

Visual recognition memory in squirrel monkeys

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Squirrel monkeys (*Saimiri sciureus*) were trained on visual recognition memory tasks in a Wisconsin General Testing Apparatus with a trial-unique procedure that used 250 objects as stimuli. In Experiment 1, acquisition of a trial-unique delayed non-match-to-sample task (DNMS) was compared with acquisition of a trial-unique delayed match-to-sample (DMS) task. The DNMS task was learned in significantly fewer trials and with significantly fewer errors. Two animals in the DNMS group demonstrated highly accurate retention of the DNMS strategy despite an 11-month hiatus in experimental testing. In Experiment 2, the same procedures were used to study the learning of lists of 3, 5, 10, or 20 serially presented items. Although the animals were able to accurately remember lists of up to 20 items, there was no evidence of serial position effects.

One of the most widely employed methods used to study memory processes in animals is the delayed match-to-sample (DMS) technique. In this visual recognition task, a sample stimulus is shown to the animal, removed from view, and, after some delay (retention interval), is again presented together with a comparison stimulus. A response to the original stimulus (matching response) is reinforced. There are several parameters of this general DMS paradigm that can be manipulated, such as the exposure time of the sample stimulus, the length of the retention interval, the presence of light and/or noise during the retention interval, and the number of retrieval cues during the choice portion of the task (see D'Amato, 1973; Jarrard & Moise, 1971; Medin & Davis, 1974, for reviews). One of the manipulations that can strongly affect the performance of animals is increasing the number of items in the set of sample and comparison stimuli. In general, it appears that small sets of sample and comparison stimuli lessen the animal's mnemonic performance either by creating a considerable amount of proactive interference (Jarvik, Goldfarb, & Carley, 1969) and/or by challenging the animal's poor ability to make rather precise temporal discriminations (D'Amato, 1971, 1973; Worsham, 1975).

The extreme case of increasing the number of sample and comparison stimuli is the use of a unique pair of

stimuli on every trial per session, that is, the trial-unique procedure. Compared to a small-stimulus-set procedure, the trial-unique method has been shown (1) to reduce by almost one-half the number of trials required for rhesus monkeys to learn a 10-sec DMS task (Mishkin & Delacour, 1975), (2) to allow pigtail macaques to perform accurately on DMS problems with retention intervals ranging from 5 sec to at least 48 h (Overman & Doty, 1980), (3) to allow monkeys to learn and accurately remember lists of serially presented stimuli of at least six items in the case of squirrel monkeys (Roberts & Kraemer, 1981) and lists of 10 to 20 items in the case of rhesus monkeys (Gaffan, 1974; Sands & Wright, 1980a, 1980b). Furthermore, through the use of trial-unique DMS procedures, there have been at least two recent demonstrations that monkeys show serial position curves in their recall of lists and that these curves are very similar to, but perhaps not identical to, those shown by human subjects (Roberts & Kraemer, 1981; Sands & Wright, 1980a, 1980b).

These results are of considerable practical and theoretical interest in light of the facts that (1) nonhuman primates are being used extensively to establish animal models for human memory and memory impairments (Mishkin, Spiegler, Saunders, & Malamut, 1981; Roberts & Kraemer, 1981; Sands & Wright, 1980a, 1980b), (2) monkeys are not capable of linguistic encoding, rehearsal, or retrieval, and (3) other animals with excellent visual abilities, such as pigeons, may be unable to learn the concept of matching-to-sample (Carter & Werner, 1978; but see Schrier and Thompson, 1980).

The present study investigated several aspects of visual recognition memory in squirrel monkeys, a species of nonhuman primates that has been rather infrequently used for visual memory research. The first experiment compared the rates at which naive

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squirrel monkeys acquired a match-to-sample task versus a non-match-to-sample task, and the second experiment measured the accuracy of object recognition memory as a function of the number of stimulus items to be remembered.

EXPERIMENT 1

More than 30 years ago, when discussing the acquisition of matching and nonmatching behaviors, Skinner (1950) predicted that both behaviors should be learned at the same rate; however, generally, this has not been the case. In tests of Skinner's prediction, pigeons were found to have better initial performance on nonmatching tasks (Cumming & Berryman, 1965) and/or faster acquisition of nonmatching tasks (Ginsburg, 1957) than of matching tasks. The theories provided to account for those results are not particularly applicable here, because these early studies used quite different procedures from those used today (e.g., only three or four stimulus objects and nonreinforcement of response to the sample). However, Mishkin and Delacour (1975), using trial-unique stimulus procedures, have shown that rhesus monkeys learn to respond to new objects (nonmatch) much more readily than they learn to respond for the second time (match) to objects seen 10 sec previously. The authors attribute the enhanced learning to an inherent tendency for rhesus monkeys to approach novel stimuli. The first experiment sought to determine whether this attraction to novelty is a learning principle in squirrel monkeys as well.

