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Primacy, Recency, and the von Restorff Effect in Rats' Nonspatial Recognition Memory

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In 2 experiments, nonspatial memory was investigated. Hungry rats obtained food in a Y maze with a continuous nonmatching-to-sample procedure, which used objects placed in goalboxes as stimuli. Rats visited 5 goalboxes, each containing 1 object. After a retention interval, the rats were presented with a choice between a goalbox identical to one in the series and a novel goalbox. Of 11 subjects, 8 displayed both primacy and recency effects, 1 displayed only recency, and 2 displayed no systematic serial position effects. Subsequently, on some sessions, the 3rd goalbox in the list was accompanied by a salient stimulus. In 8 of the 11 subjects, this procedure led to enhanced recall of the goalbox that was associated with the stimulus change.

When a number of items (e.g., nonsense syllables, pictures, words) are serially presented, humans tend to recall the items at the beginning and at the end of the list better than the items in the middle of the list (e.g., Glazner & Cunitz, 1966). Recall of the items at the beginning of the list is referred to as *primacy*, and recall of items at the end of the list is referred to as *recency*. Together, these two effects constitute a *serial position curve*. If an unusual or outstanding event occurs in an otherwise homogeneous series (e.g., a picture of an animal is incorporated into a list of pictures of plants), recall for the outstanding item is enhanced, relative to recall for a nonsalient item occupying the same serial position in the list. This effect is referred to as the *von Restorff effect* (Battacchi, Pelamatti, & Umilta, 1989; Brown & Kulik, 1977; von Restorff, 1933; Wallace, 1965).

There has been recent interest in demonstrating a correspondence between memory in human and nonhuman subjects (e.g., Ellis, Clegg, & Kesner, 1984; Kesner & DeSpain, 1988; Petrides, 1985; Wagner, Rudy, & Whitlow, 1973; Wright, Santiago, Sands, Kendrick, & Cook, 1985). The serial position curve has exerted an important influence on the development of theories regarding human memory (e.g., Atkinson & Shiffrin, 1968; Melton, 1963), and for this reason it may be considered of prime concern to those interested in the functional equivalence of human and nonhuman memory to demonstrate a serial position curve in nonhuman species. Initially, several reports demonstrated a recency but not a primacy effect in species such as dolphins (Thompson & Herman, 1977) and rhesus monkeys (Gaffan, 1977; Gaffan & Weiskrantz, 1980). However, manipulation of the retention period between exposure to the list and test, demonstrated that recency and primacy effects could be obtained in pigeons and rhesus monkeys (Wright et al., 1985). During the experiment by Wright et al., a subject was exposed to a number of stimuli and, after a retention period, was tested for recognition of these stimuli by being offered a choice between a previously presented stimulus and a novel stimulus. To obtain a reward, the subject had to respond to the novel stimulus. When the test immediately followed presentation of the list, a recency effect was noted; when the test occurred following a long retention period (e.g., 60 min), primacy was noted; but when intermediate retention periods were given, both primacy and recency effects were noted together. Similar effects were observed by Wright et al. with human subjects: primacy and recency effects were obtained together only with an intermediate retention period between list exposure and test.

Investigation of serial list learning in rats has so far been restricted to memory for spatial items (e.g., Bolhuis & van Kampen, 1988; DiMattia & Kesner, 1984). Typically, this procedure involves (a) an exposure phase, in which a rat is allowed to visit a number of food-baited arms in an eight-arm radial maze, and (b) a test phase, in which the subject has a choice between a previously visited arm and a novel arm. At test, food is placed only in the novel arm. Given an appropriate retention interval between exposure and test, rats display both primacy and recency effects (Bolhuis & van Kampen, 1988). That is, rats choose a novel arm more reliably, when comparing a novel arm with one previously visited at the start of or at the end of the exposure phase, than

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when the novel arm is compared with one visited in the middle of the exposure phase. Note that if a win–stay, rather than a win–shift, procedure is adopted, then such primacy and recency effects can be obtained with minimal retention intervals between exposure and test (e.g., DiMattia & Kesner, 1984).

Although the aforementioned studies have demonstrated primacy and recency effects in nonhuman subjects, criticisms of such studies may temper the interpretation of such effects as being equivalent to those generated with human subjects. Several reports of primacy and recency have reported these effects averaged over groups of subjects (e.g., Bolhuis & van Kampen, 1988; DiMattia & Kesner, 1984). It may be that some subjects in these studies displayed a primacy effect, and some subjects displayed a recency effect: When averaged over the entire group, these effects would have combined to produce group-mean primacy and recency effects. Such group-mean serial position curves may be produced, however, without individual subjects displaying the dual serial position effect. Although several reports have displayed data for single subjects and have noted both primacy and recency effects within individual animals (e.g., Sands & Wright, 1980; Wright et al., 1985), these studies may be criticized on procedural grounds (see Gaffan, 1983). Both the study by Sands and Wright and the study by Wright et al. presented the list contingent on a response made by the subject. This response may have conferred a selective performance advantage at test on the early members of the list (perhaps through motor mediation) and thus generated an apparent primacy effect that had nothing to do with central memory processes. Consistent with this notion is the failure to observe primacy and recency in an experiment that presented all stimuli contingent on a subject's response (Gaffan & Weiskrantz, 1980).

