TIME-PLACE LEARNING BY PIGEONS, COLUMBA LIVIA

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In each of two experiments, 2 pigeons received discrimination training in which food reinforcement for key pecking was conditional upon both spatial and temporal cues. In Experiment 1, food was available for periods of 30 s at each of three locations (pecking keys) during trials that lasted 90 s. In Experiment 2, food was available for periods of 15 min at each of four locations (pecking keys) during a 60-min trial. In both experiments, pigeons' key pecking was jointly controlled by the spatial and temporal cues. These data, and other recent experiments, suggest that animals learn relationships between temporal and spatial cues that predict stable patterns of food availability.

Key words: spatial cues, temporal cues, time-place learning, foraging, key peck, pigeons

The idea that animals' behavior is sensitive to joint control by spatial and temporal variables appears in at least three contexts in the literature on foraging. The first is in Staddon and Dale's (e.g., Staddon, 1983) theory of how animals remember to avoid spatial locations recently visited and depleted of food. Briefly, these investigators hypothesized that animals simultaneously encode spatial location and the time at which a location was visited. In tasks such as the radial maze, it is believed that animals employ lists of place-time memory codes to avoid reentering empty arms. They may do this by not entering arms with the newest temporal tags. More recently, Gallistel (1990) has hypothesized that many animals maintain a constant record of temporal and spatial information and that this information is used as the basic way in which memory is organized.

The third suggestion of joint spatial-temporal control stems from naturalistic observations that many animals appear to go to particular places at specific times of the day to forage. Although there are many field observations of this phenomenon (e.g., Daan & Koene, 1981), it is only recently that convincing experimental laboratory evidence has been provided. Biebach, Gordijn, and Krebs (1989)

tested warblers, *Sylvia borin,* in a chamber consisting of a living area that was surrounded by four rooms, each containing a feeder. Each day food was intermittently available in a particular room for a 3-hr period. If the bird entered the "correct" room it could gain access to food; if it entered an "incorrect" room, the feeder in that room remained locked and the bird could not obtain food. Food was available for 20 s during each feeding. After obtaining food, the bird had to return to the living area and wait a minimum of 280 s before reentering the correct room. The birds quickly learned to enter correct rooms and avoid entering incorrect rooms. During test sessions all four feeders were available for the 12-hr feeding period. Under these conditions the birds continued to visit the rooms at the appropriate (i.e., trained) times.

The research described in this paper also concerns joint spatial-temporal control of behavior. Our research is similar to that of Biebach et al. (1989) but differs in two major ways. First, we used shorter time intervals during which food was available at particular places (pecking keys). In Experiment 1, food was available intermittently for 30 s in each of three places (pecking keys). In Experiment 2, food was available intermittently for 15 min in each of four places (keys). Second, we used pigeons as subjects. This species has been used extensively in research on behavioral control by spatial (e.g., Cheng, 1988; Spetch & Edwards, 1986; Wilkie & Summers, 1982) and temporal (e.g., Cheng & Roberts, 1989; Spetch & Wilkie, 1983; Wilkie & Willson, 1990) cues.

Therefore, it seemed appropriate to use this animal in an investigation of the joint control of behavior by these two types of cues.

EXPERIMENT 1

In this experiment, subjects were exposed to a discrete-trial procedure in a conventional operant conditioning chamber. Trials lasted for 90 s, during which food was available intermittently on each of three identical pecking keys for 30 s—the left key for the first 30 s, the middle key for the middle 30 s, and the right key for the last 30 s. Of primary interest was the question of whether the subjects' rate of key pecking was controlled jointly by temporal and spatial location cues.

METHOD

Subjects

The subjects were 2 Silver King pigeons, Jack and FF. The subjects were maintained at 90% or more of free-feeding body weights by a diet of mixed grain obtained during test sessions and posttest feedings. The subjects lived in large plastic-coated wire-mesh cages with free access to vitamin-fortified water, grit, and crushed oyster shells. The colony was climate controlled (20 °C) and had a light–dark cycle matched to the natural sunrise–sunset times. Both subjects had previously been trained to peck keys for food reinforcement but were naive with respect to the present procedures.

