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Visual List Memory in Capuchin Monkeys (*Cebus apella*)

Anthony A. Wright
University of Texas Medical School at Houston

Memory of 3 capuchin monkeys, *Cebus apella*, was tested with lists of 4 travel-slide pictures and different retention intervals. They touched different areas of a video monitor to indicate whether a test picture was in a list. At short retention intervals (0 s, 1 s, 2 s), memory was good for the last list items (recency effect). At a 10-s retention interval, memory improved for 1st list items (primacy effect). At long retention intervals (20 s and 30 s), primacy effects were strong and recency effects had dissipated. The pattern of retention-interval changes was similar to rhesus monkeys, humans, and pigeons. The time course of recency dissipation was similar to rhesus monkeys. The capuchin's superior tool-use ability was discussed in relation to whether it reflects a superior general cognitive ability, such as memory. In terms of visual memory, capuchin monkeys were not shown to be superior to rhesus monkeys.

Capuchin monkeys, by some measures, are very intelligent. Their tool-using abilities surpass those of other monkeys and, in some respects, appear comparable with those of great apes. Indeed, based on an analysis of their tool-using abilities, Parker and Gibson (1977) and Chevalier-Skolnikoff (1989) suggested that capuchins possess a level of sensorimotor intelligence (Piagetian stage 5 or 6) typical of 12–18-month-old human infants.

More recent evidence, however, has challenged whether capuchins really can achieve such an advanced stage of cognitive development. In one situation (e.g., invisible-displacement task), a capuchin monkey appeared to learn a cause-and-effect relationship (Schino, Spinozzi, & Berlinguer, 1990), but in another situation (e.g., stick-and-tube task) they apparently do not (Visalberghi & Limongelli, 1994; Visalberghi, Savage-Rumbaugh, & Fragaszy, 1995; Visalberghi & Trinca, 1989). Also, unlike human infants at stages 5 and 6, capuchins do not imitate, raising additional concerns as to whether they have reached such an advanced stage of sensorimotor intelligence (Gibson, 1989, 1990; Visalberghi & Fragaszy, 1990).

Despite this controversy regarding developmental stages and their role in intelligence, the capuchin's tool use remains a superior talent. What their superior tool use means for cognitive capacities generally may not be resolvable from additional tool-use studies. Possibly, tests of a more general cognitive ability might shed light on this issue. These types of tests tend to transcend specialized talents (e.g., tool use) that can be confused with superior intelligence. General cognitive abilities are based on higher order relationships rather than the item-specific, context-specific behaviors of problem-solving tasks such as tool use (cf., Goldman-Rakic & Preuss, 1987). One general cognitive ability, common to virtually all measures of intelligent behavior including tool use, is *memory.*

Memory is essential in effective tool use, as it is in all learned behavior. Effective tool use may depend on remembering a specified sequence or list of behaviors. This behavior may include the making of tools and using them in a prescribed sequence (e.g., Westergaard & Suomi, 1993). The alternative to a remembered sequence of behavior is trial-and-error behavior. Trial-and-error behavior may occur initially, but as effective behaviors are learned, trial-and-error behavior should diminish and eventually drop out. In some situations, however, capuchin trial-and-error behavior persists, indicating that effective behavior and cause-and-effect behavior is not being learned (e.g., Visalberghi & Limongelli, 1994).

The evidence is mixed as to whether or not the capuchin's superior tool use reflects superior general cognitive abilities, such as memory. Therefore, testing the capuchin's list memory ability and comparing it with the list memory ability of other species (e.g., rhesus monkeys) might shed light on whether the capuchin's tool-use ability really reflects a superior general cognitive capacity or is a more isolated specific talent. The purpose of the studies in this article was to test the visual list memory of capuchin monkeys and compare it with the visual list memory of other species.

