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Rhesus monkeys (*Macaca mulatta*) show robust primacy and recency in memory for lists from small, but not large, image sets

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Abstract

The combination of primacy and recency produces a U-shaped serial position curve typical of memory for lists. In humans, primacy is often thought to result from rehearsal, but there is little evidence for rehearsal in nonhumans. To further evaluate the possibility that rehearsal contributes to primacy in monkeys, we compared memory for lists of familiar stimuli (which may be easier to rehearse) to memory for unfamiliar stimuli (which are likely difficult to rehearse). Six rhesus monkeys saw lists of five images drawn from either large, medium, or small image sets. After presentation of each list, memory for one item was assessed using a serial probe recognition test. Across four experiments, we found robust primacy and recency with lists drawn from small and medium, but not large, image sets. This finding is consistent with the idea that familiar items are easier to rehearse and that rehearsal contributes to primacy, warranting further study of the possibility of rehearsal in monkeys. However, alternative interpretations are also viable and are discussed.

Keywords

familiarity; interference; rehearsal; serial probe recognition

Most of our experience can be seen as occurring in serial order, one event after another. For example, you might attend a series of talks at a conference, read different sections in a textbook, or watch a set of four or five advertisements during a television commercial break. Because we acquire so much information in a serial order, it is important to study how serial order affects processing and subsequent memory for individual items or events. Accordingly how organisms learn, process, and remember serially-presented lists of stimuli has been the subject of many investigations across several species (e.g., Terrace, 2005; Wright et al., 1985) and remains an active area of study.

One of the most robust findings about memory for lists is that it is often characterized by enhanced memory for the first and last list items, termed primacy and recency, respectively (Atkinson and Shiffrin, 1968). The combination of primacy and recency produces a U-shaped serial position curve for accuracy. In humans, the U-shaped serial position curve is observed when lists consist of either words (Rundus, 1971), abstract visual patterns (Korsnes et al., 1996), or spatial locations (Smyth and Scholey, 1996). It is also observed in tests of both free recall (Carlesimo et al., 1996) and recognition (Wright et al., 1990). While not as extensively

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documented in nonhumans as it is in humans, the U-shaped serial position curve has been observed in Old World monkeys (Sands and Wright, 1980), New World monkeys (Wright, 1999), rats (Kesner and Novak, 1982), pigeons (Santiago and Wright, 1984), and chickadees (Crystal and Shettleworth, 1994), suggesting that it reflects fundamental memory processes common across species.

In humans, studies of memory for lists have often identified rehearsal as the underlying mechanism responsible for the primacy effect (Atkinson and Shiffrin, 1968). Because earlier list items enter our working memory first, they are rehearsed more than later items, facilitating the transfer of those earlier items into long-term memory and enhancing later accessibility to retrieval. Several types of evidence point to a critical role for rehearsal in primacy. When asked to rehearse aloud, subjects spontaneously rehearse the first list item more than the later list items (Rundus, 1971; Tan and Ward, 2000). Having subjects complete a distraction task during list presentation reduces primacy and instructions that rehearsal is unnecessary (i.e., that no memory test will follow) eliminate primacy while leaving recency intact (Glenberg et al., 1980; Marshall and Werder, 1972). Directed forgetting instructions, in which subjects are cued that rehearsal of specific list items is unnecessary, affect memory for early list items (primacy), but not later list items (Sahakyan and Foster, 2009). Amnesic patients, who have damage to the hippocampus and for whom rehearsal is ineffective at transferring information to long-term memory, have poor memory for early list items (primacy), but normal memory for later list items (recency), relative to control subjects (Baddeley and Warrington, 1970; Carlesimo et al., 1996). Taken together, this evidence strongly suggests that the primacy component of the characteristic U-shaped serial position curve observed in humans is due to rehearsal.

In contrast to studies with humans, studies with nonhumans often focus on memory interference as the underlying cause of primacy. According to the interference account, memory for initial list items interferes with later list items and memory for later list items interferes with earlier list items (Wright, 1998). Memory is worst for items in the middle of the list because those items receive both proactive and retroactive interference. These types of interference are proposed to follow different time courses, depending on the length of time elapsing from stimulus exposure (hereafter: study) to when the subject is required to make a test response (hereafter: test). Retroactive interference is strongest at short study-test delays and proactive interference is strongest at longer study-test delays. This account has been used to explain the shift from only recency at short delays, to a U-shaped serial position curve at moderate delays, and finally to only primacy at long delays (Wright et al., 1985). This shift from primacy, to primacy and recency, to recency has been termed the dynamic serial position curve and has been observed in pigeons, monkeys and people (Wright et al., 1985; but see Kerr et al., 1998; Kerr et al., 1999 for reports that did not find a dynamic serial position curve in humans).