Method

Subjects. Ten experimentally naive adolescent squirrel monkeys (*Saimiri sciureus*) were divided randomly into a match-to-sample group (M) and a non-match-to-sample group (NM) of five animals each. The animals were individually housed in standard cages, maintained on water and Purina Monkey Chow, and given pieces of fruit as reinforcement in the test situation.

Apparatus. Testing was carried out in a modified Wisconsin General Testing Apparatus (WGTA), which was inside a sound-attenuating chamber. The animal was seated in an adjustable Plexiglas restraining chair that allowed free arm and leg movement and was positioned about 5 cm in front of the horizontal sliding tray of the WGTA. The stimulus tray contained three shallow food wells spaced 5 cm apart. An opaque guillotine door separated the experimenter from the monkey and, when lowered, allowed the experimenter to manipulate the stimulus objects and the bait in the food wells. Bits of apple, grapes, and peaches were

used as reinforcement. The stimuli were small miscellaneous "junk" objects, for example, eraser, ping pong ball, bolt, keys, plastic toys, etc., mounted on a flat wooden base.

Procedure. Animals were tested in 25 trials per day, 5 days per week. In the acquisition phase of testing, there were 250 different stimulus objects that were randomly paired and never shown to the animal more than once per week (trial-unique procedure). A new set of objects was used for each subsequent experiment.

Each trial consisted of two parts: (1) presentation of the to-be-remembered sample object, which always covered the center food well and under which was a piece of fruit; and (2) presentation of the sample object together with a novel comparison object, each covering a lateral food well, the sample appearing on the left or right in an irregularly balanced sequence. In the sample presentation phase, the sample object was baited for all groups. The learning criterion was 90% correct responses for 2 consecutive days.

In delayed match-to-sample training, one group, match (M) ($N=5$), was taught to displace an object (sample) from the center well to receive a piece of fruit. The sample was removed from sight, the opaque screen was lowered, and 10 sec later the screen was raised and the animal was presented with a choice between the original sample and a comparison object which had not been used previously that week. The monkey was rewarded for displacing the sample object (i.e., rewarded for a "match" response).

In delayed non-match-to-sample training, the animals in a non-match (NM) ($N=5$) group were treated exactly as Group M, except that in the choice phase of each trial they were reinforced for displacing the novel comparison object (i.e., reward for a "non-match" response).

Results and Discussion

Individual and group learning scores are shown in Table 1. Group NM learned the non-match-to-sample task in an average of 785 trials (an average of 216.2 errors across an average of 31.6 test sessions). Group M showed unexpected difficulty in mastering the match-to-sample task in 1,630 trials (an average of 563.8 errors across an average of 65.2 test sessions). In fact, three of these five animals approached, but failed to reach, criterion on the match-to-sample task. Their performance on the last block of 50 trials was 70.5%, 74%, and 80% correct. Training for these three animals had to be discontinued after 70 sessions because they were committed to biomedical research unrelated to the present study. The group differences were statistically significant [trials, $t(8)=9.65$, $p < .01$; errors, $t(8)=5.15$, $p < .01$].

Figure 1 shows the groups' average performance over 30 blocks of 50 trials. For the first 15 blocks of trials, an analysis of variance (Kirk, 1968) showed a significant difference for training conditions [$F(1,8)$

Table 1
Trials and Errors in Learning Match- or Non-Match-to-Sample Tasks

Match Subjects	Sessions	Errors	Nonmatch Subjects	Sessions	Errors
A-1	70*	710	F-6	33	210
B-2	59	451	G-7	37	295
C-3	57	406	H-8	28	182
D-4	70*	715	I-9	27	190
E-5	70*	537	J-10	33	204
Mean	65.2	563.8		31.6	216.2

*Training terminated at 70 days (1,750 trials).

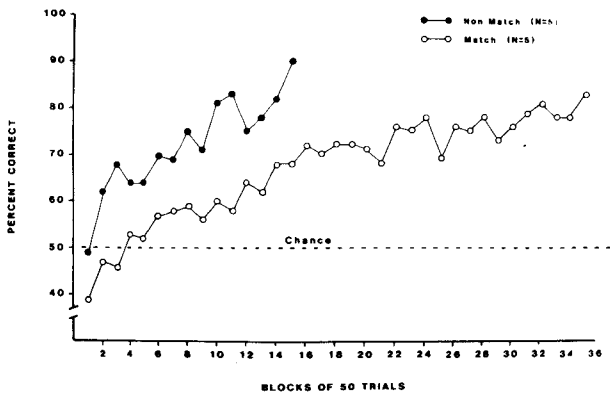


Figure 1. Average group performance in acquisition of match or non-match-to-sample tasks in blocks of 50 trials (two sessions).