Given the robust nature and importance of serial position effects in studies of human memory, if human and nonhuman memory systems are to be regarded as analogous, then serial position phenomena should readily be obtained in nonhumans under a wide variety of procedures. Before examining the functional equivalence of human and nonhuman memory, we need to verify that serial position effects can be obtained in rats in a design that is not subject to the criticisms discussed here.

In addition to examining serial position effects with nonspatial information in rats, the present study also investigated whether a von Restorff-like effect could be obtained in rat subjects. Several studies have noted that a salient event presented after a choice response allows rats to learn a spatial discrimination, in spite of a long delay between the choice response and reinforcement (Lieberman, McIntosh, & Thomas, 1979). Analogous effects have been demonstrated in Pavlovian trace conditioning with pigeons (Rescorla, 1982; Thomas, Robertson, & Lieberman, 1987) and instrumental conditioning of rats (Reed, 1989); the presence of a stimulus in the interval between the offset of the target stimulus or response and the delivery of the reinforcer facilitates the acquisition of conditioned responding. Given that memory for nonspatial information is facilitated by the presentation of a salient event (Reed, 1989; Thomas et al., 1987), one expects that a nonspatial item presented in a list may be better recalled if it is accompanied by a salient event. That is, a von Restorff-like effect should occur in nonhumans. Such an effect would extend the functional equivalence of effects noted in several procedures between humans and nonhumans.

Experiment 1

Previous demonstrations of serial position effects for nonspatial information in primates have used recognition tasks based on the nonmatching-to-sample procedure described earlier (e.g., Wright et al., 1985). An analogue of this task has been developed for rats (Aggleton, 1985; Steele & Rawlins, 1989). In this task, rats are tested on a continuous nonmatching-to-sample procedure for recognition of objects. On each trial the rat must choose between a familiar and a novel goalbox; the goalboxes contain objects similar to those used in primate testing. A three-arm Y maze is used; the rat emerges from a goalbox in one arm and must choose between goalboxes in the other two. The task is continuous in that the novel goalbox in one trial is used as the familiar goalbox in the next trial. By allowing the rat to run to a number of different goalboxes prior to the nonmatching recognition test, a list of objects may be built. One goalbox from the list can then be selected for test. By using a number of such lists during each session by testing recognition of goalboxes occupying the different serial positions in the list, we may determine a complete serial position curve for each subject on each session. In the present experiment, we used a 20-s retention interval between list exposure and the recognition test, as previous work indicated that using this interval produces both primacy and recency effects in spatial memory tasks (e.g., Bolhuis & van Kampen, 1988).

Method

Subjects

A total of 16 experimentally naive male DA strain rats (Bantin & Kingman) served in Experiment 1. The rats were 3–4 months old at the start of the experiment, had a free-feeding body weight of 250 g–285 g, and were maintained at 80% of this weight throughout the study. The animals were housed individually, except when they were tested, in which case they were transported into the test room in groups of 3 or 4. The rats had water constantly available in the home cage.

Apparatus

Testing was conducted in a Y maze (Figure 1). Each arm of the maze was 13-cm wide and 20-cm high; the distance from the center of the maze to the back wall of the goalbox was 37 cm. The maze contained a central door that, when lowered, simultaneously blocked access to all three arms of the maze. Another door, located 18 cm along each arm of the maze, blocked access only to the goalbox located at the end of that arm of the maze. The doors were manually operated by overhead cables. A small opening was mounted above each goalbox, immediately behind the goalbox door, 20 cm from the center of the maze. Through this opening reinforcement (one 45-mg food pellet) could be delivered. Also, three 24-W light bulbs, which could be used to illuminate the goalbox, were mounted over the goalbox.

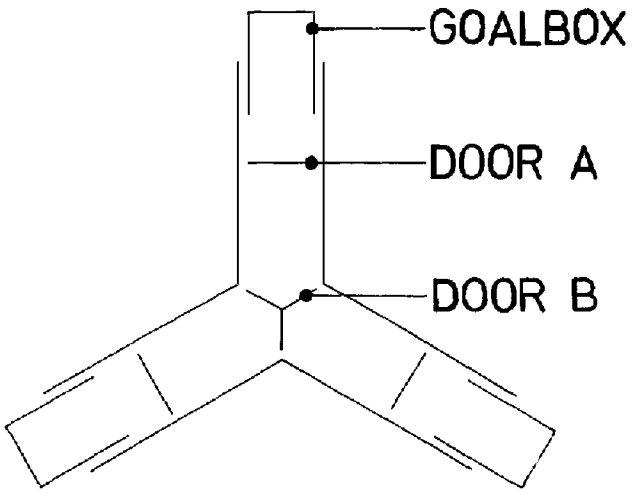

Figure 1. Schematic representation of the Y maze used in the present experiments.

Distinctive goalboxes (Figure 2) could be inserted into the ends of each arm. These goalboxes differed in texture, design, and in the objects that they contained. There were 50 pairs of goalboxes, each pair different to the human eye from every other pair (although the two members of a pair were identical). In addition to the distinctive goalboxes, three blank goalboxes that contained no object or design were used. For 8 subjects, the goalboxes were illuminated during training; for the remaining 8 subjects, the goalboxes were not illuminated. The apparatus was located in a dimly illuminated room.