The most significant comparisons between nonhuman and human performance in tests of memory for lists have been conducted by Wright and colleagues (e.g., Cook et al., 1991; Wright et al., 1985). Tests of the rehearsal account of primacy in monkeys have suggested that they do not rehearse, despite showing primacy in memory for lists. Monkeys do not show the inter-stimulus-interval (ISI) effect that is thought to be diagnostic of rehearsal in humans (Cook et al., 1991). Increasing the ISI between list items leaves more time to rehearse each item before the next one is presented. At the same time, lengthening the duration of the whole list means that items have to be remembered longer before test. Overall accuracy in humans increases when ISI is lengthened (Wright et al., 1990), consistent with the importance of rehearsal for memory, whereas accuracy in monkeys decreases (Cook et al., 1991), probably due to the longer delay before testing. A second challenge to the rehearsal account in monkeys is that rehearsal in humans is often conceived of as sub-vocal verbal behavior (e.g., Baddeley, 1992). Given that nonhumans lack verbal representations, they might consequently lack the capacity for rehearsal (but see Hourihan et al., 2009 for recent evidence that humans can

rehearse nonverbally). Given the difficulty of assessing rehearsal in nonhumans and the relative lack of studies attempting to do so, it is important to conduct additional studies using a variety of converging approaches to provide independent evidence for or against the rehearsal account of primacy in monkeys and other nonhuman species. We therefore introduce and motivate the following studies using a rehearsal framework as is dominant in the human literature (Atkinson and Shiffrin, 1968; Glenberg et al., 1980; Marshall and Werder, 1972; Rundus, 1971; Sahakyan and Foster, 2009). However, it should be noted that other theoretical frameworks have been well developed to account for the serial position curve in both humans and nonhumans (e.g., Wright et al., 1985). We will address these alternatives further in the Discussion.

If the characteristic U shape of the serial position curve is due, at least in part, to rehearsal, then we might expect it to occur only with familiar items or items that can be recoded in terms of existing representations in long-term memory. Consistent with this, most studies of memory for lists in humans use stimuli that are at least somewhat familiar to the subjects. Humans are often tested with word stimuli, and even when stimuli are not words, humans may recode them verbally (e.g., a photograph of a blue boat might be recoded as the words “blue boat”). When to-be-remembered items are coded or recoded verbally, memory for them may become dependent on activation of existing representations (i.e. words) in long-term memory, rather than on the generation of completely new memory traces. For example, when asked to study lists of nouns (Baddeley and Warrington, 1970) or travel slides (Wright et al., 1990), subjects presumably have existing representations of the nouns or the objects pictured in the travel slides. Studies in humans suggest that activation of such existing representations in long-term memory is critical for primacy. Photographs of familiar household items produce primacy in humans, whereas photographs of unfamiliar shapes do not (Swanson, 1978). Direct manipulation of familiarity by pre-exposing subjects to abstract shapes affects primacy but not recency (Dugas, 1975). This suggests that memory for lists of familiar stimuli will be more likely to result in the typical U-shaped serial position curve than memory for lists of unfamiliar stimuli. One way to increase the familiarity of to-be-remembered items in nonhumans, and presumably ensure they are represented in long-term memory, is to use a small set of repeating stimuli to generate lists for memory tests.

We examined how rhesus monkeys' memory for lists, as depicted by a serial position curve, changes based on the size of the image set from which the lists are drawn. Six monkeys performed a serial probe recognition (SPR) test with 5-item lists of photographs drawn from either large, medium, or small image sets. In SPR tests, subjects see a list of stimuli, experience a delay, and then see a single stimulus that they must judge as either from the studied list or not. Over many trials, the subject's memory is repeatedly probed using stimuli from all possible list positions, as well as distractor stimuli that were not from the studied list. The result is a serial position curve that depicts memory accuracy as a function of list position. Some studies have found that the shape of the serial position curve changes as a function of the delay between study and test, with a shift from recency only, to a U-shape with primacy and recency, and then finally to only primacy as the delay between the last study item and test increases (Wright et al., 1985). To maximize the chances of capturing such dynamic effects, if they occurred in our study, we tested memory for items from lists drawn from each set size at delays varying from 0.2 to 50 seconds. Based on results from humans showing the importance of stimulus familiarity to the primacy portion of the serial position curve (Dugas, 1975; Swanson, 1978), we hypothesized that the extent to which we obtained primacy would vary as a function of the size of the set from which images were drawn, with the smaller sets generating the most primacy.

Experiment 1

Method

Subjects and apparatus—Six adult male rhesus monkeys (*Macaca mulatta*; mean age at start of testing: 5.97 years) served as subjects. The monkeys were pair-housed, received a full food ration daily, and had ad libitum access to water. All monkeys had experience with various cognitive tests using a touchscreen computer, including delayed matching-to-sample and paired-associate learning.

