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PIGEONS' SPATIAL MEMORY: FACTORS AFFECTING DELAYED MATCHING OF KEY LOCATION

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The delayed-matching-to-sample procedure was modified to study pigeons' spatial memory. Nine pecking keys, arranged as a three-by-three matrix, served as the spatial cues. Trials began with a brief "ready" stimulus (dimming of the houselight). Then a randomly chosen key was lit briefly as a sample. After a short delay the sample key was lit again along with one of the other eight keys. A peck at the key that had served as the sample produced grain reinforcement, whereas a peck to the other key produced only the intertrial interval. After delayed matching of key location was learned, the effects of sample and delay duration, number of keys illuminated as sample and comparisons, and organization of three-key samples were studied. Matching accuracy decreased as sample duration decreased, delay increased, the number of locations serving as samples increased, the number and proximity of comparisons increased, and when the three-key samples were "discontinuous" rather than "lines."

Key words: spatial memory, delayed matching to sample, key-location samples, key peck, pigeons

In delayed-matching-to-sample (DMTS) procedures, a sample stimulus is presented and then terminated, after which choice or comparison stimuli (one of which is identical to the sample) are presented. Choice of the comparison that matches the sample is reinforced, whereas choice of a nonmatching comparison is not. The subject must remember the sample to choose the matching comparison; however, it is advantageous for it to forget or ignore the sample once the trial is over. For this reason, performance on DMTS is often characterized as "working memory" (Honig, 1978).

Various stimuli have been used in DMTS procedures with the pigeon: colors and line tilts (e.g., Carter & Eckerman, 1975), food or its absence (e.g., Wilkie, 1978), response patterns (e.g., Maki, Moe, & Bierley, 1977), and durations of lights or food presentation (e.g., Spetch & Wilkie, 1981); but, to our knowledge, spatial cues have not been employed. This neglect is surprising given the current interest in the memorability of spatial cues (e.g., Kamil & Sargent, 1981; Olton, 1978). Accordingly, we developed a variant of DMTS in which pigeons were trained to match the spatial location of visual cues and here report the results of manipulations of several variables.[1]

EXPERIMENT 1
TRAINING DELAYED MATCHING OF KEY LOCATION

We employed a three-by-three matrix of pecking keys, one of which was lit briefly as a sample at the start of a trial. After a delay, the previously lit key and one of the remaining keys were lit. A peck to the key that had been lit as the sample was reinforced, whereas a peck to the other key produced only the intertrial interval.

METHOD

Subjects

Five experimentally naive Silver King pigeons were reduced to about 80% of their free-feeding weights prior to the experiment.

Apparatus

The test chamber was a ventilated, light-proof, sound-attenuating chamber measuring 20.5 cm (l) by 30.0 cm (w) by 33.0 cm (h). Nine clear Plexiglas pecking keys (3.25 cm in diameter) were mounted (5 cm apart, center to cen-

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[1] Closely related work is described by Smith, Attwood, and Niedorowski in an article in this issue.

ter) in a three-by-three matrix on one of the long walls. The center key of the matrix was 22 cm above the floor of the chamber, 18 cm from the left, and 23 cm from the right edge of the wall. Behind each key was a Moulon ML microswitch requiring a force of about 15g (.15 N) to operate, and a FLV117 red light-emitting diode. To the right of the key matrix was a 5.5-cm by 4.5-cm opening through which mixed grain was presented by a BRS/LVE Model #114-10 feeder. A #313 light within the food enclosure illuminated the grain when presented. Mounted on the wall opposite the key matrix was a shielded #313 houselight.

Data collection and experimental control were carried out by a Data General NOVA 3 computer, BRS/LVE Interact interface, and the MANX language (Gilbert & Rice, 1979).

Procedure

Preliminary training. The birds were trained first to eat mixed grain from the raised illuminated hopper and then from the hopper when it was briefly raised at variable times. Next, the birds were trained by the method of successive approximations to peck keys lit red. Key illumination was randomly determined. Pecking a lit key produced 5-sec access to grain, extinguished that key, and caused another key to light. Training continued until the pigeons readily pecked all keys.

The experiment proper. Birds 1, 2, 3, and 4 received 43 sessions of DMTS training with key location as the sample. During initial sessions certain parameters (e.g., sample duration, number of trials per session, etc.) were varied in order to improve performance. Bird 5, which was tested for 32 sessions after Birds 1 to 4 had completed this phase, received only the final version of the procedures (described below); Birds 1 to 4 received the final version during about the last 20 sessions.

Daily sessions had 36 trials. Each trial began with .75-sec offset of the houselight as the "ready" stimulus; then, .75 sec later, one of the nine keys, randomly selected as the sample, was lit for 2 sec. This was followed by a 1-sec delay with all keys dark. After the delay the sample key again was lit along with one other randomly selected key. These comparison keys remained lit until the pigeon pecked one of them: if it pecked the comparison that had been the sample, the bird received 5-sec access to mixed grain followed by a 20-sec intertrial interval (ITI); if it pecked the other alternative, the bird received a 25-sec ITI.

RESULTS

Figure 1 shows the percentage of trials on which the birds pecked the comparison key that had been the sample for the last 10 sessions for Birds 1 to 4 and all sessions for Bird 5. Matching was acquired and reached asymptotic values by the last 10 days of the experiment (87.1, 82.3, 75.7, 86.0 and 85.5 mean percent correct for Birds 1 to 5, respectively).

