct baseline (i.e., trial-unique) performance. This last result shows the far-reaching effects of this repeated-item interference. The role that repeated-item interference might play in determining how memory works will be discussed in the next section.

Familiarity, Identity, and Episodic Memory

Related to the far-reaching effects of proactive interference shown in Figure 22 is the issue of whether this monkey was making "true" identity judgments or simply responding on the basis of familiarity. The issue of familiarity was brought into sharpest focus for researchers working in animal learning and cognition by David Premack more than 25 years ago when he questioned whether or not pigeons had the cognitive capability to learn abstract concepts (Premack, 1978, 1983). This same issue of familiarity is now at the forefront of memory research with animals and humans. Regarding single-item memory performance (i.e., delayed *same/different* performance) Premack (1983) said: "The animal simply reacts to whether or not it has experienced the item before. Old/new or familiar/unfamiliar would be better tags for this case than same/different" (p. 354). Implicit in Premack's claim was that familiarity —recognition of an item without regard to whether it was on the current trial—might differ from other processes that would explicitly limit such judgments to items of the current trial. This issue of familiarity comes up in virtually all abstract-concept learning and memory experiments, particularly with animals. One cannot avoid the issue of familiarity by using delayed nonmatching to sample (DNMS) instead of DMTS as some researchers have contended (e.g., Gaffan & Weiskrantz, 1980; Mishkin & Delacour, 1975). In DNMS, the subject could use familiarity to identify the matching stimulus (the incorrect choice) and then switch and choose the other (unfamiliar) stimulus. Likewise, using simultaneous instead of delayed same/different (S/D) does not rule out the use of familiarity as Premack (1983) would have us believe. In simultaneous S/D, subjects could first look at one stimulus (as they often do) and then look at the other stimulus, thus transforming the simultaneous S/D task into a delayed S/D task.

Familiarity has been a hot topic of research in human memory for at least as long as it has been in animal memory (e.g., Atkinson & Juola, 1974; Mandler, 1980). Indeed, human memory researchers have led the way by specifying the alternatives to familiarity (e.g., explicit memory, recollection, controlled memory, and episodic memory), unlike counterparts in animal memory. It is one thing to say that animals of some study may be *just* responding on the basis of familiarity (e.g., Mackintosh, 2000; Premack, 1983), but it is quite a different matter to specify what they *should* be doing and how to test those possibilities. Before considering alternatives to familiarity that animals might employ, it may be worthwhile considering how human-memory researchers dissociate familiarity from other types of memory. In one procedure, participants are either instructed to identify items experienced in a particular context (e.g., seen as an anagram) or in any context (i.e., items read, heard, or seen as an anagram). Measures of recollection and familiarity are computed from algebraic equations representing these different memory tests (e.g., Jacoby, 1991, 1998; Yonelinas, 2002). In another procedure, participants are asked if they actually did *remember* (episodic memory) an item, or just *know* (familiarity) that some item had been experienced (e.g., Gardiner & Richardson-Klavehn, 2000; Tulving, 1972, 1985, 2002). It is unclear (at least to me) how either of these procedures might be adapted to testing animal memory.

Nevertheless, recent experiments demonstrate that some animals have memory considerably more precise than simple familiarity memory. The most well known are the scrub-jay caching experiments by Clayton and her colleagues (e.g., Clayton, Bussey, & Dickinson, 2003; Clayton & Dickinson, 1998). Scrub jays are trained to cache perishable wax worms and non-perishable peanuts in separate and distinctive halves of two distinctive sand-filled ice-

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cube trays (2 X 7 arrays). When the jays recovered their caches after a short delay of only 4 hr, they recovered the more desirable wax worms first. After much longer delays of 124 hr, jays first recovered peanuts if they had previously learned that wax worms deteriorated in this amount of time. Reversal of their earlier preference for wax worms means that they remembered "what" (peanuts vs. wax worms), "when" (4 vs. 124 hr), and "where" (which tray side) the foods were stored. Other experiments by Clayton and colleagues showed that manipulating experience for the time of worm deterioration or degrading worm preference (satiation and taste aversion) between caching and recovery altered recovery preferences. These latter experiments demonstrated that the birds' recollective/declarative memory was flexible and *not* in Tulving's words "...a hard-wired connection between fixed behaviour prompted by fixed knowledge..." (2002, p. 283).