Subjects were tested six days a week in their home cages, using portable testing rigs. Each rig was equipped with a 15" color LCD touch-screen (3M, St. Paul, MN) running at a resolution of 1024×768, generic stereo speakers, and two automatic food dispensers (Med Associates Inc., St. Albans, VT) that dispensed into food cups beneath the screen. Correct responses were rewarded 90% of the time with nutritionally-balanced banana-flavored pellets (Bio-Serv, Frenchtown, NJ) and the remaining 10% of the time with miniature chocolate candies, intermixed according to a random schedule. One testing rig was attached to the front of each monkey's cage and remained there for seven hours, allowing the monkeys to work at their own pace throughout the day. Each day, monkeys participated in two or three computer-based studies, one of which was the study reported here. Studies were administered consecutively, with one-third or one-half of the available testing time devoted to each study in turn. During the seven-hour testing session, monkeys were separated from their partners by a protected-contact divider that allowed the monkeys to see and groom each other, but not to access other individuals' computer screens.

Stimuli—Stimuli were 2400 color photographs gathered from the online photo repository Flickr (Yahoo!, Sunnyvale, CA) using the batch downloading tool FlickrDown (<http://greggman.com>). Duplicates were eliminated using DupDetector (Prismatic Software, Anaheim, CA) and visual inspection, were shuffled randomly and renamed using 1–4a Rename (<http://www.1-4a.com>), and were cropped to 300×300 pixels using Adobe Photoshop (Adobe, San Jose, CA). Photos were excluded from this study if they depicted any primate species.

Procedure—We used a standard serial probe recognition procedure, similar to those that previously produced U-shaped serial position curves (e.g., Wright et al., 1985). Each trial began with the onset of a green start square (100×100 pixels) that the monkey touched twice (FR2) to begin the trial. The list images then appeared in order, centered on the screen and separated by 200 milliseconds of black screen. Monkeys were required to touch each list image (FR2) to progress to the subsequent image. Lists were five items long, except during initial training, when they were shorter. The last list item was followed by a delay of 0.2, 0.5, 2, 10, or 50 seconds, selected pseudorandomly to counterbalance across the testing session, during which time the screen was black. Finally, the monkey was presented with one image and a non-match symbol (Figure 1, rightmost panel). On half the trials, the image was from the studied list and on the other half of trials, the image was a distractor image that hadn't been seen on that trial. The test image and non-match symbol appeared equally often in each of the four corners of the screen. The monkey earned food, accompanied by distinctive secondary audio reinforcement ("excellent!" or "woo-hoo!" for food pellets and chocolate candies, respectively), by touching the image if it was from the list or by touching the non-match symbol if the image was not from the list. Incorrect choices – touching the test image if it was not from the list or the non-match symbol if the image was from the list – resulted in a negative auditory stimulus ("d'oh!") and a 2-second time out, during which the screen was black. Trials were separated by a 10-second intertrial interval (ITI), during which the screen was black. Accordingly, total time between trials was 10 seconds following a correct choice and 12 seconds following an error. Figure 1 depicts a representative trial.

Training: We first trained monkeys to complete the match/non-match recognition test with lists of one item drawn from a set of 1600 possible images. The delay between study and test was one second. Monkeys completed one session of 200 trials per day. After reaching criterion of 90% or more correct in a single session, we increased the list length by one image for each subsequent session, up to a list length of five items, irrespective of performance. Finally, monkeys received 15 sessions with the five-item lists to give them sufficient experience to establish stable inter-session performance prior to testing with multiple delay lengths.

Testing: To evaluate the effect of image set size and delay length on the serial position curve, we tested monkeys with lists drawn from large, medium, and small image sets (2400, 60, and 6 images, respectively). The delay between the offset of the last list image and the onset of the recognition test was 0.2, 0.5, 2, 10, or 50 seconds (pseudorandomized so each delay length was presented twice in each block of 10 trials). First, monkeys completed 21 sessions with lists from the large set of 2400 images. Then, we reduced the set size to 60 by removing a random 2340 images and tested for another 21 sessions. Finally, we reduced the set size to 6 by removing 54 more images and tested for another 21 sessions. Monkeys completed one session of 200 trials per day. Consequently, images from the large, medium, and small image sets were reshuffled and reused every two sessions, every 10 trials, or every single trial, respectively.

Data analysis—The first session with each new set size was a practice session and was not analyzed. Thus, we analyzed 20 sessions with each set size. This resulted in 80 trials for each combination of list position, set size, and delay and 400 non-match trials with each set size and delay. To better approximate normality, all proportions were arcsine transformed prior to analysis (Aron and Aron, 1999). As our study used a match/non-match recognition test, we also analyzed performance as measured by d' (Macmillan and Creelman, 2005) to give us a measure of recognition that accounted for any possible bias to choose either the match or non-match option. In cases where the pattern of results was the same, we report the more conventional measure of accuracy, proportion correct. First, we analyzed whether accuracy differed as a function of list position using a repeated measures ANOVA for each set size and delay length. For tests that violated the assumption of sphericity, we used the Greenhouse-Geisser corrected degrees of freedom to determine omnibus significance (Keppel and Wickens, 2004). In cases in which ANOVA revealed significant list position effects, we then tested for primacy and recency specifically using planned comparisons. Accuracy on the first and last list positions was compared with the least accurate of the three middle positions using paired t -tests. Because the hypothesized effects of primacy and recency are directional, one-tailed t -tests were used. We did not correct for any potential familywise error resulting from multiple comparisons because our hypothesized effect of using lists from large sets was a lack of statistical significance for the primacy effect. It was therefore more important to protect against making a Type II error.

