REPRODUCTION MEMORY OF TWO-EVENT SEQUENCES IN PIGEONS

B. KENT PARKER

WEST VIRGINIA UNIVERSITY

Six pigeons were trained to reproduce two-event sequences in an experiment that employed a discrete-trial procedure that required subjects to peck one of four possible sample sequences (left-left, left-right, right-right, right-left) signaled on a given trial by the successive illumination of response keys. Following a retention interval (0.1 to 30 seconds), a reinforcer was delivered if a subject reproduced the prior sample sequence during a test condition in which both left and right keys were illuminated. The pigeons readily reproduced the orders in which they had just seen and pecked two illuminated keys. Reproduction accuracy declined as the retention interval was increased. Homogeneous sequences (left-left, right-right) were reproduced with greater accuracy than heterogeneous sequences.

Key words: short-term memory, stimulus-response memory, behavior pattern, key peck, pigeons

Recent studies of short-term memory in the pigeon have shown that various temporal patterns of stimuli, responses, or both can gain stimulus control in delayed conditional discriminations. These investigations have shown that patterns of stimuli and responses (e.g., Shimp & Moffitt, 1974; Weisman, Wasserman, Dodd, & Larew, 1980), as well as patterns of behavior, including interresponse times (Shimp, 1981), number of pecks (Kramer, 1982; Lattal, 1975; Shimp, 1982) and response duration (Zirias & Silberberg, 1978), can function as discriminative stimuli for key pecking in delayed test periods. Of particular relevance to the present investigation are findings that pigeons remember a temporal pattern of stimuli and responses that occurred in their recent past. Typically these studies have used some variant of either the delayed matching-to-sample or the feature-probing paradigm.

Wasserman, Nelson, and Larew (1980) used a discrete-trial successive matching-to-sample task to examine pigeons' memory for two-item stimulus-response patterns. They trained pigeons to peck two-response sequences of randomly illuminated left or right keys during

sample phases. During each test phase one of four possible test stimuli was presented on the center key and responding was reinforced only if the test stimulus was uniquely associated with the preceding sample sequence (symbolic matching to sample). Discrimination ratios revealed higher rates of responding on positive than on negative test-stimulus presentations, over retention intervals of 0.5 to 4 s.

In studies employing the feature-probing method, pigeons have been trained to peck successively a two-response (Jitsumori & Sugimoto, 1982; Shimp & Moffitt, 1974) or three-response (Shimp, 1976) pattern of randomly illuminated left, center, or right keys during the first (sample) phase of a two-phase discrete-trial procedure. In the second (test) phase, following a retention interval, color cues presented on the keys prompted the pigeons' identifying the key pecked first, second, etc. during the sample phase. The results of these investigations have shown that pigeons remember the temporal organization of two- and three-item stimulus-response patterns over intervals of 0.1 to 4 s (Shimp, 1976; Shimp & Moffitt, 1974) and 1 to 9 s (Jitsumori & Sugimoto, 1982); the probability of correct choice responses (left, center, or right) was better than chance.

As Weisman et al. (1980) have noted, with discrimination ratios providing the evidence of memory for stimulus-response sequences in delayed-matching procedures, it is clear that pigeons can remember and discriminate one

Portions of these data were presented at the convention of the Psychonomic Society, Philadelphia, Pennsylvania, 1981. The author wishes to thank Janice Stern and Edward Eades, who assisted in conducting the experiment. Send reprint requests to B. Kent Parker, Department of Psychology, West Virginia University, P.O. Box 6040, Morgantown, West Virginia 26506-6040.

sequence from another, but it is not clear that they can identify and remember the position of individual stimulus-response items within a temporal sequence. Moreover, with the exception of Shimp (1976), researchers using a choice response with a feature-probing procedure did not require that subjects remember the temporal order of stimulus-response items because the ordinal position of an item and the color of the cue probing memory had been confounded (Jitsumori & Sugimoto, 1982). This confounding enabled subjects to remember and discriminate relationships between key positions and specific colors, or the temporal order of stimulus-response items, or both.