List memory is perhaps best characterized by the serial position function. Memory is typically found to be best for the first items of a list (*primacy effect*) and the last items of a list (*recency effect*), and poorest for the items in the middle of a list. This U-shaped function has long been the benchmark of list memory (Ebbinghaus, 1902). A variety of behavioral, pharmacological, and brain-lesion research has shown that primacy and recency effects can be selectively dissociated (e.g., Castro, 1995, 1997; Crowder, 1976, p. 141; Glanzer & Cunitz, 1966; Kesner, 1985; Kesner & Novak, 1982). One behavioral parameter that dissociates primacy

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Correspondence concerning this article should be addressed to Anthony A. Wright, Department of Neurobiology and Anatomy, University of Texas Medical School, P.O. Box 20708, Houston, Texas 77225. Electronic mail may be sent to aawright@nba19.med.uth.tmc.edu.

and recency effects is *retention interval.* At short retention intervals, there is only a recency effect. At long retention intervals, there is only a primacy effect. At intermediate retention intervals, both effects are present, producing the characteristic U-shaped serial position function.

Similar changes in the serial position function with retention interval have been shown for rhesus monkeys, pigeons, and humans (Wright, Santiago, Sands, Kendrick, & Cook, 1985). The time course of these changes, however, was different for the different species. For example, the recency effect dissipated in 10 s for pigeons, 30 s for rhesus monkeys, and 100 s for humans. These memory results can be used to compare and evaluate the memory results from capuchin monkeys. The pattern of changes with retention interval can be used to determine whether or not the underlying visual memory processes for capuchin monkeys are similar or different from those of these other species. The time course of changes in primacy and recency effects can be used to determine whether or not there are quantitative differences that might account for superior memory of capuchin monkeys relative to rhesus monkeys. For example, superior memory of capuchin monkeys could be shown as a prolonged recency effect relative to rhesus monkeys, possibly closer to that for humans.

Method

Subjects

The subjects were 3 male capuchin monkeys: a *Cebus apella* named Groucho and two *Cebus apella apella* named Zeppo and Chico. At the beginning of the experiment, Groucho and Zeppo were 9.5 years old, and Chico was 8.25 years old. They were maintained in state and federal approved facilities. They were fed twice daily, once after all 3 monkeys finished being tested and again about 3.5 hr later. Water was available ad libitum in their individual home cages. Fruits and vegetables occasionally accompanied the first feeding. Experimental sessions lasted about 1 hr and were conducted 5 or 6 days per week.

Apparatus

A custom aluminum test chamber was constructed so that there were no holes or openings to visually distract the monkeys from working the task (Bhatt & Wright, 1992).

A total of 720 travel-slide pictures were used in the testing. They were stored in 256 × 256 format and displayed 11.51 cm wide by 9.29 cm high on a 33-cm NEC video monitor (model JC-1401P3A Multisync color monitor with an 800 × 560 resolution). List items appeared in the upper portion of the monitor and the test item appeared 1.35 cm below the list items. A small white rectangle, 5.64 cm wide by 6.19 cm high, was located in the lower right-hand corner of the monitor. Touch responses to test pictures and the white rectangle were monitored by a Carroll Touch Infrared Smart-Frame (Model 50023801, Carroll Touch, Round Rock, TX). A Plexiglas template with cutouts matching the picture and response areas guided touch responses.

Procedure

Training the monkeys in the list memory task involved several stages. First, they were trained in a same–different task with pairs of pictures presented simultaneously. In this training stage, a pair of pictures appeared, one above the other. If they were the *same* picture, then a touch to the lower picture resulted in a banana pellet. If they were *different* pictures, then a touch to the white rectangle in the lower right-hand corner resulted in a banana pellet.

After the monkeys learned the same–different task with a pool size of 8 pictures, the size of the pool was expanded to 16, 32, 64, and 128 pictures. Same–different transfer performance was tested following this acquisition by intermixing test trials containing novel stimuli with regular training trials.

Same–different performance was then trained in a delayed format. The first (upper) picture was removed before the second (lower) picture was presented. Following good performance in this delayed same–different task, the first (upper) item was expanded to a list of two, three, and then four items. The monkeys were trained with four-item lists until performance was accurate (>90% correct) before memory was tested at different retention intervals.