Results and Discussion

Initial visual inspection of the results indicated that the serial position functions were quite stable across delays up to 10 seconds. In particular, we did not observe the dynamic serial position curve that has been observed in some previous studies (i.e., only recency at short delays, both primacy and recency at moderate delays, and only primacy at longer delays; compare Figure 2 to Wright et al., 1985 Figure 1). Separate repeated measures ANOVA were conducted for each set size and each delay and revealed that accuracy differed significantly as a function of list position for all curves at delays of 0.2, 0.5, 2, and 10 seconds, with the exception of the list from the medium-sized set at the 10-second delay (Table 1, Figure 2). At the 50-second delay, accuracy was low overall, and did not vary as a function of list position for lists from any image set size (Table 1). Statistical analyses confirmed the lack of a dynamic serial position curve seen in the initial visual inspection, as we observed significant primacy

from the shortest delays of 0.2 and 0.5 seconds (Table 1, Figure 2). Because we found no consistent effect of delay on the shape of the serial position curve, we collapsed the data across all delays that showed significant list position effects (0.2, 0.5, 2, and 10 seconds). When collapsed across delays, we found recency with lists from large, medium, and small sets, but primacy only with lists from medium and small sets (Table 1, Figure 2). The observation of U-shaped serial position curves with lists from small and medium, but not large, sets supports our hypothesis that stimulus familiarity affects the shape of the serial position curve. Furthermore, our findings are consistent with the idea that familiar items are more easily rehearsed and that rehearsal is at least partially responsible for primacy.

Experiment 2

In Experiment 1, monkeys were tested on lists from large, medium, and small image sets, in that order. They showed recency with lists from all sets, but primacy only with lists drawn from medium and small stimulus sets. This suggests that the primacy portion of the characteristic U-shaped serial position curve is affected by the familiarity of the list items. However, because the three set sizes were tested sequentially, set size was confounded with the amount of experience monkeys had with the serial probe recognition paradigm. It is therefore possible that the observed differences result from sustained training in the task generally, rather than from the changes in stimulus set size. In Experiment 2, we deconfounded set size from testing order by intermixing tests with all three set sizes. During each session, monkeys received an equal number of tests with lists drawn from large, medium, and small stimulus sets. Based on the results from Experiment 1, we hypothesized that monkeys would show U-shaped serial position curves with lists from small and medium, but not large sets.

Method

Subjects and apparatus—Subjects and apparatus were the same as those used in Experiment 1.

Stimuli—Stimuli were 990 novel photographs, gathered and processed as described in Experiment 1. Photographs were divided into three sets: 960 for the large stimulus set, 24 for the medium set, and 6 for the small set. These set sizes were selected so that the average frequency with which images repeated in Experiment 1 was maintained as closely as possible in Experiment 2. That is, every two sessions, every 10 trials, or every 3 trials for large, medium, and small image sets, respectively.

Procedure—Individual trials were run as in Experiment 1. Because we found no significant effect of list position at the 50-second delay in Experiment 1, we only used delays of 0.2, 0.5, 2, and 10 seconds in Experiment 2. Sessions consisted of 160 trials with each set size for a total of 480 trials per session. The set size used on any given trial was pseudorandomized such that lists were randomly drawn twice from each stimulus set size in each block of six trials. Randomization of delay length and match/non-match trials was done within each set size, rather than across all trials to ensure that delays and trial types were equally represented in each set size. We ran monkeys on 21 sessions, with the first session being a practice session that was not analyzed.

Data Analysis—All data analyses were conducted as in Experiment 1.

Results and Discussion

Initial visual inspection again did not show a dynamic serial position curve. Paired t-tests confirmed significant primacy and recency at almost all delays for lists drawn from the small and medium, but not large, image sets (see Supplementary material, Table S1). Consequently,

we collapsed across delays. Only the collapsed data are presented here for efficiency of presentation (see Supplementary material, Table S1 for full statistics). Repeated measures ANOVA revealed that accuracy differed as a function of list position for lists drawn from small and medium, but not large, image sets (small: $F(4,20) = 12.78, p < .001$; medium: $F(1.9,9.2) = 8.83, p = .008$; large: $F(1.6,8) = 2.43, p = .154$). We found significant primacy and recency for lists from both the small and medium image sets (small primacy: $t(5) = 2.61, p = .024$; small recency: $t(5) = 4.33, p = .004$; medium primacy: $t(5) = 3.30, p = .011$; medium recency: $t(5) = 3.78, p = .005$; Figure 3).