Other experiments with rats have shown that this mammal species, like scrub jays, can remember things that cannot be explained by familiarity alone. Rats were trained in a radial-arm maze task where they obtained a preferred chocolate reinforcement in one location and nonpreferred pellets in some of the other locations (Babb & Crystal, 2006). The chocolate reinforcer was replenished at its original location only on long-delay tests, not on short-delay tests. Pellets were never replenished at their original locations during training but were found during both short- and long-delay tests at the original unbaited locations. At long-delay tests, but not short-delay tests, the rats first visited the location of the preferred chocolate, demonstrating that this memory was unique for the particular reinforcer, chocolate, at a particular place, and at a particular time. Other tests by these researchers showed that the rat's memory was flexible by depreciating chocolate, and that time of day was not instrumental in revisiting the chocolate location. In yet other experiments, rats were trained to discriminate sand-filled cups containing distinctive odors (Fortin, Wright, & Eichenbaum, 2004). The receiver-operating-characteristic curves (ROCs) had asymmetrical and curvilinear components like those of humans (Yonelinas, 1997), suggesting the existence of both recollection and familiarity. Following selective damage to the hippocampus, the rats' ROC curves became symmetrically curvilinear suggesting that the hippocampus specifically mediates recollection (for a review, see Eichenbaum & Fortin, 2005).

Despite these clever advances in animal memory research, there is little danger that these animals will anytime soon be anointed as having episodic memory. Critics can always claim (as some do) that such behavior might be mediated by simple S–R associative conditioning, "They may just 'know' what kind of food is where, and what state it is in—fresh or rotten—without knowing how or why they know it" (Tulving, 2001, p.1512).

A New Approach to Testing Familiarity and Recollection—Interference

Notwithstanding the clever experiments previously mentioned, there is little evidence as to the particular memory processes that animals use in most laboratory memory tasks. One could point to pigeons learning a continuous-matching task (e.g., respond if it's old, not if it's new) which has aspects akin to familiarity (Macphail & Reilly, 1989; Todd & Mackintosh, 1990). But this demonstration does not prove that familiarity was the basis of this performance or what subjects might be doing in S/D and list-memory tasks. What are needed are experiments that manipulate the effectiveness of familiarity in performing a particular task and an objective assessment of how subjects use familiarity.

We have begun exploring the possibility of using repeated-item interference and the interference function (e.g., Figure 22) to determine the degree to which subjects rely on familiarity and under what conditions they might employ other memory processes. (See also Cowan, Johnson, & Saults, 2005, for the use of repeated-item interference to determine human working-memory capacity.) Consider an interference function like the one shown in Figure 22 where a subject was trained with trial-unique items. If such a subject was completely indiscriminate with regard to how far back in time he would accept a stimulus as a match (i.e., any degree of familiarity would suffice), then the PI function should be relatively flat (e.g., 64% correct, like the interference on the immediately preceding trial in Figure 22) extending back across many previous trials, possibly even the whole session.

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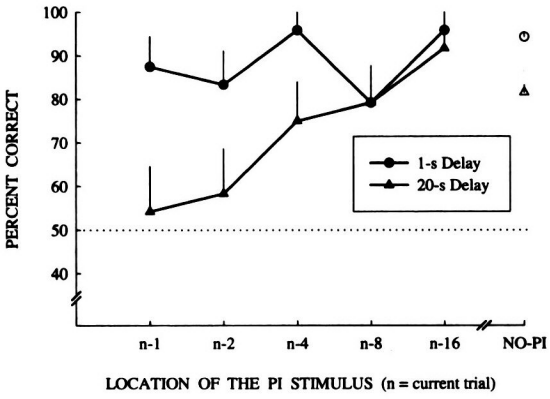

Fig. 23. Interference tests of a rhesus monkey's single-item memory performance under separate tests with 1-s or 20-s retention delays as a function of the number of items occurring between a test item on a *different* trial and its previous presentation. The NO-PI condition shows training-trial performance with no interference. The dotted line represents chance performance.

Such a case could conceivably occur, because the rule "have I seen this item before in this session" would work just as well as "was this test item in the list of the current trial." One can think of such a situation as a case of a very lax familiarity criterion. Of course, a history of having to make memory judgments under repeated-item interference (e.g. Figure 21) would likely moderate any lax familiarity criterion and produce a more graded performance, perhaps not unlike that seen in Figure 22 (see Wright, 2006, Figure 9.5, for predicted effects on the PI function with familiarity-criterion changes.) If the interference function shown in Figure 22 was due to a moderate familiarity criterion, then consider what effect making the task more difficult would likely have on the interference function. In the case of longer retention intervals, overall accuracy might suffer because when a test item matched a list item, the list item would be less familiar because it would be further in the past. Subjects could, in theory, reduce their familiarity criterion. But this would only be effective if repetitions (and interference) were minimal. Figure 23 shows the effect of varying the delay on a monkey's PI function. Tests with interfering items placed in prior trials—one to four trials prior—interfered more at the 20-s delay than at the 1-s delay. This performance difference disappears at greater separations (8 and 16 trial separations) showing that memory is not just universally affected or that any interference disrupts memory performance.