In the list memory task, each trial began with the presentation of the list in the upper portion of the video monitor. No response was required to start the list. Four list items were presented successively, each for a 1-s duration and a 1-s interstimulus interval. These were the same presentation times and interstimulus intervals used in a similar study with rhesus monkeys (Wright, Santiago, & Sands, 1984).

Following a retention delay of 0 s, 1 s, 2 s, 10 s, 20 s, or 30 s, a single test (probe) item appeared in the lower portion of the monitor. The test matched one of the list items on half the trials, and the monkey was required to touch the test item in order to receive a 96-mg banana pellet reward. The test did not match a list item on the other half of the trials, and the monkey was required to touch a white rectangle in the lower right of the monitor to receive a similar reward. Incorrect touches or failures to touch within a 4-s response period produced a 30-s time-out. There was no correction procedure (e.g., repeating incorrect trials).

The retention delay was fixed for a block of 32 trials but varied across blocks of trials. In each 32-trial block, there were 16 same and 16 different trials. The order of presentation was random for each 32-trial block. Two 32-trial blocks, each with a different delay, were tested daily. The two delays were selected quasirandomly, with the restriction that one short delay (0 s, 1 s, or 2 s) and one long delay (10 s, 20 s, or 30 s) were tested daily. The two delays to be tested daily and their testing order (short versus long) were varied and counterbalanced within the limits of the experiment. The six delays were each tested 10 times in 10 randomized blocks, which resulted in 40 tests of each serial position of each function.

The pictures on each trial were unique within a daily session, resulting in 288 pictures presented daily. The 288 pictures varied daily and were selected from a larger pool of 720 pictures.

Two studies were conducted, each for 30 daily sessions. In the first study, a 5-s intertrial interval (ITI) followed reward or time-out. In the second study, a 10-s ITI followed reward or time-out.

Results

The time required to train the monkeys in the different phases of the task was extensive. They were trained in the same–different task for 7,200 trials. They accurately (>80% correct) performed the task with 128 training pictures and with novel pictures. The upper item was then expanded to a list of four items. They were trained on the four-item list memory task for 39,000 trials before testing their list memory at the six different retention intervals.