Procedure

Maze adaptation. The rats were initially adapted to the maze in six, 40-min sessions. During Session 1, groups of 4 animals were exposed to the maze with the doors removed and food pellets scattered throughout the maze and the blank goalboxes. In Session 2, groups of 4 rats were exposed to the maze, but during this and all future sessions of adaptation, four food pellets were located only in each of the blank goalboxes. For Sessions 3 and 4, rats were placed in the maze in pairs. Finally, in Sessions 5 and 6, rats were exposed to the maze individually. By the end of this phase of training, all of the subjects were consistently eating the food pellets.

Maze running. For the following 10 sessions, subjects were taught to run down the arms of the maze to obtain food. Each of the sessions of this phase lasted until the rat had entered six goalboxes (i.e., had run down every arm twice, once each from the two other arms). The center door was removed for this phase of training, but the goalbox doors were in place. During the first 4 sessions, rats were placed in the center of the maze. One of the goalbox doors was then raised and remained raised until the rat had entered the goalbox. After approximately 10 s, the door of the goalbox containing the rat and the door to a second goalbox were simultaneously opened. The doors remained open until the rat had run down the arms of the maze and entered the second goalbox, after which reinforcement was obtained. In Sessions 5–10, the procedure was as described here, except that reinforcement was dropped into the goalbox through the delivery slot. Thus, the subject had to search the goalbox to locate the pellet. By the end of this phase, all of the subjects were running the maze for food pellets.

Nonmatching. During this phase, the center door was lowered to its resting position to block access to all three arms. A rat was placed in one of the arms with all of the doors lowered. The goalbox door for that arm was then raised, and the rat was allowed to enter one of the distinctive goalboxes (Goalbox A). On entry, the door was lowered, and a pellet was dropped into the chamber. After 10 s, all of the doors were opened, and the rat could choose between the other two goalboxes. One of these goalboxes was identical to the previously visited box (Goalbox A′); the other was novel. Subjects had to enter the novel box to obtain reinforcement. If the rat chose the novel box, the doors were lowered and food was delivered. We deemed that a choice had been made when the back legs of the animal had crossed the plane of the center door. The subject would then have 10 s in Goalbox B before being offered a choice between Goalboxes B′ and C, and subsequently between Goalboxes C′ and D. If the subject chose the familiar goalbox, no reward was given. After 10 s, the subject was offered the same choice: If the subject chose correctly, it was confined to the correct box for 10 s, but no food was given. If the subject had failed to emit a correct choice within five attempts, only the correct goalbox door was raised to force the subject to that goalbox. During each session, subjects completed 10 choice trials between pairs of different goalboxes (i.e., got up to a choice between Goalboxes J′ and K), regardless of the number of correct and incorrect choices made. The position of the correct alternative (i.e., left or right) was varied from trial to trial, hence, making the task nonspatial. The possibility that odor cues were used by individual subjects within a trial was precluded by the use of a replica goalbox, not previously visited by that subject. This phase of training lasted until the subjects had obtained a score of 75% accuracy on each of the last 5 sessions. Of the 16 subjects, 5 (2 from the illuminated goalbox group and 3 from the dark goalbox group) failed to reach this criterion within 50 sessions and were excluded from the study; the best performance of any of these animals on any session was 60% correct.

List learning. Following acquisition of the basic nonmatching rule, rats began training on the list-learning procedure. During this phase, we placed the rat in the center of the maze, opened a goalbox door, and allowed the rat to enter one of the distinctive goalboxes. We gave the rat one food pellet, which we dropped into the goalbox, and allowed the rat to spend 10 s in the box. We then raised the first goalbox door, along with the center door and the door to a second goalbox. The rat was allowed to run into the second goalbox, the doors were lowered, and a food pellet was delivered. The procedure was repeated until the rat had experienced five different, distinctive

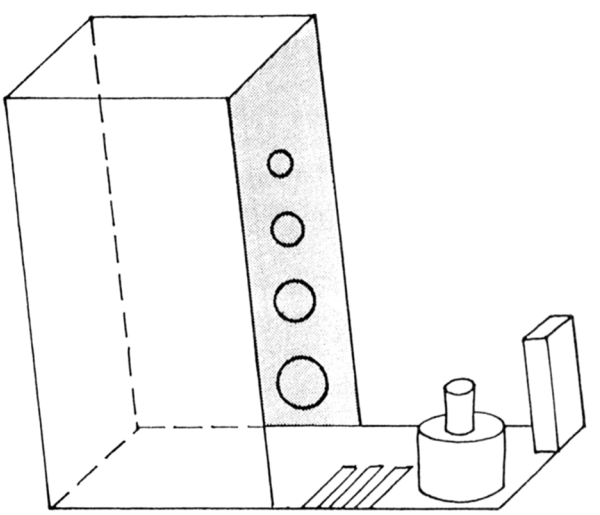

Figure 2. Schematic representation of a goalbox and the objects that it contains.