In order to investigate directly pigeons' remembering and discriminating individual stimulus-response items and their orders within sequences, the present procedure entailed delayed matching to successive samples (DMTSS). This procedure had been designed by Devine and Jones (1975) as a multiple-unit memory task for nonhuman primates. In the DMTSS task two or more samples are successively presented to the subject and then removed from view. After a retention interval, the previously shown samples are presented simultaneously and the subject is required to match the order of their presentation by selecting the first sample, then the second sample, and so on. Previous research with the DMTSS procedure has shown that monkeys can reconstruct the order of presentation of nonspatial two-event samples of form and color stimuli (Devine, Burke, & Rohack (1979) and of spatial two-event samples of lighted response keys (MacKay & Brown, 1971). In the present experiment pigeons were subjects and the stimulus-response items to be reproduced were two-peck sequences on randomly lit left and/or right keys. Following this sample-sequence phase and a retention interval (varied from 0.1 s to 30 s), both left and right key lights were lit (test phase) and the pigeon was required to reconstruct the order of the left and/or right pecks emitted in the sample phase.

METHOD

Subjects

The subjects were six experimentally naive pigeons (two homing and four White King) maintained at approximately 80% of their free-feeding weights. They were housed in in-

dividual cages with water and grit constantly available.

Apparatus

Two two-key chambers with interior dimensions of 28 by 28 by 34 cm were used. The keys, 2.5 cm in diameter, were located 22 cm from the floor and 12.75 cm apart (center to center). The keys could be transilluminated with red or white light by inline display projectors (IEE, Series 10, 28 V dc) mounted behind the key apertures. Centered beneath the keys, 8 cm from the floor, was a 5 by 5-cm opening allowing access to a hopper filled with mixed grain. Chamber illumination was provided by a houselight (7.5 W ac) mounted in the ceiling. A ventilator fan in each chamber masked extraneous sounds. Electromechanical control and recording equipment was located in an adjacent room.

Procedure

A daily session consisted of 96 discrete trials, each of which consisted of the following events: sample-sequence presentation, retention interval, test-stimulus presentation, and intertrial interval (ITI).

The sample sequence was initiated by the presentation of a red light on a randomly selected left or right key. The first response on that key turned it off and began a 0.5-s sample-stimulus interstimulus interval during which both keys were dark but the houselight remained on. When the sample interstimulus interval timed out, the red light appeared again on the left or right key with equal probability and, again, the first response turned it off. In this fashion each of 24 left-left (LL), left-right (LR), right-left (RL), and right-right (RR) stimulus-response sample sequences were randomly scheduled within a daily session.

Immediately following the sample-sequence presentation was a 0.1-s retention interval during which the keys were dark and the houselight was off. When the retention interval timed out, the test-stimulus presentation was initiated by simultaneously illuminating both keys white. The subject's task was to peck the key (left or right) that it had pecked first during the sample-sequence presentation. If the subject chose the correct side, the response turned off the keys for 0.5 s followed by the re-illumination of both keys with white light.

In the presence of this second test stimulus the subject's task was to peck the key that it had pecked second during the sample sequence. If the subject chose the correct key, the food hopper was presented for 2.5 s followed by the ITI.

Choice of an incorrect key in response to either the first or second test stimulus was followed by a 10-s timeout. During the timeout both keylights and the houselight were off. When the timeout elapsed, the test stimulus to which the incorrect response occurred was repeated. For example, if the sample sequence was LR and the bird pecked the right key in the presence of the first test stimulus, the first test stimulus was repeated following a 10-s timeout. If the bird correctly pecked the left key in the presence of the first test stimulus and then pecked the left key in the presence of the second test stimulus, the second test stimulus was repeated following the timeout. This partial correction procedure was in effect until a correct response occurred to both test-stimulus presentations. Thus, each trial ended with reinforcement followed by the ITI. During the 40-s ITI both keys were dark, but the houselight was continuously illuminated.