Visual inspection of the data (Figure 3, *Left*) appears to show a U-shaped serial position curve for lists from the large set despite the statistical lack of list position effect; however, examination of individual subject data revealed that this apparent pattern was largely due to a single subject, monkey Cy. For example, monkey Cy's accuracies on middle list items (i.e., items 2, 3, and 4) were 9.3, 9.8, and 6.0 standard deviations below the means of the other five subjects. Compare the serial position curve with lists from the large set from all subjects (Figure 3, *left*) to the same curve with this outlier removed (Figure 3, *right*), which shows much less pronounced differences in the means. Nevertheless, to prevent a possible Type II error, we ran paired t-tests to confirm the lack of primacy and recency effects with lists from the large set and with all subjects (primacy: $t(5) = 1.66, p = .079$; recency: $t(5) = 1.15, p = .151$). It is also worth noting that with all six subjects, one delay did show significant primacy and recency (see Supplementary material, Table S1, 2-second delay); however, this effect became nonsignificant after removal of monkey Cy ($F(4,16) = 1.99, p = .144$).

These results show that the effect of set size observed in Experiment 1 was not due to the testing order. Rather, the presence of primacy and recency in memory for lists drawn from small and medium, but not large, image sets is likely due to the influence of item familiarity on the shape of the serial position curve. Unlike in Experiment 1, we did not observe statistically significant recency with lists from the large set. Possible reasons for this loss of recency are suggested in the General Discussion.

Experiment 3

In Experiment 2, we found primacy and recency with lists drawn from small and medium, but not large, sets. This suggests that stimulus familiarity affects the shape of the serial position curve. However, in Experiments 1 and 2, monkeys advanced through the lists by manually touching each image, making it possible that they might have spontaneously spent more time viewing lists from certain set sizes or to items in particular list positions. For example, images from the large image set may have elicited more visual exploration because they were relatively novel. Indeed, the median response latency to touch items from the large set was over 70 milliseconds longer than to touch items from either the small or medium sets. For lists from all set sizes, the median response latency to touch the first item was around 250 milliseconds longer than to touch subsequent items. Longer exposure to lists from the large set could have potentially produced the observed difference in the shape of the serial position curve. In addition, longer exposure to the initial list item could be entirely responsible for the observed primacy effect with the small and medium lists. In Experiment 3, we controlled for the amount of time each item was viewed by automatically advancing list items after a set time, irrespective of any response made by the subject. Based on the results from Experiments 1 and 2, we hypothesized that monkeys would continue to show U-shaped serial position curves with lists from small and medium, but not large, sets.

Method

Subjects and apparatus—Subjects and apparatus were the same as those used in Experiments 1 and 2.

Stimuli—Stimuli were the same as those used in Experiment 2.

Procedure—Procedures were identical to those in Experiment 2, with the exception that the pacing of the presentation of items was fixed and not dependent on a response from the subject. For each monkey, we determined the median study latency for items in each list position in Experiment 2. In Experiment 3, we displayed each list image for the shortest of these durations for that monkey (range: 241–447 milliseconds). Thus, each monkey experienced different study durations from other monkeys, but within each monkey study duration was equivalent for all lists and all list positions.

Data Analysis—All data analyses were conducted as in Experiments 1 and 2.

Results and Discussion

Initial visual inspection again did not reveal a dynamic serial position curve. Paired t-tests confirmed significant primacy and recency at all delays for lists from the small and medium image sets, but no significant effects for lists drawn from the large set (see Supplementary material, Table S2). Consequently, we collapsed across delays. Only the collapsed data are presented here for efficiency of presentation (see Supplementary material, Table S2 for full statistics). Repeated measures ANOVA revealed that accuracy differed as a function of list position for lists drawn from small and medium, but not large, image sets (small: $F(4,20) = 16.14, p < .001$; medium: $F(4,20) = 15.59, p < .001$; large: $F(4,20) = 0.77, p = .558$). We found significant primacy and recency for lists from both the small and medium image sets (small primacy: $t(5) = 3.32, p = .011$; small recency: $t(5) = 13.56, p < .001$; medium primacy: $t(5) = 5.58, p = .001$; medium recency: $t(5) = 5.66, p = .001$; Figure 4). These results demonstrate that the effect of set size observed in Experiments 1 and 2 was not due to differences in study time between set sizes or list positions.

Experiment 4

In Experiment 3, we again found no effect of list position on memory for lists from the large set. However, accuracy with lists drawn from the large set was better than that for lists drawn from smaller image sets overall, averaging 83% correct across all list positions. It is possible that this level of performance is a ceiling for monkeys under these testing conditions and that primacy and recency effects were therefore obscured. Consequently, in Experiment 4 we attempted to bring performance with lists from the large set away from ceiling by further shortening the study time for each item to 100 milliseconds. As we were only interested in whether performance with lists from the large set would display primacy or recency when study time was shortened, we only tested lists drawn from the large image set. Based on the results from Experiments 2 and 3, we hypothesized that memory for lists from the large set would continue to show no significant variation with list position.