goalboxes. After presenting the fifth goalbox, we allowed the subject to run into a blank goalbox: No reinforcement was given in the blank goalbox, and the rat remained there for approximately 20 s. After the retention period, we gave the subject a choice between the matching pair of one of the goalboxes from the list versus a novel goalbox. Reinforcement was contingent on entry of the novel goalbox, as described earlier in the nonmatching phase of the study. The position of the novel goalbox (left vs. right) was randomized across trials. We then allowed the rat to run out of the chosen box and removed it from the center of the maze. Each rat received five such trials during a session, which allowed a complete determination of a five-item serial position curve per rat, per session. The serial position tested during each trial was randomized across sessions. We used five different goalboxes for each new list on every trial of every session, although all of the subjects experienced the same list of goalboxes and the same novel goalbox on a given trial in a given session. Subjects also received testing on the same serial position of a given trial of a given session. Between-subject use of odor cues was reduced as far as possible by wiping the goalboxes with water after each subject had been tested. The intertrial interval was approximately 6 min. This phase lasted 20 sessions.

Results

The 11 subjects that reached the acquisition criterion for the basic nonmatching-to-sample rule did so in a mean of 365 trials (range = 300–430); this score represented only the first choice between a pair of goalboxes. The 6 subjects trained with illuminated goalboxes required a mean of 383 trials (range = 350–410) to each criterion, whereas the subjects trained in the dark goalbox required a mean of 341 trials (range = 300–390) to reach criterion. A t test conducted on this data revealed no group difference ($p < .20$).

We assessed the possibility for each subject that the outcome of one trial (T1) influenced the subjects response on the next trial (T2). The data from both groups (i.e., subjects trained in the light and dark) were pooled for this purpose, and four outcome contingencies were specified: T1 correct and T2 correct, T1 correct and T2 incorrect, T1 incorrect and T2 correct, and T1 incorrect and T2 incorrect. These data are displayed in Table 1, which represents the totals for the 880 possible outcome contingencies (excluding the influence of Trial 5 from one session on the outcome of Trial 1 on the next session).

On the basis of the selection criterion, it would be expected that at the end of pretraining, the subjects would have performed at greater than 75% accuracy. Comparison of the actual with the expected data revealed no systematic differences except that fewer correct responses (64% of the total) were recorded than would have been anticipated on the basis of the selection criterion. This was confirmed by the use of a chi-square test that revealed no significant difference between the obtained and expected results ($p > .20$).

A serial position curve became apparent after the first six sessions of testing; subjects performed better during test trials when the familiar goalbox came from the beginning or from the end of the list. The mean scores pooled for all of the subjects over the initial six sessions were 70%, 50%, 66%, 68%, and 73%, for Items 1–5, respectively. However, to ensure the reliability and robustness of the effect, testing was continued and analyses were performed on the terminal levels of performance.

Table 1
Influence of the Outcome of One Trial (T1) on the Outcome of the Next Trial (T2) for All Subjects Over All Sessions of Experiment 1

Outcome contingency	T2 correct occurrences		T2 incorrect occurrences	
	Actual	Expected	Actual	Expected
T1 correct	384	493	202	167
T1 incorrect	199	167	82	53

Figure 3 displays the mean percentage accuracy on test trials, averaged over the final six sessions, for all subjects. The 6 subjects represented in the left panel of the figure were trained in the illuminated goalboxes. These data reveal that 4 of the 6 rats (Subjects R2, R4, R7, and R15) displayed both primacy and recency effects, and 2 rats (Subjects R3 and R16) displayed no consistent effect of serial position on recall of the object. The 5 subjects represented in the right panel of Figure 3 were trained in the dark goalboxes. These data demonstrate both primacy and recency effects in 4 out of 5 subjects, the exception being Subject R9, which displayed no consistent effect. We subjected the individual subject data displayed in Figure 3 to a two-factor analysis of variance (ANOVA), using serial position (i.e., 1–5) as a within-subject variable, and group (light vs. dark goalbox) as a between-group variable. This analysis revealed a significant main effect of serial position, $F(4, 36) = 10.84$, $p < .01$, but neither the main effect of group nor the interaction of the two variables was significant ($F < 1$). Given that neither the main effect of group nor the interaction between group and serial position was statistically significant, the data from the two groups were combined. This revealed a combined group-mean percentage correct for Serial Positions 1–5, respectively, of 71%, 61%, 50%, 61%, and 76%. These data are displayed in the bottom right panel of Figure 3.

Planned comparisons, using the error term derived from the ANOVA, revealed that choice accuracy for Item 3 in the list was lower than choice accuracy for any other item, minimum $t(36) = 2.4$, $p < .5$, and memory for Items 2 and 4 in the list was worse than memory for the first and last items in the list, minimum $t(36) = 2.3$, $p < .05$. There was no difference between the first and last items, maximum $t = 1.22$.