The subjects were brought to this task through several pretraining phases. First, they were trained to eat from the food hopper and to peck either the left or right key when illuminated red. Next, reinforcement occurred only after the bird had pecked a set of two keys lighted one at a time. Then, the 0.1-s retention interval and the test-stimulus presentations were added to the sample-sequence presentations to form a complete trial, but for 12 daily sessions each of the trial types (LL, LR, RL, and RR) was scheduled in blocks of 24 trials. Thus, subjects received 24 trials of one sequence (e.g., LL) before progressing to a different sequence (e.g., RL) of 24 trials. Finally, sequences were randomized within four blocks of 24 trials. Initial training with the 0.1-s retention interval lasted 130 sessions for Birds 1, 2, and 4 and 70, 80, and 100 days for Birds 5, 6, and 7, respectively.

Retention interval manipulation. Following training with a short (0.1-s) interval between the second item of the sample sequence and the presentation of the first test stimulus, the retention interval was systematically varied over sessions from 0.1 to 30 s for individual subjects. The sequence of intervals is given in

the upper panels of Figure 2 for individual birds. Subjects were exposed to each successive interval for a minimum of 20 sessions.

RESULTS

The acquisition of DMTSS performance is shown in Figure 1, which presents the percentage correct sequence reproduction during test-stimulus presentations as a function of homogeneous (LL, RR) and heterogeneous (LR, RL) sample sequences for individual subjects over blocks of five sessions. Performances during the test-stimulus presentations were counted as correct if and only if the sample sequence was reproduced on the first opportunity to do so. That is, choice of an incorrect key in response to either the first or second test stimulus was counted as an incorrect sequence reproduction.

A random choice model applied to test-stimulus presentations would predict correct reproductions on only 25% of the trials (assuming the chance probability of a correct choice at each of the two test-stimulus presentations equals 0.5). All of the subjects learned to reproduce the sample sequences at a level that far exceeded chance performance. During the last 15 days (3 blocks), the average percentage correct for all six pigeons was 78 (range 74 to 84).

For all subjects discriminative control by the homogeneous-sample sequences developed earlier in training and ultimately reached a higher level than did the heterogeneous-sample sequences. During the first 15 days (3 blocks) of training, the average percentage correct reproduction was 78 (range 56 to 90) for homogeneous sequences and 38 (range 6 to 62) for heterogeneous. During the last 15 days the percentage correct sequence reproduction for homogeneous sequences was 83 (range 79 to 89) compared to 72 (range 66 to 84) for heterogeneous samples. Moreover, Figure 1 shows that the differential control by homogeneous- and heterogeneous-sample sequences decreased over session blocks as performance on heterogeneous sequences increased more than on homogeneous. These patterns are most clear for Birds 2, 4, and 6 and least clear for Bird 1.

The results of manipulating the retention interval are summarized in Figure 2 for individual subjects. For each bird the upper pan-

Fig. 1. Percentage correct-sequence reproduction as a function of session block and type of sample sequence. The solid lines represent heterogeneous sequences (LR, RL) and dashed lines represent homogeneous (RR, LL) sequences.

els show the overall percentage correct sequence reproduction for successive retention intervals. Each data point is a 5-day average over the last 15 days at each interval. As can be seen, individual performances were affected by the length of the retention interval. In general, the overall percentage correct sequence reproduction declined as an orderly function of retention interval length. For Birds 5, 6, and 7 performance was better than chance at the 30-s retention interval.

The lower panels of Figure 2 show the percentage correct reproduction of each of the sample-sequence types (LL, RR, LR, RL, respectively) at selected retention intervals for each subject. The height of each bar represents the percentage correct sequence reproduction over the last 15 sessions at each retention interval for each type of sample sequence. While

performance declined for both homogeneous- and heterogeneous-sample reproductions as the retention intervals increased, performance declined more on heterogeneous sequences than on homogeneous. This can be seen more clearly in Figure 3, which summarizes percentage correct sequence reproduction for homogeneous- and heterogeneous-sample sequences as a function of length of retention interval, averaged across subjects and ignoring the order of presentation of conditions. It can also be seen that, at the longer retention intervals, performance on heterogeneous samples was at or near chance levels while performance on homogeneous sequences was substantially above chance. Thus, the overall better-than-chance performance at the longer retention intervals (see Figure 2) was due primarily to the reproduction of homogeneous sequences.