Apparatus

One wall of each of two conditioning chambers contained a square 3 × 3 matrix of pecking keys. The 3.5-cm-diameter keys were mounted 5 cm apart, center to center. The center key of the matrix was 20 cm above the floor. Behind each key was a microswitch that sensed pecks having a force greater than 0.15 N and a Fairchild FLV117 red light-emitting diode (about 0.15 cd/m²). A standard grain feeder was mounted below the key matrix. In the present study, only the center row of keys was used. Data collection and experimental control were carried out by the MANX language (Gilbert & Rice, 1979) running on a minicomputer.

Procedure

Because both subjects had previous key-peck training, no preliminary training was required. Each subject received approximately 45 sessions of training during this experiment. Sessions consisted of 20 trials and occurred at approximately the same time (a few hours after light onset) each day, 5 days a week. Trials, separated by 20-s intertrial intervals, began with the illumination of the middle row of three keys with red light. Trials lasted for 90 s and were divided into six 15-s periods. During the first two periods, pecks on the leftmost key produced grain reinforcers with a probability of .2. During the remaining four periods, pecks on this key were ineffective in producing food. During Periods 3 and 4, pecks on the middle key produced grain according to the same schedule. Pecks on this key were ineffective during Periods 1 and 2 and Periods 5 and 6. During the latter two periods, pecks on the rightmost key were reinforced, again according to the same schedule. Pecks to this key were ineffective during Periods 1 to 4. During each reinforcement, the grain hopper was raised for 5 s and all keylights were turned off. During each session, the number of key pecks on each key during each of the six periods was recorded, as was the number of reinforcers obtained.

RESULTS

The data appear in Table 1, which shows responding on each of the three keys during each of the six periods that comprised a trial. The data in this table are cumulated over all sessions in the experiment. During periods in which reinforcement occurred (e.g., Periods 1 and 2 for the left key), the duration of the reinforcement periods was subtracted from the period length in calculating response rate. Relative rate of pecking was calculated by dividing absolute rate of responding on a key by the total rate of responding across all periods on that particular key. A few examples will make reading of this table easier. Consider entries for FF. During Period 1 (the first 15 s of each trial) this subject pecked the left key 0.197 times per second, the middle key 0.071 times per second, and the right key 0.068 times per second. During Period 2 (the period from 15 to 30 s) this bird pecked the left, middle, and right keys 0.155, 0.122, and 0.097 times per second, respectively. Next consider relative rates. The total of response rates on the left key for the six periods was .698 (i.e., .197 + .155 + .122, etc.). Relative responding on the left key during Period 1 was .289 (i.e., .197/ .689).

Table 1

Data for Jack and FF from Experiment 1. Data for Jack are cumulated over 49 sessions; those for FF, over 43 sessions. The first datum for each subject is average response rate (pecks per second) to each key during each of the six 15-s periods that comprised a trial. The second datum is relative response rate.

	Period											
	1		2		3		4		5		6	
FF												
Left key	0.197	.289	0.155	.225	0.112	.162	0.079	.115	0.079	.115	0.067	.097
Middle key	0.071	.095	0.122	.164	0.151	.203	0.146	.198	0.128	.173	0.124	.166
Right key	0.068	.099	0.097	.142	0.105	.154	0.126	.184	0.136	.200	0.150	.220
Jack												
Left key	0.357	.407	0.186	.212	0.115	.131	0.070	.079	0.070	.079	0.081	.092
Middle key	0.181	.114	0.398	.250	0.330	.208	0.258	.162	0.239	.151	0.183	.115
Right key	0.066	.053	0.148	.119	0.207	.166	0.284	.228	0.289	.231	0.254	.204

An examination of the data in Table 1 reveals evidence of time-place learning: For both subjects, responding on the left key was initially high but then dropped. Responding on the right key occurred in the opposite pattern. Responding on the middle key tended to be lower during both early and late periods. Interestingly, responding on Key 1 was lower during the second 15-s period than during the first, despite the fact that food was equally available during both periods. This decreased rate suggests that the subjects were anticipating nonreinforcement on this key. Jack, but not FF, showed a similar pattern of responding during the third and fourth periods on the center key. These patterns of responding are displayed graphically in Figure 1, which shows relative rate of responding on the left key, middle key, and right key during each of the six periods that made up a trial. The smoothed curves drawn through the relative rate of responding data points were generated by the distance-weighted least squares smoothing option in the Sygraph® graphics system (Wilkinson, 1988, p. 540).

