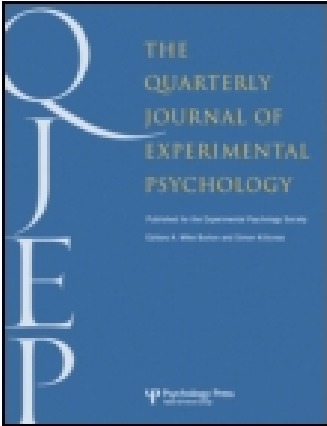


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The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology

Publication details, including instructions for
authors and subscription information:

<http://www.tandfonline.com/loi/pqjb20>

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Published online: 29 May 2007.

To cite this article: B. Buffalo, D. Gaffan & E.A. Murray (1994) A primacy effect in monkeys when list position is relevant, *The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, 47:4, 353-369

To link to this article: <http://dx.doi.org/10.1080/14640749408401364>

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A Primacy Effect in Monkeys When List Position Is Relevant

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In Experiment 1 (1a and 1b), Rhesus monkeys (*Macaca mulatta*) learned lists of two-choice visual discriminations in which list position was relevant to discrimination performance. For example, Stimulus A was the rewarded stimulus if it was presented at List Position 1, but was not rewarded if it was presented at any other position in the list; similarly, Stimulus B was rewarded only at List Position 2, and so on. In learning these lists, all animals showed a marked primacy effect. In Experiment 2 (2a and 2b), Rhesus monkeys and Cynomolgus monkeys (*M. fascicularis*) learned lists of visual discriminations in which each visual stimulus occupied a fixed position in a list, but list position was not relevant to discrimination performance. For example, Stimulus E was always rewarded, and was always presented at List Position 1. To increase the salience of list beginning as a distinctive event, successive presentations of the list were separated by 24-hr intervals. In Experiment 2 there was no primacy effect, however. These results show for the first time that a primacy effect can be obtained in visual discrimination learning by monkeys. Furthermore, they suggest that it is obtained only when list position is relevant to the discrimination learning task.

A primacy effect, defined as superior memory for the item presented first in a list of items to be remembered, is frequently seen in human memory but has not yet been established as a robust phenomenon in animal memory. Though several experiments have reported primacy effects in animals, some of these are open to methodological objections (Gaffan, 1983; E.A. Gaffan, 1992; E.A. Gaffan & Gaffan, 1992). In monkeys, experiments on list position effects have invariably employed one-trial recog-

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This research was supported by the U.K. Medical Research Council and by N.A.T.O. Grant 0184/87.

dition memory tasks such as delayed matching-to-sample or delayed non-matching-to-sample (Castro & Larsen, 1992; Gaffan & Weiskrantz, 1980; Roberts & Kraemer, 1981; Sands & Wright, 1980) or similar one-trial associative memory tasks (Gaffan, 1979). The present experiments tested for primacy effects in discrimination learning tasks, presented over many trials. The use of discrimination learning tasks rather than recognition memory tasks enables some hitherto unexplored determinants of list position effects to be investigated.

It is plausible to suppose that the first position in a list is distinctive from other list positions, and, therefore, if a subject uses memory of list position in performing a task, then the first item in the list will have an advantage over the others. In human free recall of lists, where strong primacy effects are seen, subjects spontaneously use memory of list position to guide retrieval of item information, as is revealed by the order in which the items are recalled (Deese, 1965; Deese & Kaufman, 1957). On this basis one might expect that, if monkeys were obliged to use memory of list position, a primacy effect might emerge. In Experiment 1 (1a and 1b), therefore, we obliged monkeys to use list position as a cue in discrimination learning. In these experiments discrimination of visual stimuli was by itself insufficient to predict reward or non-reward; instead, the animals had to learn that Stimulus A was rewarded in List Position 1, Stimulus B in List Position 2, and so on; stimuli in the "wrong" list position—for example, Stimulus A in List Positions 2, 3, or 4—were not rewarded.

Experiment 2 examined another factor that might determine primacy effects in discrimination learning. Clearly, if primacy is to emerge in monkeys' memory for lists, then the beginning of a list must be discriminably different from the middle or end. In fact, however, many experiments on concurrent visual discrimination learning by monkeys have employed a procedure in which the beginning of a list presentation is not consistently marked by any event that differentiates it from the end of the previous list presentation. The commonly employed procedure is to give several list presentations in each session of training. For example, in an experiment by Gaffan and Lim (1991), each session consisted of five presentations of a list of eight discrimination problems; however, the intertrial interval between the eighth problem in one list presentation and the first problem in the succeeding list presentation was the same as the intertrial interval between successive problems within one list presentation. Thus, the fact that list position effects have not been reported in experiments of this kind may simply reflect the fact that the beginning of the list was not marked in any way, except for the minority of list presentations that were the first list presentation of a session. In Experiment 2, therefore, we looked for list position effects when a list of concurrent visual discrimination problems was presented only once in each daily session. If primacy is simply produced by the salience of list beginning as a unique position in the list, then

the conditions of Experiment 2 should promote primacy effects. Experiment 2 was run twice, in two different test situations (Experiments 2a and 2b).