Another way to make the task more difficult would be to increase item repetitions and interference in the memory task generally. In this case, subjects would tend to respond *same* more often because all the items would be more familiar. But unlike the delay case with unique items, no adjustment of a familiarity criterion would be able to restore former accuracy levels (in signal detection theory terms there would be a change in discriminability, e.g., d', and raising the familiarity criterion would help performance on *different* trials but would be offset by more errors on *same* trials).

But there is a way these subjects might be able to restore their former accuracy in this memory task: They could change their memory strategy from a familiarity memory process to a more recollective memory process, or some combination of the two (cf. Wixted, 2007; Wixted & Stretch, 2004). Such a change in how they performed the memory task would mean that they might be able to recollect what memory items were in the current trial as opposed to memory items of past trials. Said otherwise, this is a context conditioning issue, where the context in question is the current trial. In the parlance of episodic memory, there would be a premium on the "when" component.

This discussion of how repeated-item interference and delay should affect bias and discriminability provides us with a framework for testing these possible changes using the function for repeated-item PI (e.g., the functions of Figures 22 and 23). In some of our memory studies we have found that monkeys slowly improve their performance under high repeated-item interference. Such changes would be expected to occur slowly if subjects were learning a different and more recollective memory process. In one case, a highly trained monkey was switched from a low-interference condition (432-stimulus set) to a high-interference condition (eight-stimulus set). This monkey's long-delay (20 s and 30 s) performance gradually improved over 2000 training trials. In addition to these indications from our work, one can see similar indications in others' single-item memory research. In a study with one monkey, there was a gradual rise and

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improvement in the delay function over 30,000 DMTS training trials under high-interference (small stimulus set) conditions (D'Amato, 1973). In another study, pigeons' memory performance improved over 15,000 DMTS training trials under high-interference (small stimulus set) conditions (Grant, 1975, 1976; Roberts, 1998). Although somewhat indirect, this evidence indicates that animals probably have the ability to adopt strategies that combat the effects of repeated-item interference. If the type of memory processing that is employed can change according to the changing circumstances, then such changes should have some direct similarities to the controlled and recollection processes of the human dissociation procedures.

CONCLUSIONS AND DIRECTIONS

The four species tested in a four-item visual list-memory task showed similar dynamic changes in their primacy and recency effects as the retention delay was increased. This finding showed qualitative similarity in visual-memory processing across species with differing evolutionary histories and neural architectures. There were, however, quantitative differences across species in the time courses by which the primacy and recency effects changed with retention delay. These similarities and differences in memory were made apparent by using short memory lists and investigating list memory over a substantial range of the effective retention delay. If longer lists (e.g., 10 items) had been used, then the changes at short-retention delays (increasing primacy effect with delay) would have already occurred while the longer lists were still being presented, and the short-delay changes would have been missed. If only one retention delay had been tested, then the particular stage of the dynamic-evolving SPF would likely have been different for different species. In that case, the conclusion might have been that these different species had qualitatively different visual memory. One future direction of our work is to explore the possibility that the effects of proactive interference from previously seen items (on later *different*-trial test performance) might reveal the type of memory processing (familiarity, recollection) used by our animal subjects. Evidence for a change from familiarity to recollection would depend upon showing that these subjects can improve their memory performance in the face of high repeated-item interference.

Experiments on the rhesus monkey's auditory memory showed that inhibition among to-be-remembered items of individual lists was instrumental in determining the shape of the SPF, and changes in inhibition with retention delay (e.g., from proactive to retroactive inhibition) changed the shape of the auditory SPF. Five experiments showed that at short retention delays, proactive inhibition among the items of auditory memory lists caused retrieval failure of the last list items. Release from this proactive inhibition caused an absolute increase in recency memory and the resulting retroactive inhibition caused retrieval failure of the first items of the list. No other explanation seems to fare as well for these auditory SPF changes. Another future direction of our work is to explore the possibility that inhibition among visual list items determines the shape of the visual SPF. If so, then we would expect to find that retroactive inhibition would dominate at short delays and give way to proactive inhibition as the retention delay increased. Our hope is that these patterns of SPF changes across retention delay for animal visual and auditory memory will provide a promising target for human as well as animal memory theories dealing with serial order and serial position effects.

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