Method

Subjects and apparatus—Subjects and apparatus were the same as those used in Experiments 1–3.

Stimuli—Stimuli were the same as those used in Experiments 2 and 3; however, only the large image set was used.

Procedure—Procedures were identical to those in Experiment 3, with the exceptions that only lists drawn from the large image set were tested and each list item was displayed for only 100 milliseconds. Sessions consisted of 160 trials.

Data Analysis—All analyses were conducted as in Experiments 1–3.

Results and Discussion

Initial visual inspection again did not reveal a dynamic serial position curve. This initial impression was confirmed, as repeated measures ANOVA revealed no effect of list position on accuracy for any delay (0.2 sec: $F(4,20) = 1.08, p = .391$; 0.5 sec: $F(4,20) = 1.87, p = .167$; 2 sec: $F(4,20) = 1.57, p = .221$; 10 sec: $F(4,20) = 1.32, p = .297$). Consequently, we collapsed across delays and again found no effect of list position on accuracy ($F(4,20) = 1.79, p = .171$; Figure 5).

To confirm that shortening study time had the desired effect of decreasing overall accuracy, we ran a repeated-measures ANOVA with two factors (experiment $\times$ list position) comparing the serial position curve in this experiment with the serial position curve for lists from the large set in Experiment 3. We found a main effect of experiment ($F(1,5) = 26.50, p = .004$), but no main effect of list position ($F(4,20) = 1.16, p = .359$), and no interaction ($F(4,20) = 0.91, p = .478$). This indicates that we successfully brought performance away from a potential ceiling that might have obscured primacy or recency. However, even when the potential for a ceiling effect was reduced, we found no effect of list position with lists drawn from the large set.

General Discussion

Across four experiments, we found robust primacy and recency with lists from small and medium, but not large, image sets. This set size difference remained even when we controlled for possible testing order effects (Experiment 2) and the amount of study time allotted to each stimulus (Experiment 3). In addition, the lack of primacy and recency in the large set appears not to be due to recognition performance being constrained by a ceiling effect, because reducing accuracy did not lead to emergence of serial position effects (Experiment 4). Images in the small and medium sets were experienced frequently and were therefore highly familiar compared to the images in the large set. It appears that that stimulus familiarity affects the shape of the serial position curve in rhesus macaques, as it does in humans (Dugas, 1975; Swanson, 1978).

Familiar stimuli may be more easily rehearsed compared to unfamiliar stimuli because familiar stimuli are ones for which subjects have existing representations in long-term memory. A previously existing representation in long-term memory may be more readily retrieved, and may contain more detail, than would a newly formed representation, making it easier to rehearse in working memory. Human subjects may compensate for being less able to rehearse unfamiliar stimuli by re-coding them as something that already exists in long-term memory (e.g., re-coding a photograph of an unfamiliar red house as the familiar words “red house”). Our finding that item familiarity is necessary for primacy is consistent with studies of memory for lists in humans that showed similar effects of familiarity (Dugas, 1975; Swanson, 1978). It is also consistent with the idea that familiar stimuli are more easily rehearsed than unfamiliar stimuli and with human studies demonstrating that rehearsal is partly responsible for the characteristic U-shaped serial position curve (Baddeley and Warrington, 1970; Glenberg et al., 1980; Marshall and Werder, 1972; Rundus, 1971; Sahakyan and Foster, 2009; Tan and Ward, 2000).

Memory for lists of images drawn from different set sizes has previously been assessed in a rhesus monkey (Sands and Wright, 1980). The monkey was tested with 3-item lists of images drawn from either a small or a large set (6 and 211 items, respectively). Although the monkey was significantly less accurate with lists drawn from the small set than with lists from the large set, set size had no effect on the shape of the serial position curve. Performance with 3-item lists drawn from both set sizes showed recency, but not primacy (based on visual inspection;

no inferential statistics were reported). It is interesting that the same monkey did show primacy for 10 item lists drawn from the same large set of 211 images. The lack of a set size effect for 3-item lists, and the lack of primacy with either set size, appears to conflict with the results reported here that show primacy only for lists drawn from smaller set sizes. It is likely, and consistent with the reported primacy effect seen with 10-item lists, that the use of relatively small 3-item lists by Sands and Wright (1980) prevented primacy in their comparison of image set size. Using the techniques described in this paper, primacy is a robust result, observed across six monkeys, multiple delays, and both small and medium set sizes. It is worth noting that the “large” set size used by Sands and Wright (1980) is closest in size to the “medium” set size used in this study. Additionally, because Sands and Wright (1980) used 10-item lists (twice the length of those used here) in the experiment for which they report primacy, their monkeys saw the 211 images very often and, thus, those images should have been very familiar. Therefore, the discrepancy between the present study and Sands and Wright (1980) may be more apparent than real.