The present experiments thus represent two parallel investigations into possible determinants of list position effects. At one extreme, one could suppose that a primacy effect is a universal feature of monkeys' memory for lists, and that the failure to observe primacy in some previous experiments such as those of Gaffan (1979), Gaffan and Lim (1991), Gaffan and Weiskrantz (1980), and Gaffan et al. (1984) is to be attributed to a simple artifact—namely, that primacy cannot emerge when list beginning is made difficult for the animal to discriminate from other list positions. If this account is true, then primacy effects should be seen in all the present experimental tasks, particularly in those of Experiment 2, where list beginning was also the beginning of a session and was therefore easily discriminable from other list positions. At the other extreme, one could suppose that primacy effects emerge only when a subject—human or non-human—uses list position as a retrieval cue. According to this account, following Deese (1965), it is supposed that human subjects use list position as a retrieval cue in the course of their spontaneous strategy of free recall. Whether non-human primates ever develop such a spontaneous strategy is an open question, but if this account is true, then a minimum predictive requirement is that non-human primates should show primacy effects when they are obliged by the task design to use list position as a retrieval cue. This prediction has not been previously tested and is tested by Experiment 1.

EXPERIMENT 1A

List Position Relevant

Method

Subjects. These were three Rhesus monkeys (*Macaca mulatta*)—S1, S2, and S3. Before beginning the present experiment, they had served as members of the normal control group in an experiment by Gaffan (1993). In the course of that experiment, they had learned visual discriminations for food reward in the same apparatus as was used in the present experiment, with complex pictures as the discriminanda. List position of the discriminanda within each daily session was randomized daily and was not relevant to discrimination performance in the earlier experiment.

Apparatus and Stimulus Material. Two colour monitor screens, each 364 mm in diagonal, were placed side by side, with a centre-to-centre separation of 390 mm. A food hopper was placed centrally beneath the screens, and pellets of food (190 mg) were dispensed automatically into

the hopper as rewards for correct choices. The monkey was brought to this apparatus in a wheeled transport cage, which was then fixed to the front of the apparatus. In each trial of the learning task, as further described below, the monkey chose one of the two pictures displayed on the two screens by reaching out through the bars of the transport cage to touch the chosen picture with its hand. The touch was detected by infrared beams passing over the centre of the monitor displaying the chosen picture.

The pictures were eight colour photographs of single objects, recorded on a laser disk. Each was displayed against a homogeneous grey background. The objects were chosen strictly at random (with a random number generator) from a recorded set of 400 photographs of objects that had been selected as being all discriminable from each other.

Procedure. The task consisted of repeated presentations of a list of four trials, each trial being a choice between two objects. The interval between trials within the list was 5 sec, and the interval between presentations of the list was 30 sec. If the monkey touched a stimulus screen during these intervals, the interval was re-started; the frequency of such responses was recorded and was typically zero in each session. The number of list presentations in each daily session was usually 60 list presentations for S2 and S3, and 72 list presentations for S1. On any trial, choice of the positive (rewarded) object was followed immediately by the delivery of a reward pellet into the food hopper and by the blanking of the other picture, the negative object; the positive object remained on the screen for 1 sec after the animal's choice had been made. Choice of the negative (unrewarded) object immediately blanked the other picture, the positive object; the negative object remained on the screen for 1 sec after being chosen, and no food reward was dispensed. Assignment of the positive and negative objects to the left and right screens was randomly determined at each trial.