An analysis of matching accuracy as a function of sample position revealed no consistent effects. A similar analysis of errors revealed that incorrect choices were not associated consistently with any key locations. However, errors were more likely when the correct and incorrect comparison keys were in close proximity. In this analysis we dichotomized the 72 possible comparison arrangements into "comparisons close together" and "comparisons distant." In a distant as opposed to a close arrangement, an unlit row or column separated the correct and incorrect comparison. Accuracy for these two groupings was tabulated for the final eight days and is shown in Figure 2 in two four-day blocks. Matching was slightly more accurate when the choices were distant than when they were close.

EXPERIMENT 2
NUMBER OF COMPARISONS

We lit either two or nine keys as comparisons to determine the effect of one or eight in-

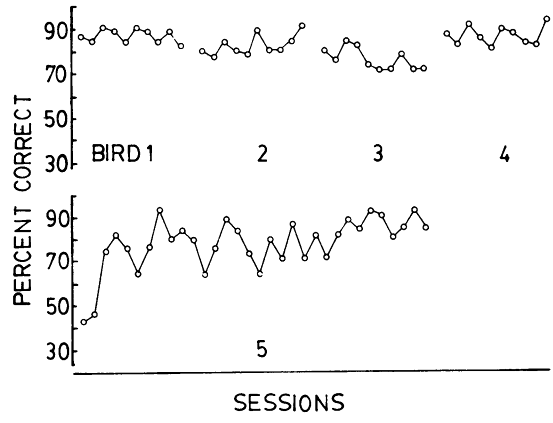

Fig. 1. Percentage of trials with correct matches in each session (Bird 5) or the last 10 sessions (Birds 1 to 4) of Experiment 1. Chance performance is 50%.

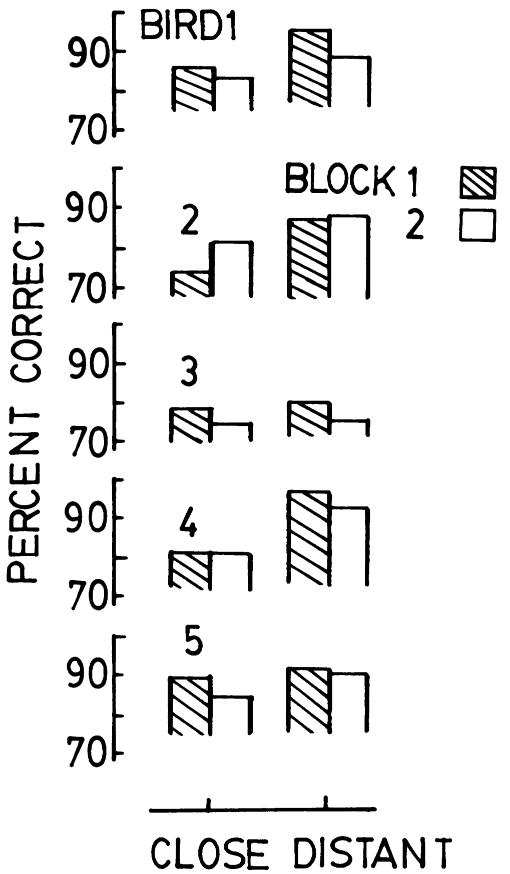

Fig. 2. Percentage of trials with correct matches when correct and incorrect comparison keys were close or distant for two four-session blocks of Experiment 1. Chance performance is 50%.

correct comparisons on delayed matching of key location. The nine-key trials also were analyzed to see if errors were more likely on keys adjacent to the correct key, as suggested by the results of Experiment 1.

Method

Subjects and Apparatus

Same as in Experiment 1.

Procedure

The same general procedures were employed as in Experiment 1. On each of the 36 trials in a session the probability was .5 that two keys would appear as comparisons; on these trials the incorrect key was chosen randomly in the same manner as in Experiment 1. On the other trials, all nine keys appeared as comparisons. Birds 1 to 5 received the following number of sessions, respectively: 40, 34, 50, 50, and 54.

Results

Figure 3 shows matching accuracy on two- and nine-comparison trials for the final 20 sessions. Despite an eightfold increase in the number of incorrect alternatives, accuracy remained well above chance (11%) on the nine-comparison trials, although there were more errors than on two-comparison trials. Mean percentage correct over the last 10 sessions for two- and nine-comparison trials for Birds 1 to 5, respectively, was: 73.8, 44.8; 92.4, 79.4; 82.9, 62.9; 73.7, 54.9; 80.1, 67.7.

Table 1 shows the proportion of nine-comparison trials during the final 20 sessions on which various key locations were chosen. Data are shown separately for each sample key (indicated by *). Sample keys always were chosen most often, and in all cases at above-chance (.11) levels. With the exception of the upper-left key for Bird 1, the nine key locations were remembered equally well. With only two exceptions (Bird 2—top-left key and top-middle key samples) the keys associated with the highest proportion of errors (indicated by a) were always adjacent to the correct key.

EXPERIMENT 3
SAMPLE AND DELAY DURATION

Performance on DMTS tasks is facilitated by increasing the duration of the sample (e.g., Roberts & Grant, 1974; Wilkie & Spetch, 1978) but is hindered by increasing the duration of the delay (e.g., Blough, 1959). We examined the effect of these variables on matching of key location.

Method

Subjects and Apparatus

Same as in Experiment 2, except that Bird 4 did not participate because of illness.

Procedure

General procedures were the same as in Experiment 1.

Sample-duration manipulation. Over 12 sessions, each bird received, in a semirandom order, three sample durations (.2, .5, and 2 sec), each presented for four complete sessions (36 trials). The delay interval was 1 sec.