Fig. 2. Upper panels: Percentage correct-sequence reproduction over all sample sequences as a function of retention interval for individual subjects in 5-session blocks for the last 15 sessions. Lower panels: equivalent data for each type of sample sequence at selected retention intervals. At each retention interval, successive bars represent LL, RR, LR, and RL sample sequences, respectively. Note that abscissa values for each panel are shown at the top of that panel.

DISCUSSION

The present experiment clearly demonstrates that pigeons not only discriminative previously presented stimulus-response sequences from one another as other studies have shown (e.g., Jitsumori & Sugimoto, 1982; Wasserman et al., 1980; Weisman et al., 1980) but also identify individual stimulus-response items and their order. That is, the pigeons in the present investigation clearly remembered the temporal order of items to the extent that

they reproduced prior series of stimulus-response events. The pigeons' reproduction of prior events extends the findings of Shimp (1976), who showed that pigeons remember the temporal order of stimulus-response items using a choice procedure in which key color and the ordinal position of the items were not confounded as in other investigations (Jitsumori & Sugimoto, 1982; Shimp & Moffitt, 1974), which used the feature-probe procedure. Moreover, the pigeons' reproduction of spatial two-event samples extends the findings of Mackay

Fig. 3. Percentage correct-sequence reproduction for the last 15 sessions at each retention interval value as a function of type of sample sequence, averaged across subjects. The solid line represents heterogeneous sequences (LR, RL) and the dashed line represents homogeneous (RR, LL) sequences.

and Brown (1971), who showed that rhesus monkeys could be trained to remember a two-event serial-position sequence using a matching-to-sample procedure that required the subject to press two consecutively lighted keys and then press the same two keys in the same order but without the lights.

Several factors affected the accuracy of sequence reproduction. First, homogeneous sequences were differentiated earlier in training than heterogeneous sequences. This finding is consistent with that of Grayson and Wasserman (1979), who found that the learning of LL and RR sequences occurred more rapidly than LR and RL sequences using a discrete-trial procedure in which reinforcement depended on the order of two-peck sequences. However, the continued superiority of performance on homogeneous samples through successive retention-interval manipulations contrasts with results of Wasserman et al. (1980), who failed to find differences in the stimulus control exerted by homogeneous and heterogeneous sequences using a relative response measure.

Second, consistent with other investigations of sequence memory using feature-probe procedures (e.g., Shimp, 1976) and discrete-trial

successive matching-to-sample procedures (e.g., Wasserman et al., 1980), performance depended upon the retention interval. As the interval separating the second item of the sample sequence from the first item of the test sequence was lengthened, there was a systematic loss of control by the sample sequence. Moreover, there was a differential loss of control as the retention interval was lengthened. Homogeneous-sequence reproduction remained at better-than-chance levels as the interval was lengthened to 20 and 30 s, while heterogeneous-sample sequence reproduction decreased to chance levels at these values.

A possible explanation of this differential loss of control at longer retention interval values is that the subjects employed behavioral mediators (see, e.g., Meltzer & Nobbe, 1980; Wilkie, 1983) with homogeneous-sequence reproduction. Although the birds did not peck during the delay interval, their bodily orientations may have mediated correct responding on homogeneous trials. An alternative interpretation is that the superior performance on homogeneous sequences occurred because homogeneous patterns have a higher likelihood of occurrence than heterogeneous patterns. Wasserman et al. (1980) found that homogeneous patterns are emitted more than five times as often as heterogeneous patterns under nondifferential reinforcement.