Discussion

The demonstration of primacy and recency effects is not of itself novel; there have previously been demonstrations of both primacy and recency in several species, including rats (Bolhuis & van Kampen, 1988; DiMattia & Kesner, 1984; Wright et al., 1985). The present results do, however, extend and improve some of these reports in a number of ways. First, the presentation of data from individual subjects allows a clearer assessment than has previously been possible of whether primacy and recency effects occur together in indi-

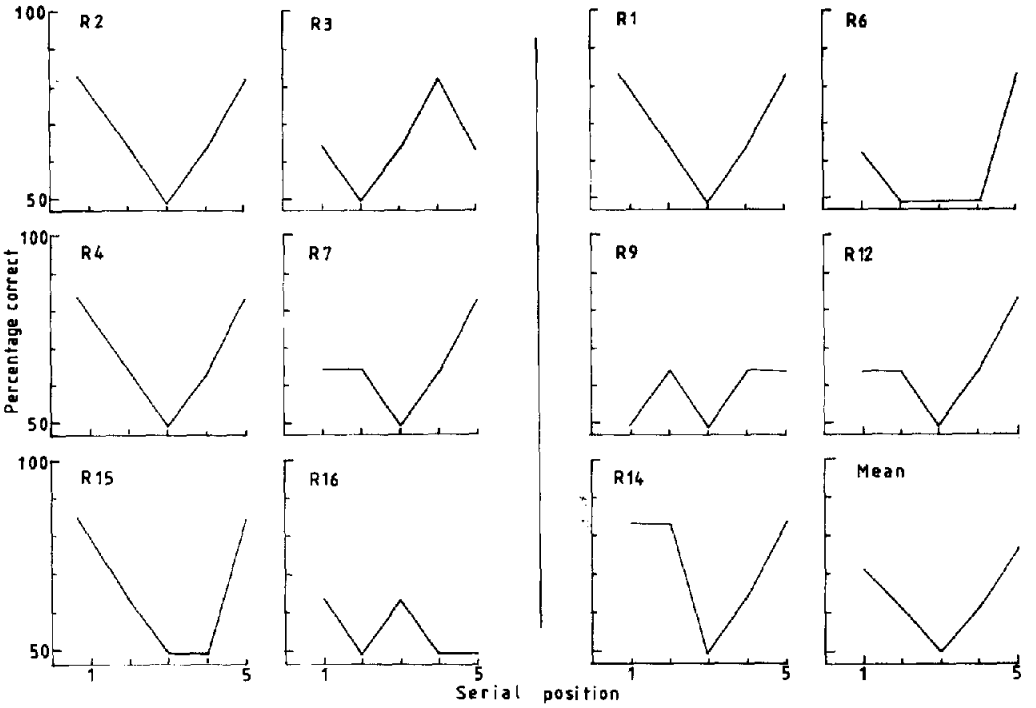

Figure 3. Results from Experiment 1: Mean recall over the last six sessions of training for each subject. (Subjects represented in the left panel were trained in illuminated goalboxes; subjects in the right panel were trained in dark goalboxes. The bottom right panel represents the mean for all subjects over the last six sessions.)

vidual subjects; some previous studies that have relied on pooled scores are open to the criticism that such mean scores generate serial position curves for the group, although no individual animal has shown both effects (see Wright et al., 1985, for similar individual subject analysis). Examination of the individual data in the present study demonstrates that this is not the case for the present experiment: Eight out of 11 subjects provided evidence of a clear primacy and recency effect occurring together. Second, it is possible that the procedures used in previous studies conferred a selective advantage in the recognition of items presented early in the list, leading to the production of primacy effects through mechanisms other than those connected with memory. For example, Gaffan (1983) has argued that in the studies of list learning in which the subject initiates the presentation of the list by a response (e.g., Sands & Wright, 1980; Wright et al., 1985), this response provides an additional cue whereby the recall of items early in the list may be facilitated. A study reported by Gaffan and Weiskrantz (1980) in which the subject produced all the items in the list by a response found no consistent serial position effects. The present experiment treated all stimuli of the list in the same manner; all were experienced after the rat had run down the arm of a maze, yet clear primacy and recency effects were noted. These data support the suggestion made by Bolhuis and van Kampen (1988) that Gaffan and Weiskrantz's failure to note a serial position curve was likely to be due to the use of inappropriate retention intervals. Thus, the present data provide convincing support for the view that comparable list learning effects occur in rats and humans.

Experiment 2

Effects similar to those of the serial position curve have been noted in human and nonhuman subjects in a number of other aspects of memory, for example, in the use of prospective and retrospective codes (Kesner & DeSpain, 1988) and in paired associate learning (Petrides, 1985). The similarity between human and nonhuman memory may be further demonstrated by examining the effect of enhancing the salience of one of the list items presented to the subject. In human subjects, this procedure leads to improved recall of the outstanding item; that is, a von Restorff effect occurs (see Wallace, 1965, for a review). It is possible to generate enhanced recall in nonhuman subjects by presenting salient stimuli following a target stimulus or response (e.g., Lieberman et al., 1979), but such results stem from procedures (e.g., classical and instrumental conditioning) radically different from those used in the study of list learning in humans. Thus, having established that primacy and recency effects occur in the present procedure with rats, the present method offers a way to determine whether a von Restorff-like effect also occurs in rats.

Method

Subjects and Apparatus

Subjects and apparatus from Experiment 1 also served in Experiment 2.