Figure 1 shows the individual results from both of the

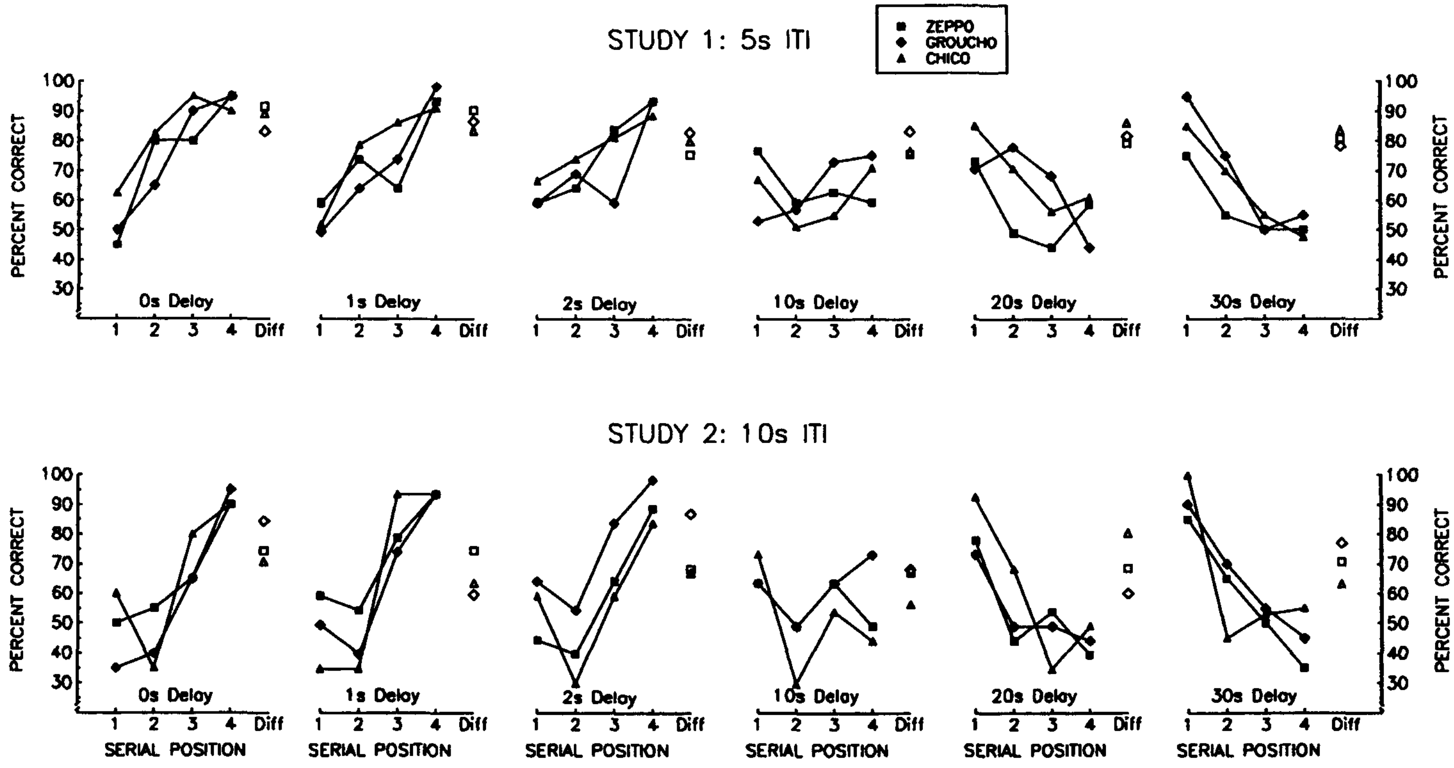

Figure 1. Two studies of serial list memory with three capuchin monkeys (Zeppo, Groucho, and Chico). Lists of four pictures were followed by a retention *Delay,* a single-test picture, a choice response, and an intertrial interval (ITI). Serial position 1 refers to memory performance in which the test item matched the first item in the list. Unfilled points (Diff) indicate performance in which the test did not match a list item.

studies. The shapes of the serial position functions and the changes with retention interval were similar for the 3 subjects in each of the studies. Also, the pattern of changes with retention interval shown in the two studies was similar, despite the longer intertrial interval in the second study. The similar pattern of changes from the two studies adds to the reliability of the overall results.

The short delay serial position functions (0-s, 1-s, and 2-s delays) show good memory for items at the end of the list (i.e., strong recency effect) but poor memory for items at the beginning of the list (i.e., no primacy effects). The 10-s delay serial position functions show emergence of primacy effects and thus are U-shaped. The long delay serial position functions (20-s and 30-s delays) showed strong primacy effects but poor memory for items at the end of the list (i.e., no recency effects).

These dynamic changes in the serial position functions were supported by statistical tests. Analyses of variance showed significant ($p < .01$) effects of serial position, $F(3, 48) = 4.58, 18.1$; and delay × serial-position interaction, $F(15, 48) = 8.50, 11.3$, for the two studies, respectively. Significant ($p < .02$) linear (monotonic increasing or decreasing) trends were shown for delays of 0 s, 1 s, 2 s, 20 s, and 30 s in the first study: $F(1, 10) = 37.5, 38.7, 24.8, 7.6$, and 29.2, respectively. Similar significant ($p < .02$) linear trends were found for the same delays of 0 s, 1 s, 2 s, 20 s, and 30 s in the second study: $F(1, 10) = 25.7, 27.5, 11.2, 16.4$, and 27.1, respectively.

Discussion

These studies began with an expectation that capuchin monkeys might be superior to rhesus monkeys in these memory studies. Evidence from their tool-use indicated a possible superior intelligence (Chevalier-Skolnikoff, 1989; Parker & Gibson, 1977). Their ability to maintain their position in an active and changing troop of wild foraging monkeys indicated a possible predisposition for list learning and memory (e.g., Janson, 1990).