Although both the mediation and the likelihood-of-occurrence accounts are tenable bases for the superior performances on homogeneous sequences, they are, respectively, less appealing or simply not applicable in the case of heterogeneous sequences. For heterogeneous-sequence reproduction, a possible interpretation is that pigeons remember their own recent behavior. Accuracy on heterogeneous sequences for all six subjects declined to chance levels at values ranging from 15 to 20 s. It is interesting to compare this performance to the performance of pigeons on a procedure for delayed matching of key location (Wilkie & Summers, 1982) in which responses to sample locations were not required. Since their pigeons remembered key location for only a few seconds, this difference suggests that the pigeon's memory for its own behavior (i.e., key pecks) may play a role in heterogeneous-sequence reproduction. Although the present data do not conclusively show that pigeons remember key pecks rather than locations of key illumination, they are

consistent with Kramer's (1982) recent findings that pigeons can remember a small number of responses for 30 s or more.

REFERENCES

- Devine, J. V., Burke, M. W., & Rohack, J. J. (1979). Stimulus similarity and order as factors in visual short-term memory in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes*, 5, 335-354.
- Devine, J. V., & Jones, L. C. (1975). Matching to successive samples: A multiple-unit memory task with rhesus monkeys. *Behavior Research Methods & Instrumentation*, 7, 438-440.
- Grayson, R. J., & Wasserman, E. A. (1979). Conditioning of two-response patterns of key pecking in pigeons. *Journal of the Experimental Analysis of Behavior*, 31, 23-29.
- Jitsumori, M., & Sugimoto, S. (1982). Memory for two stimulus-response items in pigeons. *Journal of the Experimental Analysis of Behavior*, 38, 63-70.
- Kramer, S. P. (1982). Memory for recent behavior in the pigeon. *Journal of the Experimental Analysis of Behavior*, 38, 71-85.
- Lattal, K. A. (1975). Reinforcement contingencies as discriminative stimuli. *Journal of the Experimental Analysis of Behavior*, 23, 241-246.
- Mackay, H. A., & Brown, S. M. (1971). Teaching serial position sequences to monkeys with a delayed matching-to-sample procedure. *Journal of the Experimental Analysis of Behavior*, 15, 335-345.
- Meltzer, D., & Nobbe, D. E. (1980). Mediating behavior of the pigeon during delayed responding. *Bulletin of the Psychonomic Society*, 16, 69-72.
- Shimp, C. P. (1976). Short-term memory in the pigeon: Relative recency. *Journal of the Experimental Analysis of Behavior*, 25, 55-61.
- Shimp, C. P. (1981). The local organization of behavior: Discrimination of and memory for simple behavioral patterns. *Journal of the Experimental Analysis of Behavior*, 36, 303-315.
- Shimp, C. P. (1982). On metaknowledge in the pigeon: An organism's knowledge about its own behavior. *Animal Learning & Behavior*, 10, 358-364.
- Shimp, C. P., & Moffitt, M. (1974). Short-term memory in the pigeon: Stimulus-response associations. *Journal of the Experimental Analysis of Behavior*, 22, 507-512.
- Wasserman, E. A., Nelson, K. R., & Larew, M. B. (1980). Memory for sequences of stimuli and responses. *Journal of the Experimental Analysis of Behavior*, 34, 49-59.
- Weisman, R. G., Wasserman, E. A., Dodd, P. W. D., & Larew, M. B. (1980). Representation and retention of two-event sequences in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 6, 312-325.
- Wilkie, D. M. (1983). Pigeons' spatial memory: II. Acquisition of delayed matching of key location and transfer to new locations. *Journal of the Experimental Analysis of Behavior*, 39, 69-76.
- Wilkie, D. M., & Summers, R. J. (1982). Pigeons' spatial memory: Factors affecting delayed matching of key location. *Journal of the Experimental Analysis of Behavior*, 37, 45-56.
- Ziriax, J. M., & Silberberg, A. (1978). Discrimination and emission of different key-peck durations in the pigeon. *Journal of Experimental Psychology: Animal Behavior Processes*, 4, 1-21.

Received March 22, 1983

Final acceptance November 30, 1983