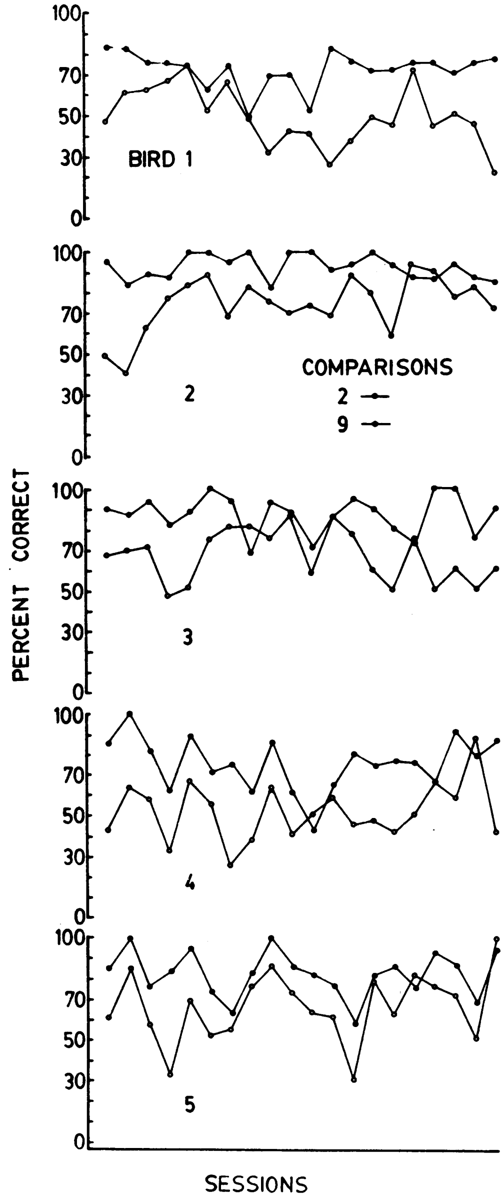

Fig. 3. Percentage of trials with correct matches when two or nine keys appeared as comparisons for the last 20 sessions of Experiment 2. Chance performance is 50% and 11% for the two- and nine-key trials, respectively.

Delay manipulation. This condition followed the sample-duration manipulation and lasted 40 sessions. Each session employed five different delays (1, 2, 4, 8, or 16 sec) presented in an order randomized within the constraint that the 1-sec delays occurred with a probability of .333 as opposed to .166 for the other four delays. Sample duration was 1 sec.

Table 1

Proportion of trials key location was chosen when all nine keys were illuminated during choice phase of trial: data matrix is isomorphic to key matrix.

				Bird 1				
.280*	.098	.105	.031	.503*	.114[a]	.000	.013	.715*
.085	.138[a]	.098	.038	.114[a]	.076	.000	.059	.132[a]
.059	.105	.032	.025	.063	.031	.026	.039	.013
.015	.038	.038	.006	.013	.034	.026	.019	.013
.404*	.160[a]	.114	.000	.714*	.108[a]	.006	.052	.690*
.068	.068	.091	.034	.040	.047	.026	.072	.092[a]
.000	.012	.006	.000	.012	.006	.000	.007	.007
.012	.049	.043	.031	.043	.074	.007	.043	.079[a]
.701*	.111[a]	.062	.031	.720*	.080[a]	.014	.079[a]	.762*
				Bird 2				
.795*	.032	.008	.007	.877*	.000	.000	.007	.896*
.040	.016	.032	.000	.022	.007	.000	.000	.039[a]
.016	.000	.057[a]	.007	.030	.045[a]	.007	.007	.039[a]
.049	.032	.032	.000	.048	.032	.000	.008	.057
.680*	.032	.024	.016	.707*	.032	.008	.000	.743*
.098[a]	.024	.024	.032	.089[a]	.040	.000	.003	.148[a]
.009	.018	.056	.000	.000	.016	.007	.000	.022
.093[a]	.046	.000	.008	.144[a]	.008	.000	.022	.090[a]
.682*	.028	.065	.008	.768*	.048	.000	.037	.818*
				Bird 3				
.703*	.040	.000	.024	.717*	.024	.016	.091[a]	.724*
.046	.069[a]	.034	.006	.055[a]	.042	.000	.032	.059
.023	.052	.029	.024	.049	.055[a]	.027	.010	.037
.051	.015	.010	.010	.054[a]	.005	.000	.031	.021
.744*	.040	.020	.027	.786*	.043	.026	.031	.820*
.056[a]	.030	.030	.016	.038	.016	.005	.021	.042[a]
.032	.038	.000	.004	.024	.014	.005	.010	.005
.175[a]	.058	.045	.004	.128[a]	.024	.005	.027	.125[a]
.554*	.064	.032	.044	.719*	.034	.016	.038	.765*
				Bird 4				
.756*	.024	.004	.043	.548*	.082	.025	.076	.624*
.082[a]	.014	.043	.087[a]	.053	.087[a]	.040	.045	.081[a]
.024	.024	.024	.038	.024	.033	.030	.025	.050
.013	.013	.004	.005	.021	.021	.016	.021	.076[a]
.801*	.073[a]	.013	.047	.629*	.158[a]	.065	.048	.695*
.041	.032	.004	.037	.052	.026	.027	.027	.021
.005	.005	.000	.004	.029	.034	.013	.004	.041
.105[a]	.036	.010	.068	.108	.103	.032	.060	.218[a]
.763*	.063	.010	.128[a]	.443*	.078	.009	.023	.595*
				Bird 5				
.439*	.031	.037	.045	.543*	.035	.022	.045	.555*
.158[a]	.052	.052	.025	.126[a]	.086	.018	.036	.178[a]
.068	.047	.111	.035	.045	.055	.022	.032	.087
.011	.011	.055	.024	.009	.014	.000	.010	.005
.662*	.033	.022	.029	.694*	.024	.010	.032	.686*
.088[a]	.066	.049	.053	.101[a]	.048	.032	.065	.153[a]
.000	.010	.020	.000	.000	.000	.019	.000	.009
.035	.010	.010	.027	.009	.009	.029	.009	.038
.800*	.085[a]	.030	.086[a]	.821*	.045	.009	.097[a]	.786*

*Correct key location; i.e., this key location appeared as the sample.