Procedure

Experiment 2 began immediately after Experiment 1. The same list learning procedure described in Experiment 1 was used for one half the sessions in Experiment 2. Interspersed with these sessions in a quasi-random order were sessions in which a stimulus change occurred on entry into Goalbox 3. The goalbox lights were turned off for the subjects trained with illuminated goal boxes, and the goalbox lights were turned on for the subjects trained in the darkened goalboxes. This stimulus change occurred approximately 4 s after the rat had entered the third goalbox in the list and lasted for 4 s. In a given session (i.e., for all five serial positions tested on a given day), the stimulus change occurred in Goalbox 3, regardless of whether that goalbox was to be used in the test on that particular trial. In all other details the procedure was as described in Experiment 1. Experiment 2 continued for 24 sessions.

Results

Data from the first 6 sessions of training under each contingency (i.e., with and without the stimulus change associated with Goalbox 3) revealed that both groups (illuminated and darkened goalboxes) continued to display primacy and recency effects and demonstrated enhanced recognition of Goalbox 3 on those sessions in which there was a stimulus change. For subjects trained with the illuminated goalboxes, scores for the mean percentage accuracy on sessions lacking the stimulus change were 74%, 70%, 52%, 68%, and 75%, for Serial Positions 1–5, respectively. Scores on the sessions in which a stimulus change occurred for Goalbox 3 were 72%, 63%, 69%, 65%, and 76%, respectively. A highly similar pattern of results emerged for the subjects trained with the darkened goalboxes. On the first 6 sessions of the experiment, on those sessions without a stimulus change associated with Goalbox 3, the scores for recognition were 72%, 65%, 58%, 60%, and 78% respectively. These scores became 70%, 61%, 71%, 55%, and 75%, for Goalboxes 1–5, respectively, on sessions with a stimulus change. These data suggest that a von Restorff effect occurred early in training, consistent with the suggestion made about marking effects by Thomas et al. (1987). However, to examine the reliability of this effect, training was continued for 12 more sessions.

The mean percentage of test trial choices that were correct, averaged over the last six sessions of each session type (i.e., with and without stimulus change) are displayed in Figure 4 for each subject. The 6 subjects represented in the left panel of Figure 4 were trained in the illuminated goalboxes, with

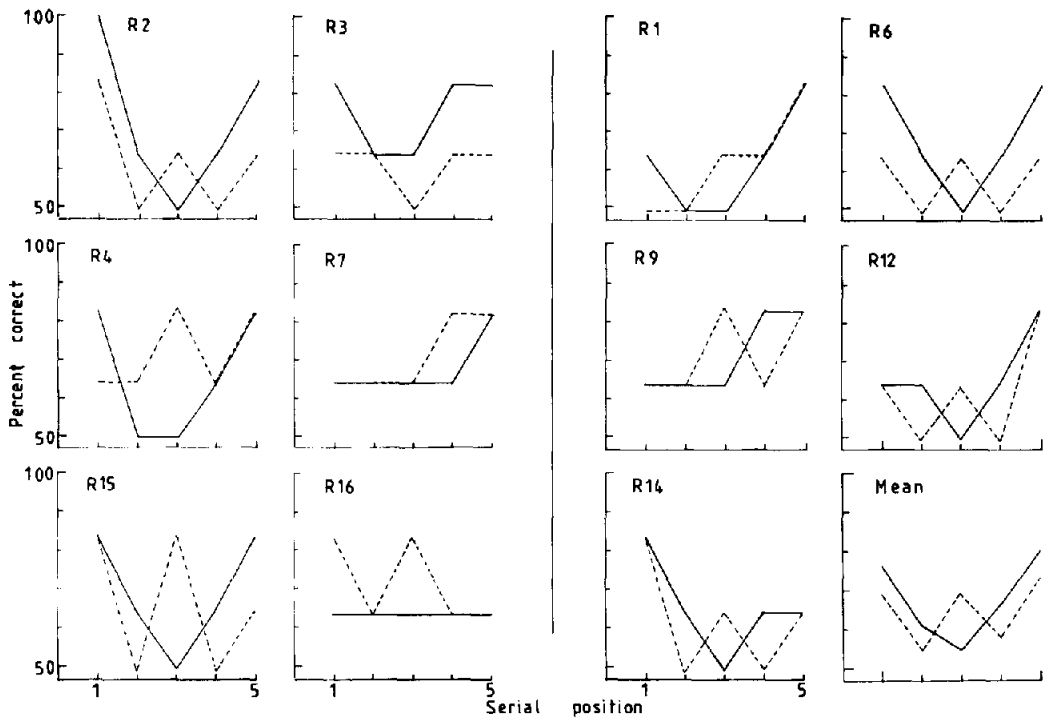

Figure 4. Results from Experiment 2. (Solid lines represent the mean recall over the last six sessions without an illumination change on entry to Goalbox 3; the dotted lines represent the mean percentage recall over the last six sessions when there was an illumination on entry to Goalbox 3. The subjects in the left panel were trained in illuminated goalboxes with a darkening of the goalbox as the salient event. The subjects in the right panel were trained in dark goalboxes with an illumination of the goalbox as the salient event. The bottom right panel represents the mean for all subjects pooled.)

darkening of the chamber as the stimulus change. Inspection of these data reveals that on the sessions without illumination of Goalbox 3, the serial position effect was similar to the one noted in Experiment 1. Subjects R2, R3, R4, and R15 displayed pronounced primacy and recency effects; Subject R7 displayed only a recency effect; and Subject R16 displayed no systematic serial position effect. Inspection of the data from the sessions in which Goalbox 3 was darkened (dotted lines) reveals that, for 4 of the 6 subjects, recall for Goalbox 3 was greater than when no stimulus change occurred.