Based on research in humans suggesting that manipulations of rehearsal selectively affect the primacy portion of the serial position curve (Baddeley and Warrington, 1970; Glenberg et al., 1980; Marshall and Werder, 1972; Rundus, 1971; Sahakyan and Foster, 2009; Tan and Ward, 2000), we hypothesized that manipulating set size, and thus the familiarity of images, would selectively affect primacy in monkeys. Subjects failed to show primacy, but did show recency, in memory for lists drawn from the large image set in Experiment 1. However, recency was not obtained with lists from the large set in subsequent experiments. The reason for the lack of recency with the large set in Experiments 2–4 is unclear. Because this pattern of recency without primacy was only observed for lists from the large image set in Experiment 1 (which were the first lists tested), it is possible that subsequent experience with the serial probe recognition paradigm used in this study changed the way that monkeys remembered all future lists (see Wright, 2007 for evidence that experience can change the shape of the serial position curve in monkeys). It is also possible that lengthening the ISI for list items from the large set would lead to more discrepancy in the relative memory strength of individual items, resulting in a more pronounced recency effect. This is supported by previous work examining rhesus monkeys’ memory for 6-item lists, which shows a flat serial position curve with a short ISI of .08 seconds and only recency with longer ISIs of 1, 2, or 4 seconds (Cook et al., 1991).

We do not see clearly how existing interference accounts would explain the current finding of primacy only with highly familiar items. Because images from small sets repeat frequently, memory of previous presentations of a given image could interfere with memory for the most recent presentation of that image, making it difficult to determine whether it was remembered from the current trial or a previous trial. Lists from the large set repeat much less frequently and memory therefore does not suffer as much from between-list interference. However, interference theory, as applied to serial position effects, stresses the effects of within-list rather than between-list interference (Wright, 1998). That is, within-list interference affects middle items more than end items, producing serial position effects. In contrast, between-list interference should affect all list items equally, lowering overall performance, but not changing the shape of the serial position curve. Consequently, it is unclear why decreasing the amount of between-list interference would selectively reduce primacy in Experiment 1 or produce the flat serial position curves from Experiments 2–4. Additionally, in the current study we did not find a dynamic serial position curve, one of the findings on which the interference account is based (Wright et al., 1985), making it unclear how the interference account would explain the current results. However, the interference account certainly explains much of how organisms remember lists and it may be possible to apply this versatile framework in a way that explains the current findings.

Another alternative explanation to the rehearsal account is that the current results are due to a shift in retrieval strategy from familiarity judgments with large sets to recollection of the studied stimulus with small sets, as suggested by Wright (2007; see Yonelinas, 2002 for a review of recollection and familiarity). In tests of lists drawn from the large set, distractor items are unfamiliar and, therefore, monkeys can perform accurately by making judgments of absolute familiarity. With lists from the small set, distractor items are almost as familiar as target items, making comparatively coarse absolute familiarity judgments ineffective. Even more sensitive judgments of relative familiarity would become increasingly difficult as the set size from which lists were drawn became smaller. The demands of making difficult familiarity judgments might lead monkeys to abandon relative familiarity and adopt a recollection strategy. It is possible that using familiarity judgments, as can be done with lists drawn from large image sets, produces only recency (as in Experiment 1) or equal performance across list items, as in Experiments 2–4. By contrast, using a recollective strategy, as potentially required for lists drawn from small sets, might produce primacy and recency because the monkeys naturally retrieve end items first when recollecting the list. This would be consistent with the idea that tests of human recall show a U-shaped serial position curve partly because subjects naturally adopt an explicit retrieval strategy of recollecting the end list items first (Baddeley and Hitch, 1993; Carlesimo et al., 1996). It is also possible that monkeys got better at using a familiarity strategy for lists from the large set over the course of training, flattening out the serial position curve and leading to the observed loss of recency. Finally, a recently developed computational model (SIMPLE; Brown et al., 2007) has been applied to serial position effects and suggests that subjects may discriminate list items based on temporal distinctiveness. However, it does not appear that this model would predict primacy with small but not large image sets, as we report here. Rather, items from the small set would become less temporally distinct due to their frequent repetition, reducing primacy, which was not observed here. In any case, the possibility that manipulating set size changes monkeys' retrieval method, which then changes the shape of the serial position curve, is plausible and one that deserves further study.

In summary, rhesus monkeys' memory for lists of visual stimuli is characterized by robust primacy and recency when those lists are drawn from small, but not large, image sets. This effect is possibly because the small sets consist of familiar images that are relatively easy to rehearse. However, other interpretations, such as the use of different retrieval strategies for lists from different set sizes, are plausible and deserve further study.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Schematic of the progression of events in the serial probe recognition trials used in Experiment 1. Monkeys touched the green start box to initiate a trial (leftmost panel), touched each of the five list images in sequence, experienced a delay, and then were presented with a test (rightmost panel). The test screen displayed a “non-match” symbol and an image that was either from the studied list or not. If the image was from the list, touching it was rewarded. If the image was not from the list, touching the “non match” symbol was rewarded. A black screen lasting 200 milliseconds separated images in the list during study.