[a] Key location(s) to which most errors were made.

RESULTS

Matching accuracy as a function of sample duration is shown in Figure 4, in two blocks of two sessions each. Accuracy was clearly inferior at the .2-sec duration, but even at this duration matching was considerably above chance.

Matching accuracy as a function of delay is shown in Figure 5, in four 10-session blocks. For all birds, accuracy was generally above chance at delays of 1, 2, or 4 sec but generally did not exceed chance at the 8- and 16-sec delays. There was little evidence of improvement at the longer delays over the course of the experiment.

EXPERIMENT 4
ONE OR THREE KEYS AS SAMPLES

One variant of the DMTS task is the "shared attention" procedure (e.g., Maki & Leith, 1973). The sample consists of either an element (such as one of two color fields or one of two line tilts) or a compound of elements (such as a color ground and a line tilt). The comparisons are always elements. On trials with compound samples, either of the elements of the compound may be presented in the comparison phase of the trial. For example, with a compound sample consisting of red and vertical line, pigeons may receive red and green fields or vertical and horizontal lines as comparisons. Typically, matching is less accurate with compound samples than with element samples. Here we examined a similar variable: the number of keys lit as a sample. We lit one or three sample keys and then, as comparisons, lit just one of the sample keys and one key that had not been a sample.

METHOD

Subjects and Apparatus

Same as in Experiment 3.

Procedure

The same general procedures were employed as in the earlier experiments. In the first phase (22 sessions), sample and delay durations were 1 sec. On each of the 36 trials in a session the probability was .5 that a single key would serve as sample; on these trials each of the nine keys was used equally often as sample. On the other trials each of eight three-key patterns was used equally often as sample. The patterns were the three rows, three columns, and the two major diagonals. On trials with one-key samples each of the other eight keys had an equal chance of appearing as a comparison along with the sample key. On trials with three-key samples each of the three sample keys had an equal chance of appearing as the correct comparison, and each of the six keys not used in the sample had an equal chance of appearing as the other comparison.

In the next phase (12 sessions), the duration of three-key sample presentations was increased from 1 to 5 sec. One-key sample presentations remained at 1 sec.

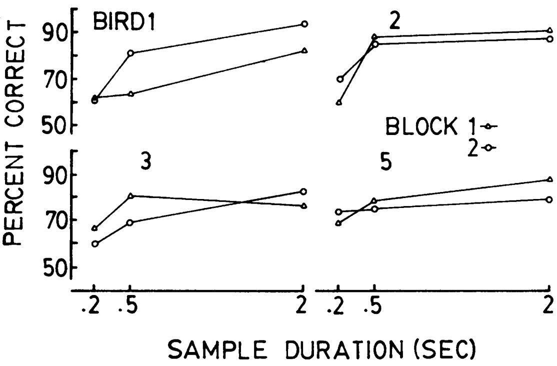

Fig. 4. Percentage of trials with correct matches when sample durations were .2, .5, and 2 sec (Experiment 3). The data are from four sessions at each sample duration, shown as two blocks of two sessions. Chance performance is 50%.

RESULTS

Matching accuracy for trials with one-key samples and three-key samples is shown in Figure 6. In general, more errors were made on trials with three-key samples, although the correct comparison was chosen more often than would be expected by chance.

Choice of the correct comparisons trials on three-key samples was not improved by lengthening the duration to 5 sec from 1 sec.

Figure 7 shows matching accuracy, in two blocks of 11 sessions, for three types of trials with three-key samples: row samples, column samples, and diagonal samples. Although there was little consistent difference in accuracy between row and column arrays (except for Bird 5, who did better on rows), all birds performed less well with the diagonal patterns.

EXPERIMENT 5
ORGANIZATION OF THREE-KEY SAMPLES

The previous experiment showed that three-key samples produced more errors than one-