On the first trial of every list presentation, the positive (rewarded) object was always Object A; similarly, on Trial 2 the positive was always Object B, on Trial 3 Object C, and on Trial 4 Object D. The negative (unrewarded) objects were of two types. On *easy* trials the negative was an object that was never rewarded. There was a negative object of this kind for each list position—objects W, X, Y, and Z. Thus, if Trial 1 in the list was an easy trial, it would always present a choice between A (positive) and W (negative); if Trial 2 was an easy trial, it would always present a choice between B (positive) and X (negative); and so on. On *hard* trials, however, the negative object was a misplaced positive object. On a Hard Trial 1 in the list, the negative object could be either B, C, or D; on a Hard Trial 2 in the list, the negative could be A, C, or D; and so on. Half the trials were hard trials and half were easy trials. Of the hard trials, one third at each list position presented each of the three possible negative objects for a

hard trial at that position. Within each block of six lists, each list position was tested with three easy trials and with one each of its three possible hard trials. Therefore, within each block of six lists, each of the stimuli A, B, C, and D occurred as the positive in three hard trials and as the negative in three hard trials.

Before beginning the main task as described above, the animals had one session in which all the trials were easy trials. All animals made very few errors in learning to respond correctly on easy trials, and very few errors on easy trials were recorded during the main task. The main analysis of results (below) is concerned with performance on hard trials.

The total number of list presentations was not the same for all animals. Our initial plan had been to train to a criterion of 90% correct performance, but this plan was abandoned when it became clear that the animals would require many thousands of trials to reach 90% correct performance on hard trials. S1 received 990 list presentations, S2 received 540 list presentations, and S3 received 642 list presentations.

Results

On easy trials, all animals performed above 95% correct in all sessions after the first. On hard trials, no animal achieved perfect performance, but all were above chance at the end of training. S1 chose correctly on 71% of the hard trials in the final session, S2 on 83%, and S3 on 57%.

To compare performance at the four list positions, the total number of correct choices in hard trials at each list position was calculated for each animal over the whole experiment. Table 1 shows the results in detail from each animal. For each animal, the first row in the table, labelled response C (correct), is simply the total number of correct responses at the four successive list positions; correct responses at List Position 1 are correct responses to Stimulus A, correct responses at List Position 2 are correct responses to Stimulus B, and so on. From this first row in the table alone for each animal, it can be seen that every animal made more correct responses at List Position 1 than at any other list position. To test the statistical significance of this primacy effect we performed χ^2 tests, comparing correct and incorrect responses at List Position 1 with correct and incorrect responses at the three other list positions combined. Within the data of individual animals, the tendency to make more correct responses at List Position 1 than at other list positions was significant at $p < 0.01$ in S1, $\chi^2(1) = 21.458$, and in S3, $\chi^2(1) = 44.613$. Within the data of S2, although the effect was in the same direction, it did not reach statistical significance, $\chi^2(1) = 1.607$. Combining these effects in the three animals by addition of the three chi-square values, the overall primacy effect was significant, $\chi^2(3) = 67.678$, $p < 0.01$.

TABLE 1
Experiment 1a: Results from Hard Trials

Monkey	Trials	Response	Stimulus A	Stimulus B	Stimulus C	Stimulus D	Total
S1	1980	C	366 (73.9)	346 (69.9)	257 (51.9)	323 (65.3)	1292 (65.3)
		FP	120 (24.2)	197 (39.8)	162 (32.7)	209 (42.2)	688 (34.7)
		AC	246	149	95	114	604
S2	1080	C	177 (65.6)	175 (64.8)	160 (59.3)	159 (58.9)	671 (62.1)
		FP	86 (31.9)	115 (42.6)	92 (34.1)	116 (43.0)	409 (37.9)
		AC	91	60	68	43	262
S3	1284	C	221 (68.8)	148 (46.1)	164 (51.1)	142 (44.2)	675 (52.6)
		FP	186 (57.9)	133 (41.4)	154 (48.0)	136 (42.4)	609 (47.4)
		AC	35	15	10	6	66

Note: For each stimulus the table shows the number of correct responses to it (C) and the number of false positive responses to it (FP). Each of these is also expressed in brackets as a percentage of all those trials on which there was an opportunity for a response of that type to occur. AC is the adjusted total of correct responses, C - FP.

The analysis presented above, relying only on the analysis of correct and incorrect responses at each list position, is sufficient to indicate a primacy effect; but it neglects the possibility that a finer analysis might be made possible by taking into account the negative (unrewarded) stimulus at each trial, as well as the positive. (The positive, rewarded stimulus was always A at List Position 1, for example, but the negative stimulus at List Position 1 on hard trials could be either B, C, or D.) For example, there might be response biases towards particular visual stimuli, irrespective of list position; these would be reflected in a high total of false positive responses to those stimuli. We therefore also calculated the total of false positive responses to each of those four stimuli when they were negative stimuli, presented at one of the three list positions other than the position at which they were positive. The resulting totals are presented in the row labelled response FP (false positive) in the table. It can be seen that, for example, S1 made more responses overall to stimuli B and D than to stimuli A and C, combining correct and false positive responses. From inspection of the other values in the table, it appears that individual monkeys' response biases towards particular stimuli were idiosyncratic.