= 26.3, $p < .01$] and for blocks of learning trials [$F(14,112) = 18.0$, $p < .01$] but not for an interaction between the groups across trials [$F(14,112) = 1.4$, $p > .05$]. Post hoc tests revealed that on the first blocks of trials the match group performed significantly below chance [$t(4) = 5.02$, $p < .05$].

Because of the lack of a significant interaction between the groups, the poorer attainment of criterion by animals in the M group does not appear to be due to slower learning rates, but rather to the fact that at the outset of training they performed at a level below chance. On the first block of 50 trials, the M group performed at only 39% correct whereas the NM group performed at nearly 50% correct. Throughout the course of acquisition, this initial difference generally was maintained, so the curves remained roughly parallel.

These results confirm and extend similar findings by Mishkin and Delacour (1975), which showed that rhesus monkeys learn a nonmatch task significantly faster than a match task. While the testing procedures were designed to be identical, the present squirrel monkeys required approximately nine times as many trials to learn a match task as did rhesus monkeys (Mishkin & Delacour, 1975). The present learning scores would be considerably higher if all animals in Group M had been trained to criterion.

It is noteworthy that, in the study by Mishkin and Delacour (1975), rhesus monkeys in the nonmatch and match groups, respectively, performed at 80% and 38% correct response on the first day of testing. This is in contrast to the present experiment, in which scores on the first block of 50 trials were 48% and 39%, respectively, for the NM and M groups. This discrepancy between rhesus and squirrel monkeys may reflect subtle and unknown differences in experimental procedures; however, a more interesting speculation is that rhesus monkeys have an innate preference for novel objects but that squirrel monkeys do not. However, if the initially high nonmatch performance of the macaques (Mishkin & Delacour,

1975) is attributable to an innate attraction to novelty, then one would expect that the initial match performance of the macaques not only would be below chance, because they tend to incorrectly respond to novelty, but also that it would be lower than the match performance of the present squirrel monkeys in the M group. This was not the case, however, as both macaques and squirrel monkeys initially performed the match task at about 39% correct. These data suggest that squirrel monkeys may, in fact, have some degree of initial attraction to novel objects. The tendency of the M group to respond (incorrectly) to the novel object apparently opposed and outweighed the effects of the reward contingency until the 6th and 7th blocks of trials, when they began to perform consistently above chance (Figure 1). This tendency to approach the novel object continued to be so strong throughout testing that three of the five animals in the match group were performing at 75% correct on the final block of testing. Other investigators have also found that squirrel monkeys have difficulty learning match-to-sample problems. For example, in a study by Roberts and Kraemer (1981), squirrel monkeys required up to 2,000 trials to learn a simultaneous matching task.

If squirrel monkeys have only a weak attraction to novel objects, the question remains as to why the nonmatch group acquired a preference for novelty quickly enough to allow them a significantly faster attainment of criterion. An explanation may lie in the use of a large set of sample and comparison stimulus objects, that is, the trial-unique procedure. For both groups, on the sample exposure part of each trial, the animals were reinforced for displacing a relatively novel object (at least novel that week). On the choice part of each trial, the nonmatch animals were reinforced for displacing a second novel object and the match animals were reinforced for selecting the familiar member of the choice pair. In other words, animals in the NM group were required to learn only one principle, "approach novelty," whereas the animals in the M group were required to learn the dual principles of "approach novelty" and then "approach familiarity." Apparently, the latter task demand is the more difficult.

When the factors of novelty and task demand are considered together, the current data are interpreted to mean that, during the choice phase of a trial-unique two-choice recognition memory task, there are two forces at work that determine which stimulus object will be chosen: (1) the animal's preference for a novel stimulus, which seems to be weak in squirrel monkeys, and (2) whether the animal is reinforced for responding to the previously seen stimulus or to the unique, comparison stimulus. The non-match-to-sample task combines a favorable reward contingency with a natural attraction to novelty and thus allows much faster acquisition than the match-to-

sample task in which the two factors are in competition.