The 5 subjects represented in the right panel of Figure 4 are the subjects trained in the darkened goalboxes. Inspection of the data for sessions lacking a stimulus change reveals that both primacy and recency effects occurred in Subjects R1, R6, and R12; Subjects R9 displayed a recency effect; and Subject R14 displayed a primacy effect. Inspection of the data from the sessions in which Goalbox 3 was illuminated reveals enhanced recall of Goalbox 3, relative to the sessions in which Goalbox 3 was not illuminated.

We subjected the individual subject data displayed in Figure 4 to analysis by a three-factor ANOVA (Serial Position × Session Type × Group). This analysis revealed a significant main effect of serial position, $F(4, 36) = 10.15$, $p < .01$, and an interaction between serial position and session type, $F(4, 45) = 7.71$, $p < .01$, but no other main effect or interaction was significant. As there were no significant effects involving the group variable the data for the two groups were combined. This revealed a combined group-mean percentage choice trials correct for the sessions without a stimulus change of 76%, 61%, 54%, 67%, and 80% for Serial Positions 1–5, respectively. This replicates the serial position curve observed in Experiment 1. The combined group-mean percentage choice trials correct for the sessions with a stimulus change for Goalbox 3 were 69%, 55%, 69%, 58%, and 73% for Serial Positions 1–5, respectively. This shows a quite different form of serial position curve. These mean data are displayed in the bottom right panel of Figure 4.

Subsequent planned comparisons revealed that changing the illumination of Goalbox 3 resulted in increased choice accuracy for this item, relative to normal trials, $t(45) = 3.65$, $p < .01$. There was also a significant drop in choice accuracy for Item 4, $t(36) = 2.10$, $p < .05$; however, although choice accuracy for each of the other items in the list was slightly lower on those days when an illumination change was imposed, none of those other reductions was significant (maximum $t = 1.51$).

Discussion

For those sessions in which no stimulus change was used, subjects continued to display the serial position effect generated during Experiment 1. (This constitutes a within-subjects replication of the results of Experiment 1.) A stimulus change associated with Goalbox 3, however, enhanced recall of that goalbox relative to those trials in which no stimulus change was associated with that goalbox. This effect is similar to the von Restorff effect obtained with humans (Wallace, 1965); such findings extend the similarity between findings of human and nonhuman memory experiments to a novel situation. The present von Restorff-like effect could not be attributed simply to the perceptual effect of illuminating Goalbox 3. Thus, by allowing better encoding of the objects located in that goalbox, as both illuminating and darkening, the goalbox produced similar von Restorff effects. That the object accompanied by the change of illumination was recalled better than an object occupying the same serial position but lacking the stimulus change is especially striking given the findings of Wagner et al. (1973). Wagner et al. reported that a salient event occurring after a stimulus–reinforcer pairing disrupted learning about that association. This effect was attributed to the salient event displacing the representations of the stimulus and reinforcer from short-term memory, preventing conjoint processing of the two events. The presentation of the stimulus in the present experiment had the opposite effect, as has been found in a number of other paradigms (e.g., Lieberman et al., 1979; Reed, 1989; Rescorla, 1982).

General Discussion

The present experiments investigated rats' ability to learn lists of nonspatial stimuli and offered evidence that primacy and recency effects do occur in rats' nonspatial memory.

Some investigators (e.g., MacPhail, 1986; Olton, 1985) have suggested that nonspatial memory in rats is less robust than spatial memory. The present results, however, add to the growing body of evidence that nonspatial items are remembered at least as well as spatial items. Rats have been found to remember long lists of nonspatial items over substantial periods of time (Steele & Rawlins, 1989). Such lists are longer than lists built of spatial information in the radial maze (e.g., Olton & Samuelson, 1976). In the present experiments, nonspatial information was retained over intervals of 70 s, with a number of intervening items presented during this period. Although both the temporal duration and resistance to interference of the nonspatial memory investigated in the present study compares well with that noted for memory for spatial items, training on the present procedure took substantially longer to complete than that reported in similar experiments for nonspatial items (e.g., DiMattia & Kesner, 1984). This suggests that irrespective of the subsequent memory for such items, rats have more difficulty learning about nonspatial than about spatial tasks.