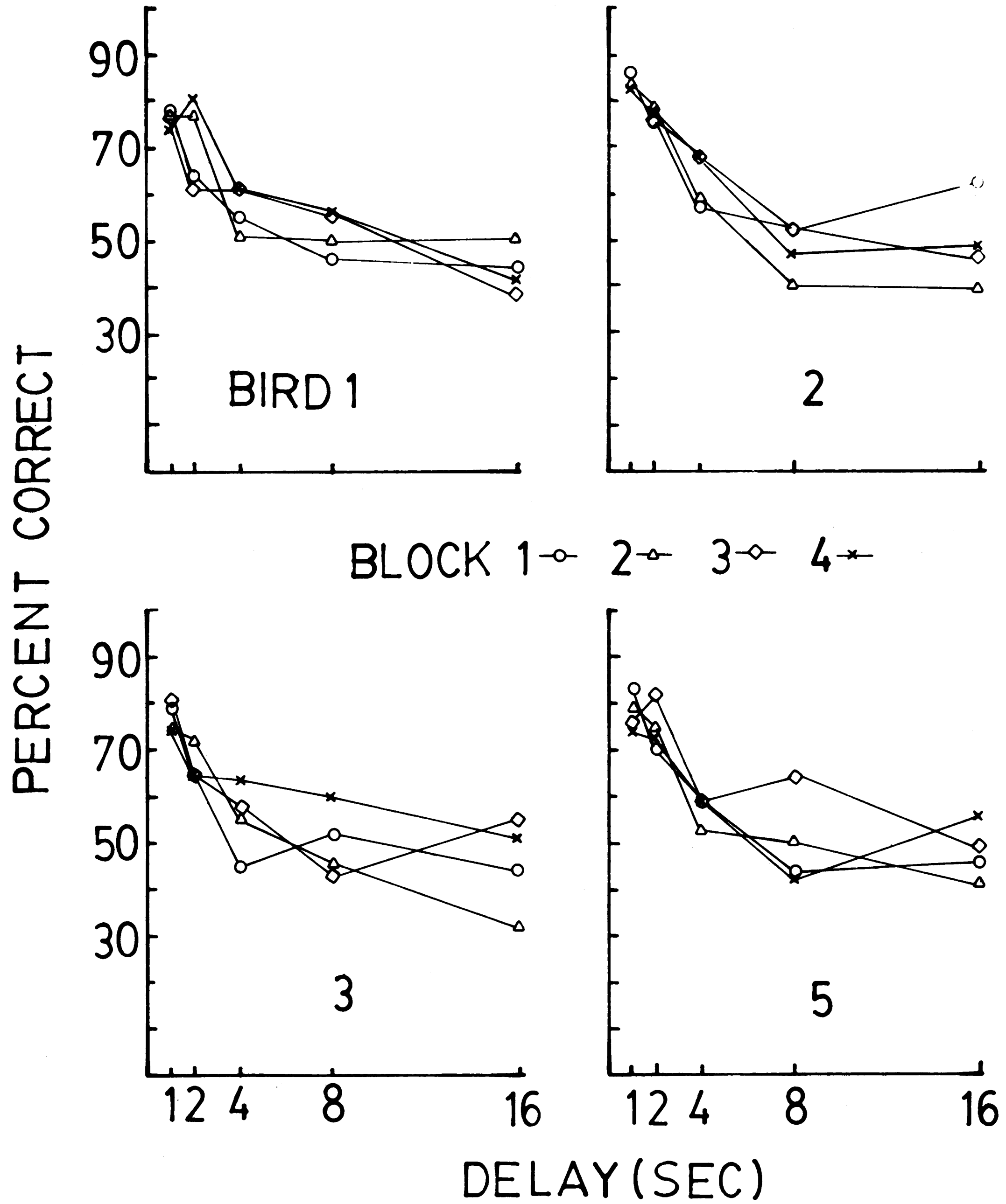

Fig. 5. Percentage of trials with correct matches when delay interval was 1, 2, 4, 8, or 16 sec (Experiment 3). Data are shown as four blocks of 10 sessions. Chance performance is 50%.

key samples and that certain three-key samples (diagonals) produced more errors than others (rows or columns). The present experiment was a more detailed examination of errors on the eight three-key samples used in Experiment 4. As well, eight, nonlinear, discontinuous, three-key samples were used (see Table 2).

METHOD

Subjects and Apparatus

Same as in Experiment 4.

Procedure

General procedures were the same as in Experiment 4. In the first phase (56 sessions),