Long-term retention of nonmatch strategy. A subsequent finding demonstrated that despite their original difficulty in learning the DNMS task, some monkeys showed prolonged retention of delayed nonmatch behaviors. Two animals in the NM group were retrained on a nonmatch task after 11 months of no behavioral testing. During the break in testing, they were housed in an indoor-outdoor colony cage. Prior to the 11-month hiatus, the monkeys had been trained to criterion on a 10-sec DNMS task and then tested on DNMS lists of 3, 5, 10, or 20 items (Experiment 2). Three hundred and thirty days later they were retrained on a 5-sec DNMS task.

Figure 2 shows the learning curves for nonmatch animals F-6 and J-10 before and after the hiatus. Although both monkeys originally required 34 days to reach criterion, upon reacquisition each achieved criterion in only 6 days, including the 2 criterion days of 90% correct response. The substantial savings scores are further underscored by the fact that the animals performed at 70% and 80% correct on the first 10 reacquisition trials. Since it is unreasonable to assume that during the hiatus the animals' tendency to approach novel objects dramatically increased, the only other explanation for these results is that for 11 months they remembered the procedural strategies involved in DNMS tasks—that is, they remembered the rules of the testing situation.

EXPERIMENT 2

Investigations of memory of a single object are limited in providing information about more complex mnemonic processes such as storage capacities, memory scanning, or retrieval strategies. These processes may be better studied by memory tests that require the subject to register, retain, and later retrieve multiple, serially presented items or lists

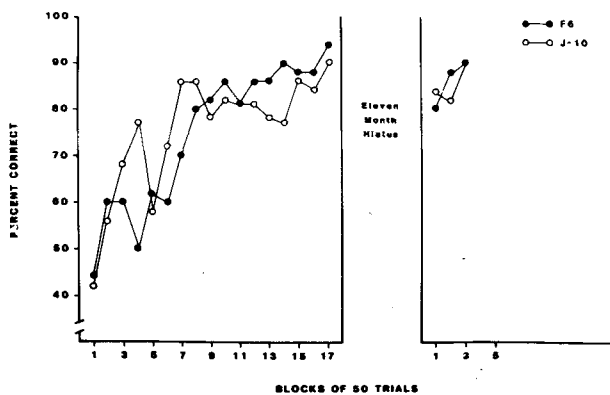


Figure 2. Individual acquisition and reacquisition performance before and after an 11-month break in testing for two monkeys in non-match-to-sample paradigms.

(Thompson & Herman, 1977). Macaques have demonstrated the ability to remember lists of 10 items over intervals of several minutes (Gaffan, 1974; Mishkin, 1978; Sands & Wright, 1980b), and squirrel monkeys have shown accurate retention of at least 6 items (Roberts & Kraemer, 1981). The second experiment investigated list learning in seven of the squirrel monkeys used in the first experiment.

Method

Subjects. The seven squirrel monkeys that mastered the match or nonmatch task in Experiment 1 served as subjects.

Apparatus. Monkeys were tested with the same equipment used in Experiment 1.

Procedure. The testing procedure was generally identical to that of the previous experiment. Each animal remained in its original match group ($N=2$) or nonmatch group ($N=5$), and each was presented with lists of 3, 5, or 10 consecutive, but unique, sample objects. For example, in a list of three objects, stimuli A, B, and C were presented for food reward, one at a time, in 10-sec intervals. Ten seconds after the presentation of the last items in the list, the stimuli were re-presented in the same order, each being paired with one novel object (e.g., A vs. X, B vs. Y, C vs. Z) at 10-sec intervals. The animals were given 5 days of 30 trials per day of each list (10 lists of 3 items/day, 6 lists of 5 items/day, 3 lists of 10 items/day). A pool of 300 new stimulus objects was used so that no object was used more than once a week. At the end of testing in lists of 10 items, the five nonmatch animals received an additional 20 days of training on lists of 20 items, one new list being presented daily.

Since, for all list lengths, the interitem presentation rate was 10 sec, retention interval per item was confounded with list length. This procedure was deliberate and based on two facts. First, the animal had up to 2 min to respond when a pair of objects was chosen, and data from the first experiment showed that response times varied widely. Thus, attempts to strictly control for retention time across lists would have been futile. Secondly, and more importantly, Roberts and Kraemer (1981) have shown that neither item presentation time nor delay interval significantly affects memory accuracy in squirrel monkeys.

Results and Discussion

Table 2 shows the individual and average group performance for lists of 3, 5, 10, and 20 items. The nonmatch group tended to perform better than the match group on lists of 3, 5, and 10 items; because of the relatively poor performance of a single nonmatch animal on the list of 10, however, the group differences were statistically significant only on lists of 3 and 5 items (Mann Whitney U tests, $U=0$, $p < .05$). While there was a tendency for the performance of both groups to decrease as list length increased, this trend was not statistically significant. For the nonmatch group, a one-way analysis of variance did not reveal a significant effect of list length [$F(3,12) = 2.04$, $p > .05$]. No reliable within-group statistics could be performed for the match group since $N=2$.