To take into account these response biases, each animal's total of correct responses at each list position was therefore adjusted by subtracting from it the total of that animal's incorrect responses to the same stimulus when it was the negative stimulus at some other list position. (As explained in the Method section, each of the stimuli A, B, C, and D appeared as a negative stimulus, in a hard trial at some list position other than its rewarded position, on the same number of trials as those on which it appeared as a positive stimulus, in a hard trial at its rewarded position.) For example, the adjusted total of correct responses by S1 to Stimulus A at List Position 1 is 246 (366 minus 120, see Table 1). This adjusted total allows for response bias and also allows for chance responding; if an animal's responses are unrelated to list position, with or without response bias towards particular stimuli, then the adjusted total of correct responses at each list position will be zero. The adjusted total was then expressed as a percentage of the adjusted total of correct responses for that animal in the whole experiment; for S1 at position 1, 246 is 40.7% of 604 (1292 minus 688—see Table 1). These percentages of all correct responses thus adjust not only for response bias towards particular stimuli irrespective of list position, but also for the differences among animals in their overall average level of correct responses. The percentages of all correct responses, thus derived, are shown in Panel A of Figure 1. The expected value if there is no primacy effect is 25% at each list position for each animal; all animals exceeded this value at List Position 1. The four successive list positions showed a monotonic decline in the group average correct responses.