DISCUSSION

Both subjects showed evidence of time-place learning. The subjects responded at different locations at different times; they responded primarily to the left key early in the trial, the center key in the middle of the trial, and the right key later in the trial. The temporal control of the location of pecking was strongest early and late in the trial. Although there tended to be a peak in responding on the middle key in approximately the middle of the period, responding on this key was less differentiated temporally than responding on the other locations. This result may be due to the fact that the endpoint on a spatial continuum (left and right keys) or on a temporal continuum (early and late in a trial) are more discriminable than left from middle and middle from right, or early from middle and middle from late. That is, the apparent weaker control of responding during the middle portion of the trial may be due to generalization or to a failure to discriminate.

EXPERIMENT 2

The results of Experiment 1 were suggestive of time-place control of pigeons' pecking for food reward. The purpose of the second experiment was to replicate systematically the findings of Experiment 1, and to attempt to find stronger evidence of time-place control. In this experiment, a new apparatus was used so that the key locations that provided food availability were much more spatially distinct and separated. In addition, trials were much longer in duration. In brief, each of four pecking keys, located on the walls of a large transparent test chamber, provided food intermittently for 15 min during each 60-min trial. Subjects received one trial per day.

METHOD
Subjects

The subjects were 2 Silver King pigeons, Gandolf and Cindy. The subjects were maintained under conditions identical to those in Experiment 1. As in that experiment, both subjects had previously been trained to peck
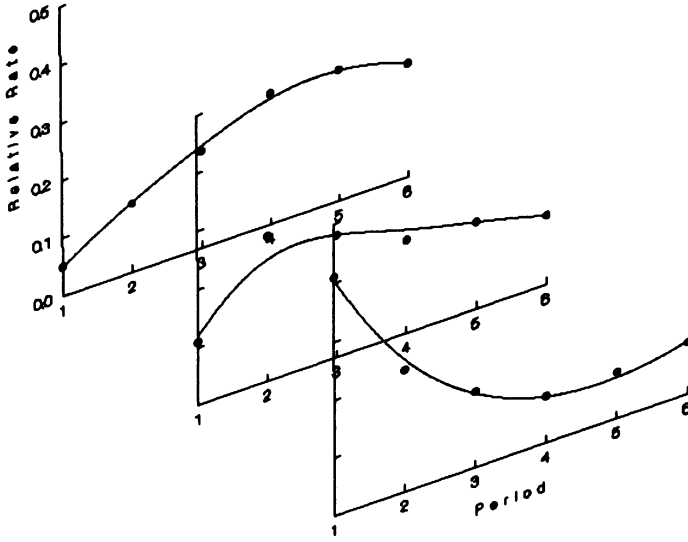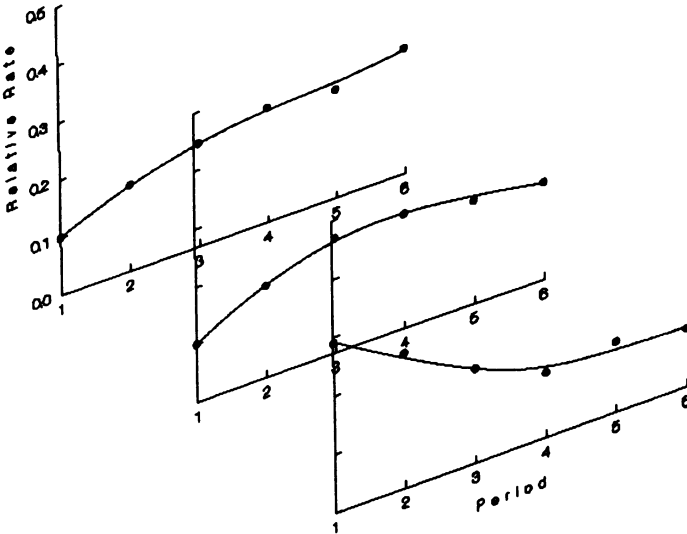
Fig. 1.   Relative response rate across periods of the session for Jack and FF. Front panels show data from the left key, center panels show data from the center key, and rear panels show data from the right key. See text for details about the fitted curves.