This is the first demonstration that a species of New World monkeys is capable of remembering long (20-item) lists of serially presented items. Of greater significance, these results, when considered with demonstrations of robust memory by rhesus monkeys (Mishkin, 1978; Overman & Doty, 1980), strongly

Table 2
Average Percent Correct Response on Lists of 3, 5, 10, or 20 Items by Animals in Match or Nonmatch Paradigms

Group	List Length			
	3	5	10	20
Match Subject				
B-2	74	73	65	*
C-3	67	73	69	*
Mean	70.5	73	67	
Nonmatch Subject				
F-6	84	80	75	75
G-7	81	77	77	74
H-8	79	82	84	78
I-9	83	84	85	81
J-10	87	80	69	79
Mean	82.6	80.6	78	77.4

*Not tested.

indicate that neither language nor linguistic-like operations is a prerequisite for accurate long-term storage and accurate retrieval of memory traces in the primate nervous system.

Serial position. One of the prominent features of list learning by human subjects is the serial position effect; that is, recall is best for the initial items in the list (primacy effect) and the final items in the list (recency effect) and worst for the middle items. Traditionally, two methodologies have been used to study serial position. In the first paradigm, free recall, a subject is presented sequentially with a number of items and later is required to recall as many items as possible. In the second paradigm, serial probe recognition (SPR), a subject is presented a list of items and later a probe stimulus is presented alone or with a nonlist item and the subject is required either to (a) classify the probe as being from the list or not, or (b) to respond to the previously seen item of the presented pair. The latter SPR task is a variation of the delayed match-to-sample task.

Serial position curves have been demonstrated in squirrel monkeys (Roberts & Kraemer, 1981) and rhesus monkeys (Sands & Wright, 1980a, 1980b) through the use of SPR paradigms. However, in the present experiment there was no evidence of serial position curves for lists of any length. With the non-match group used for analysis (only two animals in the match group learned lists), analysis of variance for number of errors as a function of serial position for lists of 3, 5, 10, or 20 items did not reveal a statistically significant treatment effect (serial position) at any list length [List 3, $F(2,8) = .03$; List 5, $F(4,16) = 1.83$; List 10, $F(9,36) = .55$; List 20, $F(19,76) = 1.23$; all $ps > .05$].

The failure to find serial position curves in the present study is understandable on both procedural and conceptual grounds. Procedurally, the present task differed considerably from either free recall or SPR paradigms in that the current monkeys were required to respond to the novel member of up to 20

pairs of objects that were presented sequentially. Inasmuch as the serial position curve is regarded as reflecting both long-term memory (primacy effect) and short-term memory (recency effect) (see Atkinson & Shiffrin, 1971, for review), the present procedure would not be expected to yield either effect, since every list item was retained for approximately equal lengths of time. These data strongly suggest that investigations of serial-position phenomena should use free recall or probe techniques rather than procedures that involve exposing the animal to the entire list of items during the test phase.

CONCLUSIONS

Experiment 1 showed that squirrel monkeys learn a non-match-to-sample strategy much faster than they do a match-to-sample strategy, as is the case for rhesus monkeys (Mishkin & Delacour, 1975). It appears that when required to match-to-sample, both squirrel and rhesus monkeys have a tendency to respond to the novel object, and that this tendency, along with the demands that are inherent in trial-unique test procedures, act as potent error factors which must be overcome before accurate match-to-sample behaviors are manifest. While the theoretical implications of attraction to novelty and task demands are sufficiently interesting to be tested independently, the practical implications are very clear: The most efficient learning of large-stimulus-set recognition memory tasks results from the use of non-match-to-sample methodologies. Once learned, the non-match-to-sample strategy seems to be resistant to passive decay over long periods of time.

Experiment 2 showed that squirrel monkeys can remember lists of up to 20 items with considerable accuracy. These findings, along with data from rhesus monkeys, suggest that the processes that underlie complex visual memory are comparable in a wide variety of nonhuman primates, including squirrel monkeys.

To the extent that nonhuman primate memory resembles that of human memory (e.g., in memory capacity, length of retention of specifics and rules, and serial position), the data increasingly suggest that robust visual memory in the primate nervous system is not necessarily predicated on the existence of linguistic mechanisms of encoding, storage, or retrieval. Thus, highly manipulative animal models for human memory functions and dysfunctions are increasingly feasible.

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