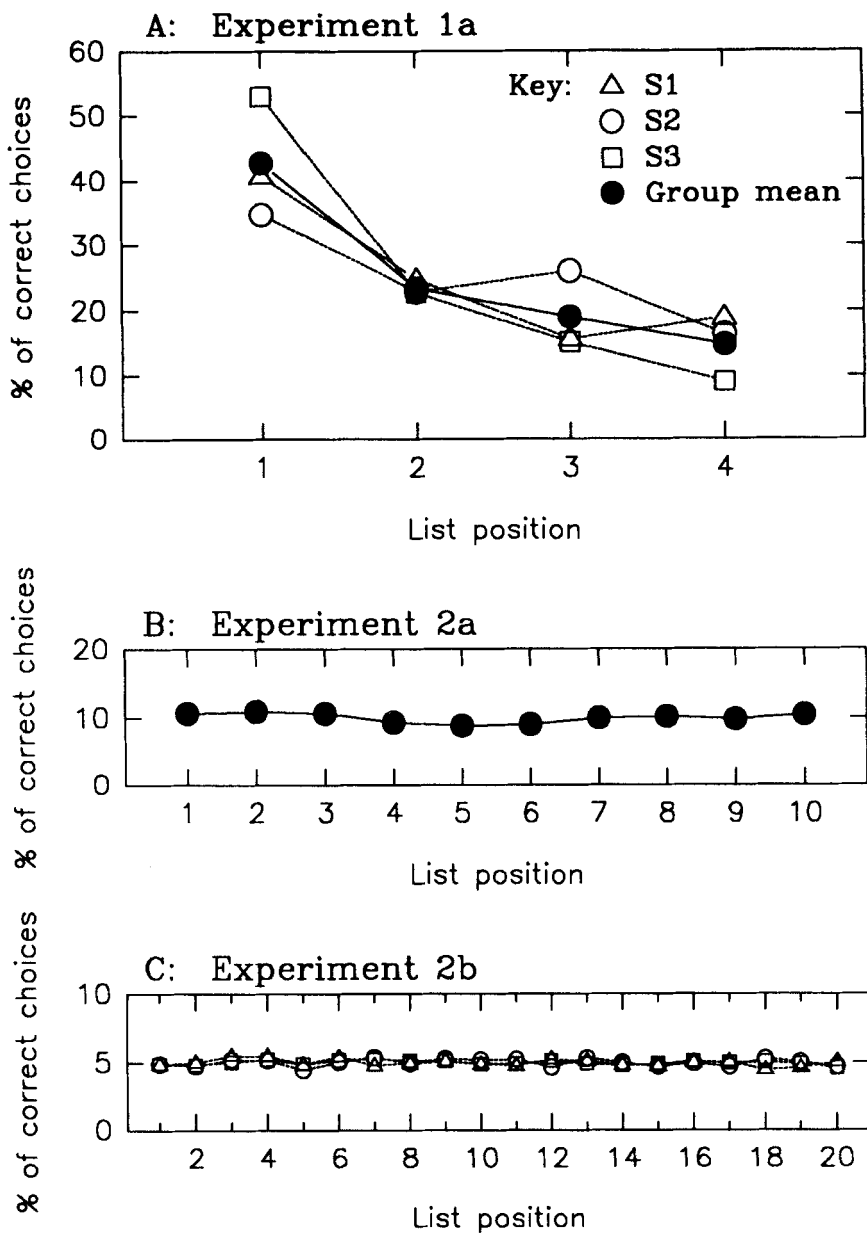


FIG. 1. Results from Experiments 1a, 2a, and 2b. The symbols in Panel A are explained in the key. The symbols in Panel B show the mean performance of a group of nine monkeys, S4 through S12. The symbols in Panel C show the performance of S13 (triangle), S14 (circle), and S15 (square).

TABLE 2
 Experiment 1a: Evidence for a Specific Advantage for the First Stimulus in the List, Stimulus A

Monkey	Response	A Present	A Absent	$\chi^2(I)$
S1	C	741	551	80.412*
	W	249	439	
S2	C	361	310	10.236*
	W	179	230	
S3	C	356	319	4.276*
	W	286	323	

* $p < 0.05$.

Note: All hard trials are classified as having A present or absent, and as eliciting either a correct (C) or wrong (W) response.

Within each animal's data, the statistical significance of the primacy effect was computed from a further χ^2 test, which took into account the negative stimulus as well as the positive stimulus on each trial. Trials were classified into those with A present, either as a negative or as a positive stimulus, and those with A absent. For each animal, the proportion of correct responses was higher when A was present (Table 2). This result shows that the animals learned more about A than about the other stimuli, and that their high proportion of correct choices of A as a positive stimulus in List Position 1 was not simply the result of a bias towards A, independent of list position.

EXPERIMENT 1B Replication of Experiment 1A

The purpose of this experiment was to show that the results of Experiment 1a were not limited to the particular objects that happened to play the roles of the Stimuli A, B, C, and D in that experiment, but would also be seen with other stimuli in the same task.

Method

The subjects were S1 and S2, two of the subjects from Experiment 1a. They performed the present experiment immediately after completing Experiment 1a.

The apparatus was the same as that used in Experiment 1a.

The task was exactly the same as in Experiment 1a, except that different stimuli played the role of Stimulus A, B, C, and so on, as described above.

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Designating the list in Experiment 1a as List 1, three further lists—Lists 2, 3, and 4—were generated for the present experiment by selecting for each list eight new visual stimuli at random from the available pool of stimuli, described above. Monkey S1 was trained on List 2 and List 3, and Monkey S2 was trained on List 4. As before, training on the main task with each list was preceded by a session in which no hard trials were presented. Following this preliminary training, S1 had 72 list presentations in the main task, including a total of 144 hard trials, with each of Lists 2 and 3, and S2 had 420 list presentations in the main task, including 840 hard trials, with List 4.

Results

In each list an adjusted total of correct responses was calculated as described above in Experiment 1a. Also a χ^2 value was calculated, as described above in the final paragraph of the results of Experiment 1a, to test the hypothesis that performance was superior in the presence of Stimulus A (either as a positive or as a negative stimulus) than in the absence of Stimulus A. In List 2, 40.4% (21/52) of the adjusted correct responses were made to Stimulus A; in List 3, 61.1% (11/18) of the adjusted correct responses were made to Stimulus A; in List 4, 32.7% (81/248) of the adjusted correct responses were made to Stimulus A. All these values are above 25%, the value expected if there is no advantage for Stimulus A. Performance in the presence of Stimulus A was superior to performance in the absence of Stimulus A in all three lists. For List 2, $\chi^2(1) = 8.177$; for List 3, $\chi^2(1) = 4.792$; and for List 4, $\chi^2(1) = 7.533$. Each of these values is significant at $p < 0.05$.

EXPERIMENT 2A

Lists in a Wisconsin General Test Apparatus

Method

Subjects. Of the nine monkeys in the present experiment, six (S4–S9) were experimentally naive Cynomolgus monkeys (*Macaca fascicularis*). For these animals, the present task was the pre-operative training phase of a longer experiment (Gaffan & Murray, 1992). The remaining three (S10–S12) were Rhesus monkeys (*M. mulatta*). They learned the present task subsequent to a discrimination learning task with complex pictures (Gaffan, 1992), similar to that which the monkeys in Experiment 1 had previously learned (Gaffan, 1993).