Results from the initial learning phase were encouraging. Capuchins learned the same–different task in 7,200 trials. This represented only one-third of the number of trials required for rhesus monkeys to learn a similar phase of the task (Wright, Santiago, & Sands, 1984).

Results from the next learning phase were not so encouraging. Training in the four-item list memory task required over 2.5 years and 39,000 trials. Rhesus required only one-fifth as much training for similar performance in a similar phase of the task. The capuchin's slow learning of this phase was surprising in light of their rapid same–different acquisition. Related to this finding may be persistent errors noted by experimenters when testing capuchins in a food-trap variation of the stick-and-tube task (Visalberghi & Limongelli, 1994; Visalberghi, Savage-Rumbaugh, & Fragaszy, 1995; Visalberghi & Trinca, 1989). These investigators concluded that capuchins did not learn the critical cause-and-effect relationship essential for solving this problem. In the same–different task in this article, however, capuchins did learn the critical relationship; they could solve novel problems. The same–different relationship is the basis of the list memory task. Why the list memory phase of this task was difficult for the capuchins is unclear. Nevertheless, they did eventually learn the list memory task to a high degree of accuracy, which is the important result from the standpoint of testing their memory.

Because the results from the two memory tests were similar, they were averaged and were compared with results from three other species—rhesus monkeys, pigeons, and humans—in Figure 2. These experiments with different species used similar procedures, including a similar serial probe recognition procedure, four-item lists, single-item tests, retention interval tests in a similar blocked design, and a large item pool of memory items presented trial-unique each session.

One procedural aspect that was somewhat different for the capuchins was that they did not initiate presentation of the lists. Because primacy effects were found in the absence of list-initiation responses, this is evidence against the hypothesis that animal primacy effects are artifacts (e.g., increased attention, distinctiveness, etc.) of list-initiation responses (D. Gaffan, 1983; E. A. Gaffan, 1992). This evidence adds to the evidence already against the list-initiation hypothesis where primacy effects for rhesus monkeys were found in the absence of list-initiation responses. In a visual list memory experiment, monkeys did not initiate lists but showed primacy effects (Castro & Larsen, 1992). In auditory list memory experiments, monkeys in one condition initiated lists and in another condition did not initiate lists; similar primacy effects were shown in both conditions (Wright, 1998; Wright & Rivera, 1997). In summary, all relevant evidence (of which I am aware) contradicts the list-initiation hypothesis and none supports it.

In comparing the memory results for the different species, perhaps the most striking feature is the similarity in the shapes of the functions. On the immediate test (0-s delay), the functions are upward-sloping, resulting in all-recency functions. Primacy comes in after a short delay. At long retention delays, recency dissipates, leaving downward-sloping or all-primacy functions.

Some differences across species occur in the time course for dissipation of the recency effect. Capuchins and rhesus monkeys show similar time courses for dissipation of the recency effect that occurs in about 30 s. This contrasts with the much shorter 10-s dissipation of the recency effect for pigeons and the longer 100-s dissipation of the recency effect for humans. Capuchins and rhesus differ slightly in their time course of the primacy effect. Capuchins develop a primacy effect at a 10-s delay, whereas rhesus develop it at a 1-s delay. Capuchins more closely resemble humans than rhesus in this regard. Experiment 2 (Figure 1) does show a hint of a primacy effect developing at a 1-s delay but nothing approaching the magnitude of the rhesus primacy effect at this delay.