Primacy and recency effects were obtained together, a finding that extended the generality of the serial position curve phenomenon in nonhuman subjects. Previous investigators have observed serial position effects in monkeys and pigeons (Wright et al., 1985) and when lists of spatial items were used with rats (e.g., Bolhuis & van Kampen, 1988; DiMattia & Kesner, 1984). These studies demonstrate that both primacy and recency effects are robust in nonhuman subjects. Such findings contrast with earlier studies that generally obtained only recency effects (e.g., Thompson & Herman, 1977). Two suggestions have been made to account for such apparently contradictory results. First, it is possible that the retention period presented between list exposure and the recognition test is crucial in determining whether the serial position effect will appear. The present experiments did not address that issue: They used a 20-s retention period similar to those

experiments that have noted both primacy and recency effects; in contrast to earlier work, they used a nonspatial task. A second suggestion to account for the joint occurrence of primacy and recency effects on some occasions, but not on other occasions, focuses on differences in the degree of processing required for the information contained in the to-be-remembered stimuli. Serial position effects have been obtained with immediate recall when rats are presented with a spatial list in the radial maze, but have to obtain food at testing with a matching-to-sample (win–stay), rather than a nonmatching-to-sample (win–shift) rule (DiMattia & Kesner, 1984; Kesner & Novak, 1982). DiMattia and Kesner (1984) suggested that the occurrence of the more elusive primary effect may be the result of the "effortful information processing" required by the more difficult win–stay task (Olton & Schlosberg, 1976; but see Reed, Maxwell, & Rawlins, 1990). It may be that the stimuli used in the present task, being highly complex and multimodal, provoked a greater degree of information processing than did the relatively simple spatial information used in the radial maze. Such enhanced processing may underlie the generation of the primacy effect in the present experiments; this would imply that a lesser amount of processing is needed for spatial information.

The serial position curve in humans has been interpreted according to a number of theories. For example, serial position effects have been taken to reflect the action of interference produced by two sources: Items in the middle of the list are subject to interference from both the preceding items (i.e., proactive interference) and from the items that follow (i.e., retroactive interference). In contrast, items at the beginning or end of the list are subject only to one type of interference, retroactive and proactive, respectively (e.g., Melton, 1963). Alternatively, it is possible that primacy and recency effects are the product of a dual memory store. Items presented at the beginning of the list undergo a greater amount of rehearsal and consequently gain access to long-term memory store, from which they are readily retrieved. Items presented at the end of the list are still being actively rehearsed at the time of test and are also readily retrieved. Items in the middle of the list, however, have not yet gained access to the stable long-term memory store and are subject to displacement from the limited capacity short-term store; these items are therefore not as readily available for retrieval. Such an account is consistent with the model of memory presented by Atkinson and Shiffrin (1968). Both of these theories have been applied to nonhuman subjects (cf. Maki, 1986; Wright et al., 1985) and may account for the present data.

In Experiment 2, a von Restorff-like effect was noted: Recognition of an item in the list was enhanced if it was associated with a stimulus change. This effect could have several alternative explanations. It may be that the stimulus change leads to increased levels of arousal, and the increased arousal leads to better processing of, and memory for, the object located in that goalbox. Such an effect may underlie similar signal-induced potentiation of classical and instrumental conditioning (e.g., Lieberman et al., 1979; Thomas et al., 1987). However, experiments conducted to examine signal-induced enhancements of conditioning suggest that an account in terms of arousal is incomplete (Thomas, Lieberman, McIntosh, & Ronaldson, 1983). The "marking hypothesis" (Lieberman et al., 1979) supplies a somewhat different account of the signal-induced potentiation of conditioning and may also provide an explanation of the present von Restorff-like phenomenon. This view suggests that a salient event such as a stimulus change triggers a backward search through memory for the putative cause of that event. The enhanced processing of the preceding (i.e., marked) event enables better subsequent recall of that event. Neither increased arousal nor marking has been used to account for data from human subjects.

A different explanation of this signal-induced effect suggests that the salient stimulus facilitates recall of the preceding event by enhancing the discriminability of that item relative to all other similar events that occur in the experimental context. There are a number of ways that a salient stimulus could enhance the discriminability of preceding events. Fedorchak and Bolles (1986) suggested that a salient stimulus presented after a target event enhances the discriminability of the target event by making its outcomes different from the outcomes associated with the other nontarget events. Consistent with this suggestion, Honey and Hall (1989) have found that stimuli are more likely to be treated as equivalent if they have similar, rather than different, outcomes. A second possibility is that the salient event provides a contrast that renders representations of the target event perceptually distinct from the representation of other events and, thus, allows easier retrieval from memory (Reed, 1990). Alternatively, the salient event may protect the target from proactive interference that would otherwise accrue during the list exposure phase (e.g., Melton, 1963). These discrimination notions are similar to those posited as underlying the von Restorff effect in humans (Hitch, 1985; Wallace, 1965). Such views of human list learning effects suggest that retrieval of an item presented in a list is dependent on the discriminability of an item from other items; if the discriminability is somehow enhanced—perhaps by presenting an item from a different conceptual category from the rest of the items in the list—then retrieval of that item is facilitated.

In sum, the present experiments provide data that suggest that remarkable convergence between properties of human and nonhuman memory may be achieved by the integration of a number of lines of research. Despite the apparent promise of these encouraging data, it should be noted that although there appear to be similar serial position and von Restorff effects in humans and rats, a procedural difference does exist between the experiments conducted to reveal such effects in the two species. For example, the target stimulus occurred twice in the present study (at exposure and at test), whereas in the human literature—because of the widespread use of free-recall tests—the target stimulus is only presented once (see Wallace, 1965). The existence of such procedural differences may initiate the operation of different processes that, nevertheless, promote the apparently similar effects on memory in the different species studied (see Gaffan, 1983). Further integration of procedures used in human and nonhuman subjects might ensure that the results from these traditionally independent areas of research yield an equivalent convergence between theories of memory.

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