Apparatus. Training was conducted in a Wisconsin General Test Apparatus. During intertrial intervals, an opaque screen separated the animal from the stimulus tray and the experimenter. A one-way-vision

screen allowed the experimenter to observe the animals during trials without being seen. Free-standing stimulus objects covered the food wells in the stimulus tray at the beginning of a trial. There were two food wells, 25 mm in diameter, 300 mm apart centre to centre. The stimulus objects differed from each other in shape, size, and colour. The rewards were either peanut halves or food pellets (190 mg).

Procedure. The animals first learned to displace objects for food reward in the test apparatus; objects used in this preliminary training were not used in subsequent discrimination training. They then learned a set of 10 discrimination problems (pairs of objects) presented concurrently. The left-right position of the correct object was determined pseudorandomly from trial to trial. There was one trial with each pair in each daily session of 10 trials. For any individual monkey, the pairs were presented in the same order each day; different monkeys had different orders, however (see below). Training was continued with each animal until the animal reached a criterion of acquisition by making a total of 3 errors or fewer in the 30 trials of 3 successive days' sessions (90% correct choices).

Each monkey started the list with a different pair of objects, but the order in which pairs of objects succeeded each other was the same for all monkeys. Thus the list for Subject S4 was pairs 1 through 10, in order; for S5, 2 through 10, then 1; S6, 3 through 10, then 1, 2; S7, 4 through 10, then 1 through 3; and so on. The intertrial interval was 10 sec throughout; the transition from Pair 10 to Pair 1 in a list as experienced by monkeys S5-S12 was identical to any of the other transitions between pairs.

Results

The choices made by each animal on the first session with the list (one trial at each list position) were discarded from analysis, as these choices reflect guesswork rather than memory. Across all the remaining trials, including those in the criterial sessions, correct responses were summed for each list position for each animal. Analysis of the correct responses for all ten list positions showed no significant effect of list position, $F(9, 72) < 1$. Table 3 presents the results in detail. It can be seen that no individual animal gave a strong indication of a primacy effect.

Panel B in Figure 1 shows the average of correct responses at each list position, expressed as a percentage of each animal's total correct responses, as in the comparable analysis of Experiment 1a (Panel A). The result expected by chance in the present experiment, if there are no list position effects, is 10% at each list position. It can be seen that the obtained results were close to those expected by chance and gave no indication of a primacy effect.

TABLE 3
Experiment 2a: Correct Responses by Individual Subjects at Each List Position

Monkey	LP1	LP2	LP3	LP4	LP5	LP6	LP7	LP8	LP9	LP10
S4	19	17	19	17	17	10	8	18	19	10
S5	10	12	10	7	10	11	10	13	7	11
S6	19	16	18	19	7	17	11	11	16	17
S7	15	15	9	15	14	3	13	11	13	15
S8	9	8	9	10	7	7	9	10	9	9
S9	17	11	15	15	5	14	15	14	14	16
S10	9	12	10	11	10	9	12	12	10	12
S11	4	8	8	2	7	8	8	5	4	7
S12	11	11	10	5	10	10	11	9	11	8

Note: S10, S11, and S12 are Rhesus monkeys, and the remaining subjects are *Cynomolgus* monkeys.

EXPERIMENT 2B

Lists in an Automated Apparatus

Method

Subjects. These were three Rhesus monkeys (*Macaca mulatta*), S13, S14, and S15. They were trained in the present task as members of the normal control group in an experiment by Murray et al. (1992).

Apparatus. The monkey was brought to the training apparatus in a wheeled transport cage, which was then fixed to the front of the apparatus. The monkey could reach out through bars at the front of the transport cage to touch a monitor screen, which was 210 mm from the front of the cage. Discriminative stimuli were displayed on the monitor screen on the left or right of the screen. The left and right positions were separated by 150 mm. A capacitance-sensitive touch screen indicated to the computer which stimulus the animal had touched. Food rewards were delivered into a hopper placed centrally underneath the monitor screen. The food rewards were 190-mg food pellets. The discriminative stimuli were constructed by superimposing one coloured text character upon a different larger text character in a different colour—for example, a small magenta curly bracket on a large grey-green T. These stimuli had a maximum height of 50 mm.

Procedure. All the monkeys learned the same seven lists of 20 discrimination problems (pairs of stimuli). Training on each list was completed before training on the next list began. Each list was presented for 20

successive daily sessions of 20 trials, one trial per discrimination problem per day. The order in which the 20 problems were presented in the session (list position) was the same every day. Each trial proceeded as follows. Two simultaneously presented stimuli occupied the left and right positions on the screen. One was the positive (rewarded) stimulus in the problem, the other the negative. Their left-right position on the screen was determined randomly. The stimuli remained on the screen until the monkey chose one by touching it; both stimuli then disappeared. If the monkey chose the positive stimulus, a food reward was delivered. If the monkey chose the negative stimulus, no food was delivered. Before the next trial began, there was an intertrial interval of 12 sec, during which any touch to the screen would reset the interval.