In summarizing the comparison of capuchin and rhesus memory, their similarities far outweigh any differences. Both species show similar qualitative changes in primacy and recency effects with retention interval. They show a similar time course of dissipation of the recency effect,

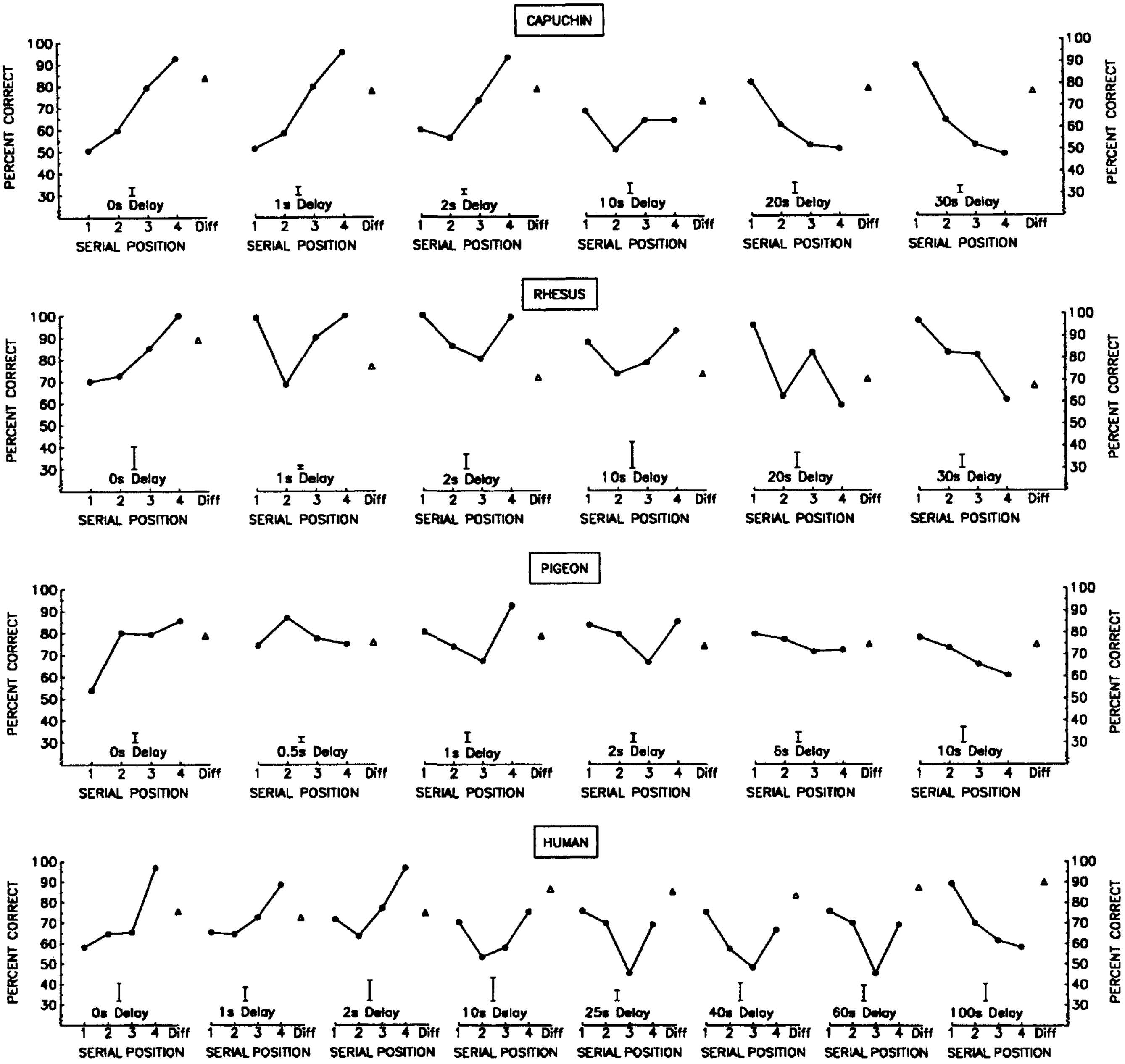

Figure 2. Average performance for three capuchin monkeys from Figure 1. Also shown are average performances for rhesus monkeys, pigeons, and humans (after Wright, Santiago, Sands, Kendrick, & Cook, 1985). Delay is the retention interval between the last list item (serial position 4) and the test. Unfilled points (Diff) indicate performances for trials in which the test did not match a list item. Error bars are the average standard error of the mean for the four serial positions of each function.

which differs from that for pigeons and humans. Dissipation of the recency effect is one measure of how long items can be held in memory.