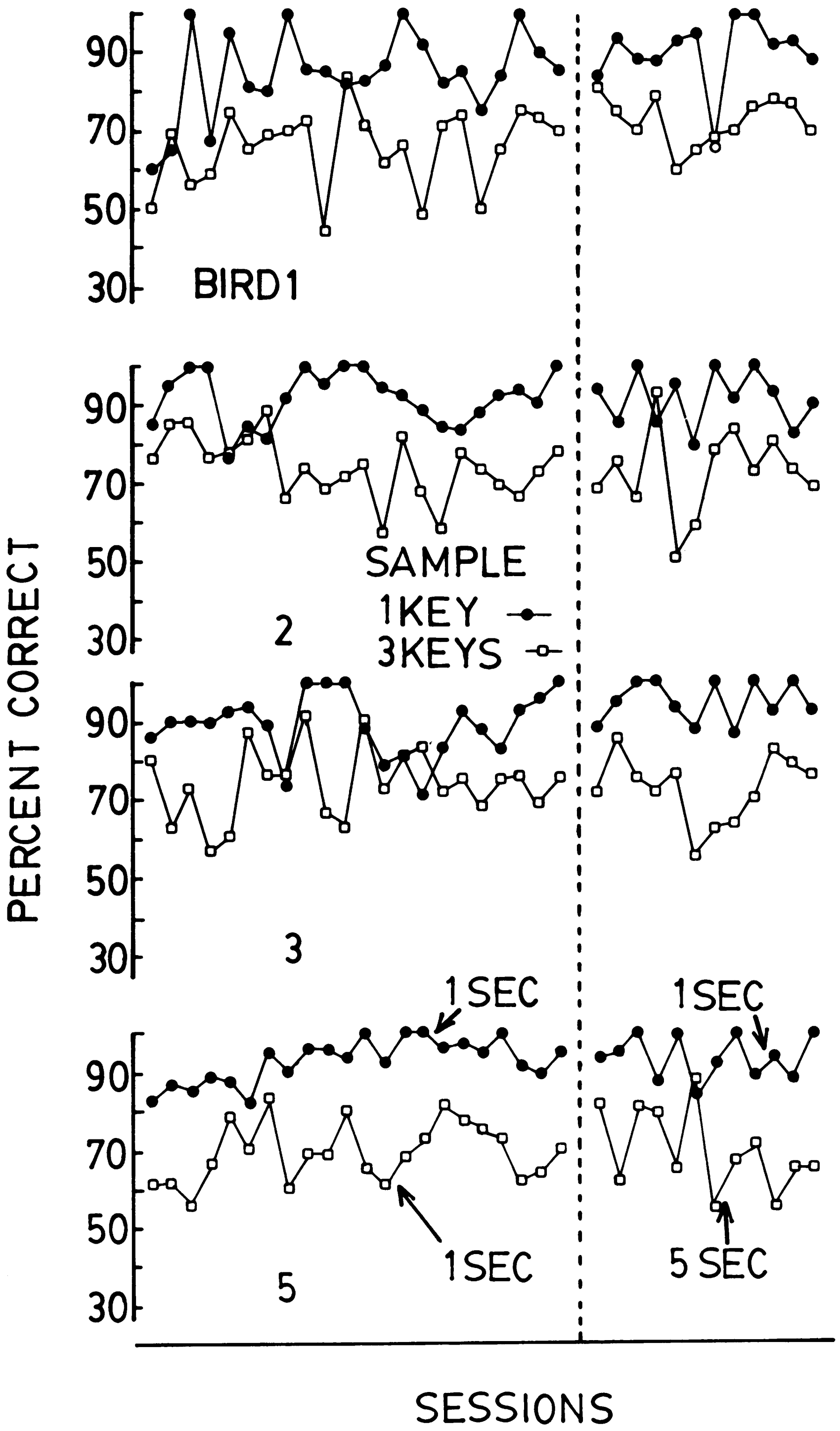

Fig. 6. Percentage of trials with correct matches for one- and three-key samples (Experiment 4) for the last 22 sessions of Phase 1 (both types of samples appeared for 1 sec) and all sessions of Phase 2 (one-key samples appeared for 1 sec, whereas the three-key samples appeared for 5 sec). Chance performance is 50%.

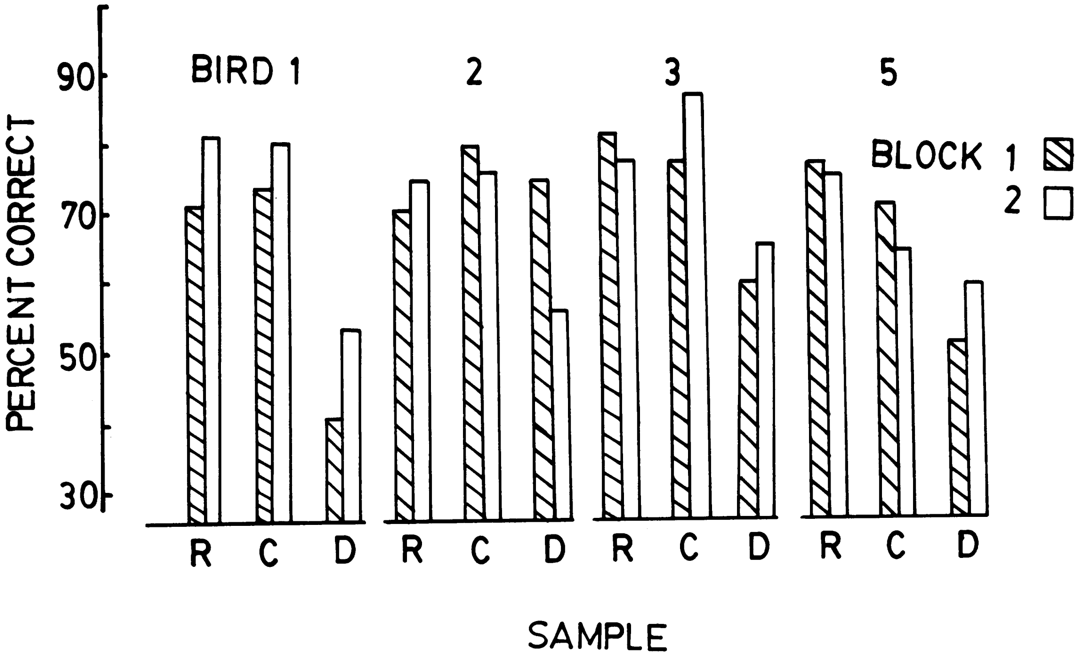

Fig. 7. Percentage of trials with correct matches for three-key samples arranged in a row (R), column (C), or diagonal (D). Data are shown as two 11-session blocks (Experiment 4). Chance performance is 50%.

each of 16 three-key samples appeared with an equal probability on the 36 trials. Eight of the samples were the same as in Experiment 4 (three rows, three columns, two diagonals). The other eight samples did not form a straight line (see Table 2, Samples 9 to 16, for a schematic representation of these arrays). Each sample appeared for 1 sec and was followed by a 1-sec delay. Comparisons were a randomly selected one of the sample keys and a randomly selected one of the remaining six keys.

In the second phase (10 sessions), Samples 9 to 16 appeared for 5 sec; Samples 1 to 8 continued to appear for 1 sec.

RESULTS

Figure 8 shows matching accuracy for Samples 1 to 8 and 9 to 16 for the last 20 sessions of the first phase and all sessions of the second phase. More errors were made on trials with Samples 9 to 16. Increasing the presentation time for Samples 9 to 16 produced little if any improvement in matching accuracy.

Matching accuracy in two 10-session blocks for each of the 16 samples is shown in Table 2. Overall, more errors were made on diagonal arrays (Samples 7 and 8) and on the discontinuous arrays (Samples 9 to 16). Individual differences and exceptions to these overall trends also were apparent. For example, Bird 5 did unusually well on the middle- and bottom-row displays, whereas Bird 1 did unusually poorly on the left-column sample. The bottom row produced the fewest errors for all birds, whereas Pattern 11 produced the most errors. Pattern 15 produced fewer errors than several of the line arrays.