Results

All the animals exhibited proficient learning of the lists of discriminations. In Sessions 2 through 20 with each list, S13 made, on average, 83.1% correct responses, S14 made 86.3% correct responses, and S15 made 88.6% correct responses. For each animal, the total across all seven lists of correct responses at each list position was calculated across Sessions 2 through 20 with each list. The percentage for each animal of the animal's total overall correct responses on Sessions 2–20 was then calculated for each list position, as in Experiment 2a. The value expected by chance, if there is no effect of list position, is 5%. The results from the three individual subjects are shown in Panel C of Figure 1. It can be seen that no individual showed a primacy effect.

DISCUSSION

The task in the first experiment was to choose between visual stimuli on the basis of their position in a list. This type of discrimination has not been studied extensively in monkeys. Swartz, Chen, and Terrace (1991) showed that monkeys are capable of this type of learning and argued that an understanding of visual serial order learning would shed light on broader questions relating to the temporal organization of action. Our results support the conclusions of Swartz et al. (1991) and show that monkeys can also learn serial order discriminations with a procedure slightly different from theirs, although the fact that S3 in Experiment 1a learned the task rather poorly may indicate that their method of training is more reliable than is ours. The advantage of our procedure for present purposes is that, unlike that adopted by Swartz et al. (1991), it allows primacy effects to be assessed. These proved to be powerful and replicable (Experiment 1b). Thus, it appears that primacy effects reliably emerge in discrimination learning when list position is relevant to discrimination performance.

Much of the interest in primacy effects in animals centres on comparison with human memory. The task of Experiment 1 is a more constrained task than human free recall, as the task overtly requires the monkeys to discriminate the serial position in which an item occurs. Nevertheless, human subjects frequently and perhaps universally exhibit a spontaneous tendency to use serial order as one important retrieval strategy in free recall of items from lists (Deese & Kaufman, 1957; Deese, 1965). In discovering parallels between memory in human and non-human primates, one important future goal will be to find conditions in which non-human primates spontaneously make use of serial position information in memory for lists of items. The present data suggest that the emergence of a primacy effect might serve as a useful marker to indicate the spontaneous use of serial position as a retrieval cue; of course, independent evidence of such a retrieval strategy would also be required if it was to be firmly established.

Experiments 2a and 2b employed discrimination learning tasks in which there was no overt requirement for the monkey to discriminate serial position, but list beginning was made easily discriminable from other list positions by presenting each list only once in each daily session. These experiments showed no primacy effects. The main importance of these results is to show that, contrary to the expectation outlined in the introduction, primacy effects cannot be obtained simply by ensuring that the beginning of the list is clearly differentiated from other parts of the list.

A subsidiary result in all of the present experiments was that there was no superiority for items at the end of the list. In discussing memory for items at the end of a list, it is essential to distinguish between two possible sources of enhanced memory for these items, as compared with items in the middle of a list. One of these two possible sources is a *recency* effect defined by time. A superiority for items at the end of a list can arise from the fact that in many experimental paradigms (such as probe recognition, as used, for example, by Castro & Larsen, 1992, or reverse-order testing, as used, for example, by Gaffan, 1979) the retention interval, between acquisition of an item in memory and the subsequent retention test for that item, is shorter for items at the end of the list than it is for items earlier in the list. The other of the two possible sources is an *acquisition-order* effect determined by position at the end of the list, irrespective of retention interval for individual items at a subsequent retention test. In delayed non-matching-to-sample, Gaffan and Weiskrantz (1980) showed that the superiority for items at the end of a list of samples in delayed non-matching-to-sample was a recency effect rather than an acquisition-order effect; for example, it could be abolished by interpolating an unfilled interval between the end of the list of samples and the beginning of the retention tests, thus making the retention interval similar for all items. In one-trial associative-memory tasks, experiments with immediate retention

tests of lists of discrimination problems have shown a strong superiority for items at the end of the acquisition list (Gaffan, 1979; Gaffan et al., 1984; Gaffan, 1985); but these experiments confounded recency effects with acquisition-order effects. In the present Experiments 2a and 2b, all items were equally recent at their retention tests, as they had all been seen 24 hr before. Thus, the present results suggest that the superiority for items at the end of the list, seen in the earlier experiments (Gaffan, 1979; Gaffan et al., 1984; Gaffan, 1985), was a recency effect rather than an acquisition-order effect. These results are unsurprising, because they indicate that what was earlier established for delayed non-matching-to-sample (Gaffan & Weiskrantz, 1980) is also true of associative memory tasks. Similarly, in Experiment 1 there was no evidence of a superiority for items at the end of a list; and here, also, there was no recency advantage for these items, as retention interval between successive presentations of each positive stimulus was the same (30 sec) for all list positions. Thus, in all these experiments, there were no differences of recency and no superiority for items at the end of the list, and therefore no evidence of an acquisition-order effect independent of temporal recency.