The pattern of changes of primacy and recency effects indicates that the underlying memory mechanisms for capuchin monkeys, a New-World species, are similar to rhesus monkeys, an Old-World species. This pattern of changes challenges memory models and theories that have been used to explain serial position functions. The primacy effect is often associated with long-term memory (e.g., Atkinson & Shiffrin, 1968; Glanzer, 1972; Waugh & Norman, 1965). But the primacy effects shown in Figure 2 actually increase in absolute value with time. Such increases in memory over time are counterintuitive. Memory typically is thought to fade with time, not improve. Hypothetical processes of decay, unlearning, and displacement (see Crowder, 1976) that have been proposed to account for fading of memory cannot account for memory improvements with time.

These results, along with those from other procedures to dissociate primacy and recency effects (e.g., Castro, 1995, 1997; Crowder, 1976), implicate two passive memory processes with different time courses. Among the passive memory processes that might be instrumental in these dynamic serial position function changes are those of interference. Retroactive interference from the last list items might initially interfere with the subject's memory for the first list items and thereby produce a recency dominated function. As time passes, proactive interference from the first list items might grow as retroactive interference wanes, producing a primacy-dominated function. Whether interference will prove instrumental in producing these serial position effects, to the exclusion of other passive memory processes such as distinctiveness (see Neath, 1993), requires further study.

These memory experiments with capuchin and rhesus monkeys highlight some issues involved in any comparison of cognitive capacities or intelligence across species (e.g., Macphail, 1987). The superior tool use by capuchins clearly does not carry over to a general cognitive skill, such as memory, as would be expected if capuchins really were of superior intelligence (see Gibson, 1989, 1990, for a modification of the superior intelligence claim).

There is no compelling evidence to suggest that the capuchin's memory is superior to that of the rhesus. Indeed, the slower learning of the list memory task by capuchin monkeys could be interpreted that capuchins are less intelligent than rhesus (see Cheney & Seyfarth, 1990; Gallistel, 1980; Roitblat, 1987, for intelligence based on adaptive learning). I prefer not to interpret this acquisition difference in such strong terms. Some modification of the training procedure, such as touching each list item, conceivably could diminish the difference or even produce an acquisition advantage for capuchins.

No matter how slow or fast the learning, once performance is accurate and stable in this list memory task, the results of memory testing should be comparable. This is contrary to Macphail's (1987) claim that all animal performance comparisons are invalid because they are subject to perceptional, motivational, or motor-skill differences. Although such differences might affect acquisition, they would not likely be important factors in steady-state list memory performance. A perceptual difference across species is not likely to be an important factor because the stimuli are robust and multidimensional, and are easily discriminated by all of these species. Motor-skill differences are unlikely to be an important factor because only a simple choice response is required, which is relatively independent of speed or dexterity. Finally, motivational differences are unlikely to be an important factor because accuracy of well-learned list memory performance is roughly independent of motivation. Motivation can affect acquisition, but, in my experience, well-trained capuchin or rhesus monkeys perform this task accurately even when sated; they may stop working, but if they work, they are generally accurate. Furthermore, motivational differences would not be expected to affect the pattern of changing serial position effects with retention interval.

The list memory task is particularly advantageous in this regard because it contains built-in monitoring of task performance. At most retention intervals, either the primacy effect or the recency effect is strong. These points of good memory serve to verify that the subject is performing at or near the limits of its capacity and is not being hampered by aspects of perception, motivation, motor skill, or attention.

As a practical matter, rhesus monkeys seem better suited than capuchin monkeys to experimental memory tasks. Rhesus learn the list memory task more rapidly overall, are less disrupted by parameter changes (e.g., intertrial–interval changes, list-length changes, retention-interval changes, etc.), and hence seem better suited than capuchins as a primate model for memory studies.

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