Figure 2.

Serial position curves for lists drawn from large (*black dots*), medium (*gray dots*), and small (*white dots*) sets of images in Experiment 1. Curves are pictured for delays of 0.2, 0.5, 2, and 10 seconds combined (*leftmost panel*) and for each of those delays separately (*right four panels*). Accuracy at 50 second delay not shown because accuracy did not vary as a function of list position for lists from any set size, see Table 1 for more information. Each dot represents proportion correct for tests with images from the given list position or tests on non-match trials. First and last list positions depicted as an asterisk indicate significant primacy and recency, respectively.

Figure 3. Serial position curves for lists drawn from large (*black dots*), medium (*gray dots*), and small (*white dots*) sets of images in Experiment 2, in which lists from all set sizes were intermixed. *Left:* Serial position curves for all six subjects. *Right:* Serial position curves for five subjects, excluding monkey Cy, whose extreme scores most contributed to the appearance of a serial position curve for lists from the large set. Curves are pictured for delays of 0.2, 0.5, 2, and 10 seconds combined. Each dot represents proportion correct for tests with images from the given list position or tests on non-match trials. First and last list positions depicted as an asterisk indicate significant primacy and recency, respectively.

Figure 4.

Serial position curves for lists drawn from large (*black dots*), medium (*gray dots*), and small (*white dots*) sets of images in Experiment 3, in which study time was controlled. Curves are pictured for delays of 0.2, 0.5, 2, and 10 seconds combined. Each dot represents proportion correct for tests with images from the given list position or tests on non-match trials. First and last list positions depicted as an asterisk indicate significant primacy and recency, respectively.

Figure 5.

Serial position curves for lists drawn from a large set of images in Experiment 4, in which study time was 100 milliseconds. The pictured curve is for delays of 0.2, 0.5, 2, and 10 seconds combined. Each dot represents proportion correct for tests with images from the given list position or tests on non-match trials.

Table 1

Repeated-measures ANOVA and paired t-test values for Experiment 1

Delay:		Collapsed	0.2 seconds	0.5 seconds	2 seconds	10 seconds	50 seconds
Large Set	Omnibus	$F(4,20)=7.84$ $p=.001$	$F(4,20)=6.37$ $p=.002$	$F(4,20)=4.27$ $p=.012$	$F(4,20)=4.36$ $p=.011$	$F(4,20)=7.21$ $p=.001$	$F(4,20)=1.30$ $p=.303$
	Primacy	$t(5)=0.71$ $p=.254$	$t(5)=0.95$ $p=.193$	$t(5)=0.90$ $p=.204$	$t(5)=0.49$ $p=.333$	$t(5)=0.86$ $p=.215$	n/a
	Recency	$t(5)=4.27$ $p=.004$	$t(5)=4.06$ $p=.005$	$t(5)=2.68$ $p=.022$	$t(5)=2.89$ $p=.017$	$t(5)=3.34$ $p=.010$	n/a
Medium Set	Omnibus	$F(4,20)=15.56$ $p<.001$	$F(4,20)=9.07$ $p<.001$	$F(4,20)=17.14$ $p<.001$	$F(4,20)=11.06$ $p<.001$	$F(4,20)=2.54$ $p=.072$	$F(1,9,5)=3.68$ $p=.067$
	Primacy	$t(5)=4.76$ $p=.003$	$t(5)=2.55$ $p=.026$	$t(5)=2.84$ $p=.018$	$t(5)=3.52$ $p=.009$	n/a	n/a
	Recency	$t(5)=5.97$ $p=.001$	$t(5)=5.75$ $p=.001$	$t(5)=5.59$ $p=.002$	$t(5)=3.98$ $p=.006$	n/a	n/a
Small Set	Omnibus	$F(1,8,9)=17.34$ $p=.001$	$F(4,20)=15.58$ $p<.001$	$F(4,20)=23.00$ $p<.001$	$F(4,20)=10.05$ $p<.001$	$F(4,20)=3.21$ $p=.035$	$F(4,20)=0.95$ $p=.458$
	Primacy	$t(5)=2.98$ $p=.016$	$t(5)=1.69$ $p=.076$	$t(5)=2.19$ $p=.040$	$t(5)=2.72$ $p=.021$	$t(5)=3.00$ $p=.015$	n/a
	Recency	$t(5)=4.49$ $p=.003$	$t(5)=4.22$ $p=.004$	$t(5)=9.07$ $p<.001$	$t(5)=5.90$ $p=.001$	$t(5)=1.52$ $p=.095$	n/a

Note: Collapsed = Delays of 0.2, 0.5, 2, & 10 seconds combined. Shaded cells mark statistically significant tests.