In conclusion, there are two main features of the present results, one negative and one positive. A primacy effect was not obtained simply by making list beginning easily discriminable from other list positions (Experiment 2), but a primacy effect did appear when monkeys were overtly required to use list position as a cue for discriminative performance (Experiment 1). These two results are clearly compatible with Deese's (1965) argument that primacy effects are not a universal or necessary feature of human memory but, rather, are specifically generated by the subjects' use, spontaneously or under overt instruction, of list position as a retrieval cue. Of course, the negative results of Experiment 2 cannot rule out the possibility that primacy effects in non-human primates might emerge reliably under some other, as yet unexplored, conditions of testing; indeed, the possibility should not be dismissed that non-human primates might spontaneously generate a recall strategy based on list position in some circumstances. Nevertheless, the present results are clearly compatible with Deese's (1965) account, which should receive more attention in future experiments designed to explore the non-human analogues of human list-position effects in memory.

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Effet de primauté chez des singes lorsque la position dans la liste est pertinente

Lors de l'Expérience 1 (1a et 1b), des singes Rhesus (*Macacca mulatta*) apprennent des listes de discriminations visuelles à double choix, dans lesquelles la position dans la liste est pertinente pour la performance. Par exemple, le choix du stimulus A était récompensé si ce dernier était présenté en tête de liste; il n'était pas récompensé s'il apparaissait à une autre position; de même, le choix du stimulus B était récompensé seulement si ce dernier apparaissait en seconde position, etc. Tous les sujets manifestent un net effet de primauté lors de l'apprentissage des listes. Dans l'Expérience 2 (2a et 2b), des singes Rhesus et *Cynomolgus* (*M. fascicularis*) apprennent des listes de discriminations visuelles dans lesquelles chaque stimulus visuel occupe une position fixe, cette dernière n'étant cependant pas pertinente pour la performance de discrimination. Par exemple, le choix du stimulus E était récompensé dans tous les cas et ce stimulus était toujours présenté en tête de liste. Afin d'accroître la discriminabilité du début de liste comme événement distinct, les présentations successives de la liste étaient séparées par des intervalles de 24 heures. L'effet de primauté n'est cependant pas apparu lors de l'expérience 2. Les données montrent pour la première fois qu'un effet de primauté peut être obtenu lors d'un apprentissage de discrimination visuelle chez les singes. De plus, elles suggèrent que cet effet survient seulement si la position dans la liste est pertinente pour l'apprentissage de la discrimination.

Efectos de primacía en los monos cuando la posición en la lista es relevante

En el Experimento 1 (1a y 1b), unos macacos rhesus (*Macaca mulatta*) aprendieron listas de discriminaciones visuales de doble alternativa en las que la posición en la lista era relevante para la actuación discriminativa. Por ejemplo, el estímulo A era recompensado si era presentado en la posición 1, pero no si era presentado en cualquier otra posición de la lista; igualmente, el estímulo B era recompensado sólo en la posición 2, y así sucesivamente. Al aprender estas listas, todos los animales mostraron un fuerte efecto de primacía. En el Experimento 2 (2a y 2b), macacos rhesus y macacos cangrejeros (*M. fascicularis*) aprendieron listas de discriminaciones visuales en las que cada estímulo ocupaba una posición fija que no era relevante para la actuación discriminativa. Por ejemplo, el estímulo E era siempre recompensado y aparecía siempre en la posición 1. A fin de aumentar la saliencia del comienzo de la lista como evento distintivo, las presentaciones sucesivas de la misma fueron separadas por intervalos de 24 horas. Sin embargo, en el Experimento 2 no se observó el efecto de primacía. Estos resultados muestran por vez primera que es posible obtener un efecto de primacía en el aprendizaje de discriminaciones visuales por monos e indican además que este efecto sólo se obtiene cuando la posición en la lista es relevante para la tarea de aprendizaje discriminativo.