DISCUSSION

Much of our knowledge of animals' working memory for spatial cues has come from experiments utilizing the radial-arm maze (e.g., Olton, 1978) and related field procedures (e.g., Kamil, 1978; Menzel, 1978). The present study shows that delayed matching of key location, which is similar to a task developed by Medin (1969) to study pattern recognition in monkeys, is also a viable paradigm for investigating working memory for spatial cues. Delayed matching permits the study of effects of certain variables not present or easily manipulated in maze or field procedures. Delayed matching,

Table 2

Percentage of trials matching comparison was chosen for 16 types of samples during last 20 sessions of the first phase, presented in two 10-session blocks.

Sample	Block	Bird 1		Bird 2		Bird 3		Bird 5	
		1	2	1	2	1	2	1	2
1	OOO[a] XXX XXX $\bar{X} = 66.1$	77.3	78.3	48.0	64.0	51.8	66.6	63.6	79.1
2	XXX OOO XXX $\bar{X} = 84.5$	78.3	78.3	79.1	78.2	88.0	86.3	95.2	95.6
3	XXX XXX OOO $\bar{X} = 90.0$	86.3	91.3	86.9	83.3	85.7	95.8	95.8	95.2
4	OXX OXX OXX $\bar{X} = 77.9$	57.1	33.3	95.8	87.5	84.0	92.0	81.8	91.3
5	XOX XOX XOX $\bar{X} = 73.7$	78.9	80.0	68.0	86.3	54.1	62.5	80.0	80.0
6	XXO XXO XXO $\bar{X} = 76.3$	83.8	87.5	84.6	71.4	60.0	91.3	52.6	78.9
7	OXX XOX XXO $\bar{X} = 53.3$	50.0	52.3	50.0	41.6	39.1	70.0	71.4	52.3
8	XXO XOX OXX $\bar{X} = 66.0$	68.4	77.2	91.6	66.6	80.0	68.1	29.1	47.3
9	OXX XXO OXX $\bar{X} = 47.8$	60.0	33.3	41.6	48.0	55.0	39.1	50.0	55.0
10	XOX XXX OXO $\bar{X} = 57.6$	60.0	47.8	77.2	60.8	50.0	64.0	38.0	63.1
11	OXO XXX XOX $\bar{X} = 43.2$	39.1	36.3	30.0	38.0	40.0	59.0	59.0	44.4
12	XXO OXX XXO $\bar{X} = 56.7$	62.5	59.0	76.1	47.6	57.8	63.6	36.8	50.0
13	OXX OXO XXX $\bar{X} = 50.8$	28.0	56.5	25.0	57.1	40.0	52.3	71.4	76.4
14	XXO XXX OOX $\bar{X} = 54.8$	62.5	54.5	65.0	45.4	66.6	57.5	50.0	36.8
15	XXX OXO XXO $\bar{X} = 79.2$	76.9	70.8	70.0	86.3	90.4	78.9	75.0	85.0
16	XOO XXX XOX $\bar{X} = 60.2$	76.0	82.6	55.0	68.4	47.0	50.0	45.0	57.8

[a] O = key in this location on; X = key in this location off.

because it is such a widely used procedure in studies of animals' working memory, has an added advantage of permitting a closer integration of the spatial-memory literature with the literature on remembering cues such as visual stimuli, responses, reinforcers (e.g., Maki et al., 1977), and duration (Spetch & Wilkie, 1981).

Several factors affect delayed matching of spatial cues. First, as in the case with other cues (e.g., Wilkie & Spetch, 1978), accuracy of delayed matching of key location is hindered by decreases in sample-presentation time and by increases in the delay interval. Presentations longer than .2 sec resulted in superior performance, but the above-chance performance with .2-sec presentations shows that pigeons can remember quite-brief key presentations. Pigeons can remember key location for roughly 4 sec, a result similar to retention intervals effects for other cues but surprisingly short for spatial cues.

Second, accuracy of delayed matching of key location is hindered by proximity of correct and incorrect choices, a result similar to one reported by Medin (1969). In his Experiment 2, two cells of a four-by-four matrix were lit briefly; after a delay the monkey had to respond to both cells to obtain reward. Accuracy was higher when the two cells were farther apart. Theoretically this effect could be due to two mechanisms. In the first place, subjects could "generalize" between correct and incorrect keys when they were adjacent. Alternatively, the sample "representation" could become "distorted," but not completely "lost" over the delay. Either mechanism could account also for the fact that in the nine-choice procedure, errors tended to occur to locations adjacent to the correct location.

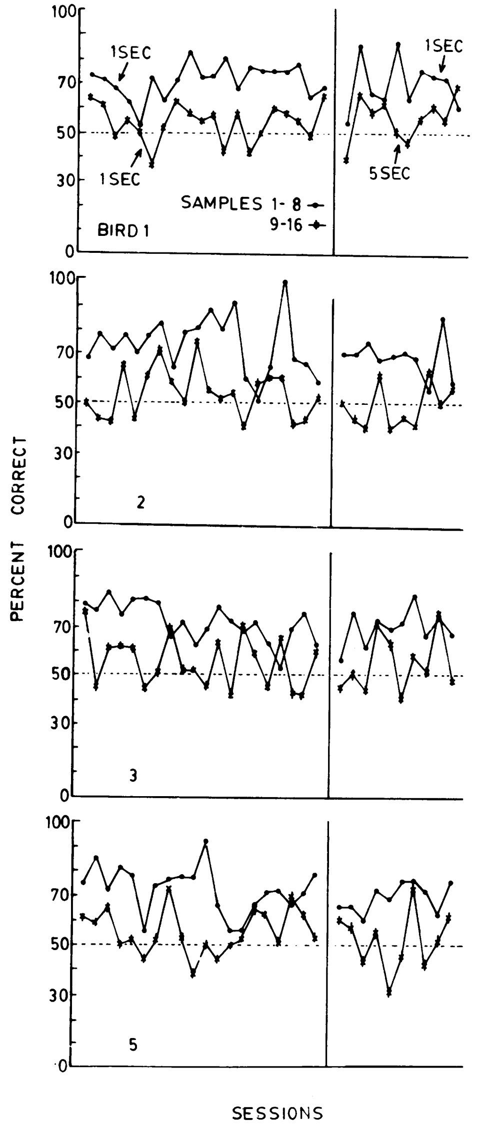

Fig. 8. Percentage of trials with correct matches when three-key samples formed straight lines (Samples 1 to 8) or were discontinuous (Samples 9 to 16) for last 20 sessions of Phase 1 (1-sec durations of both types of samples) and all 10 sessions of Phase 2 (discontinuous samples, 5 sec in duration) of Experiment 5.

It is interesting that this proximity effect has not been found in the radial-arm maze. Olton (1978) reported that when rats entered previously entered (and consequently empty) arms, there was no tendency for them to choose arms adjacent to unentered (and consequently still baited) arms. This discrepancy between the results in delayed matching and radial-arm maze procedures obviously could be due to several factors. One is the greater spatial separation (and hence less opportunity for spatial generalization or distortion) of cues in the radial-arm maze.

Third, accuracy of delayed matching of key location is adversely affected by increasing the number of incorrect comparisons from one to eight. Although several mechanisms might account for this effect, the simplest is that when forgetting occurs with nine choices, there is a lower chance of being correct by guessing.

Fourth, accuracy of delayed matching of key location is hindered by increasing the number of keys illuminated as samples. This effect resembles the "shared attention" effect (e.g., Maki & Leith, 1973) described earlier and parallels the finding that more errors are made in radial-arm mazes having more arms (e.g., Olton, 1978). This effect is perhaps related to the ability of animals to remember only a finite amount of information (but see discussion below). Poorer performance on three-key trials did not seem to be due to an inadequate opportunity to view the sample because lengthening presentation time by a factor of five did not result in any improvement in performance.

When one key serves as the sample it is possible to invoke the "mediation hypothesis" (e.g., Meltzer & Nobbe, 1980) to explain how pigeons match key location. According to this hypothesis the pigeons may have pecked at the sample or oriented to it during the delay. Although it is not clear if such behavior is the actual mechanism of remembering or only anticipates the correct response, the above-chance matching on three-key samples allows the hypothesis to be rejected. Because only one of the sample keys was randomly chosen as the correct comparison, any mediating response such as pecking or orienting toward a key presumably would result in only 67% correct choices rather than the higher percentages obtained for certain sample patterns in Experiments 4 and 5.

Fifth, accuracy of delayed matching of key location on three-key samples depended upon the configuration of the three keys. Diagonals produced more errors than rows or columns, replicating an effect that has been observed in many species in many contexts (see Corballis & Beale, 1976). Overall, linear patterns produced fewer errors than nonlinear discontinuous patterns, even when the discontinuous patterns were presented for five times as long as the line patterns. This result meshes well with the Gestalt proposition that "good figures" are most easily perceived and remembered (Koffka, 1935). Lamb and Riley (1981) also have found that sample organization affects remembering. Using a "shared attention" procedure, these investigators found that delayed-matching accuracy was lower when the white-line and colored-square elements of the compound were separated spatially compared to when the elements were close together.

Although the delayed-matching-of-key-location task is a viable paradigm for studying factors that influence working memory for spatial cues, it perhaps is limited as a procedure for determining the upper limit of the pigeons' spatial-memory capacity. The only slightly better-than-chance performance on the discontinuous three-key patterns and the finding that key location is remembered for only a few seconds is surprising given the remarkable performance of birds in field foraging studies (e.g., Gass & Montgomerie, 1981; Kamil, 1978). Nectar-feeding birds avoid returning to depleted flowers even when the flowers number in the hundreds and the foraging bout extends over a period of hours. One way of resolving this apparent paradox is to attribute only a minimal memory capacity to the pigeon. Bond, Cook, and Lamb (in press) used this strategy to account for the pigeon's performance in an eight-arm radial maze: they estimated that the pigeon can remember only three locations. However, such a limited ability to remember spatial location seems inconsistent with the pigeon's homing ability (e.g., Keeton, 1974) and with our finding (Wilkie, Spetch, & Chew, 1981) that a close relative of the pigeon, the ring dove, performs at well above chance levels in a 14-arm radial maze. Our doves, in contrast to the pigeons of Bond et al., flew rather than walked between arms and did not develop the strategy of frequently visiting adjacent arms, differences which may account for the superior performance of the doves.

We think that our findings that pigeons remember three-key locations with some difficulty reflects the effects of procedural variables rather than memory limitations. Several factors present in the field are absent in delayed matching and may prove to be important for remembering. First, the key matrix, in contrast to the radial-arm maze or the distribution of food in the natural environment, occupied an area of only a few square centimeters. Closeness of the locations to be remembered may have increased the difficulty of the task. Second, although food does not seem to be any more memorable than other cues (Cohen, Calisto, & Lentz, 1981; Wilkie, 1978), the presence of food in a spatial location may potentiate the distinctiveness of that location. In delayed matching, food was not associated with the locations to be remembered. Third, it may be easier to remember "where you have been" compared to "where you have looked," which would give a clear advantage to animals in foraging paradigms.

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