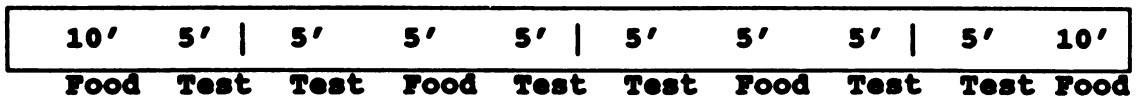| 10′	5′	5′	5′	5′	5′	5′	5′	5′	10′
Food	**Test**	**Test**	**Food**	**Test**	**Test**	**Food**	**Test**	**Test**	**Food**

Fig. 2. Schematic representation of the 10 components that comprised the probe sessions in Experiment 2. Vertical bars mark the divisions between the 15-min periods.

keys for food reinforcement but were naive with respect to the present procedures.

Apparatus

A 3.5-cm-diameter key was mounted on the center of each wall in each of two large square Plexiglas chambers. Each key was mounted 20 cm above the floor. Behind each key was a microswitch that sensed pecks having a force greater than 0.15 N and a 28-VDC 313 lamp covered by a red gelatin filter (about 1.5 cd/m^2). A standard grain feeder was mounted directly below each key. Each chamber was located in a small (about 2 m by 2 m) well-lit testing room. Subjects could see a variety of room cues (window, door, wall posters, etc.) through the transparent Plexiglas walls of the boxes. The floor area of the first box (Gandolf) was 3,600 cm^2; the floor area of the other box (Cindy) was 2,025 cm^2. Data collection and experimental control were again carried out by the MANX language (Gilbert & Rice, 1979) running on a minicomputer.

Procedure

Because both subjects had previous key-peck training, no preliminary training was required. The subjects received several training sessions, followed by probe sessions. As in Experiment 1, subjects were tested at about the same time each day, 5 days per week. Testing was done a few hours after light onset.

Training sessions. Both subjects received one 60-min session each day. Each session began with the simultaneous illumination of the four identical pecking keys. During the first 15 min, one key (Key 1) provided access to 5-s grain reinforcers according to a variable-interval 45-s schedule. During this period the cumulated number of pecks made on this and the other three nonreinforced keys was recorded, as was the number of reinforcers obtained. During the next 15-min period, the adjacent key (Key 2), counterclockwise to Key 1 from the room entrance, provided grain reinforcers on the same schedule. Responding on all four keys was again recorded. Similarly, during Period 3,

Key 3 provided food, and during Period 4, Key 4 provided food. Thus during the course of a session, food availability depended jointly upon temporal and spatial cues. Gandolf received 32 training sessions before probe sessions began; Cindy received 15.

Probe sessions. In training sessions, subjects' responding on a particular key may be controlled jointly by place-time cues. However, the occurrence and nonoccurrence of food reinforcers may also be a factor controlling responding. That is, responding for a period and not receiving food is predictive (not perfectly, of course) that food is available on some other key. Similarly, obtaining food, especially for the first time on a key, is predictive that additional food is available. To demonstrate joint place-time control of responding unambiguously, food cues must be omitted. With the current procedure this was not possible, because subjects would surely extinguish responding over a 60-min test session. Consequently, a different type of test for place-time control was arranged during probe sessions.

As shown in Figure 2, probe sessions were divided into 10 components. The first 15-min period (when pecks on Key 1 were normally reinforced) was divided into an initial 10-min component and a second 5-min component. Food was available during the first component but not during the second. The second 15-min period (pecks on Key 2 normally reinforced) consisted of three 5-min components. Food was available during the middle 5-min component but not during the first or last component. A similar arrangement occurred in the third period (Key 3 pecks reinforced). In the last 15-min period (Key 4 pecks reinforced), food was available during the last 10 min but not during the first 5 min. The critical aspect of this design was that food was not available during the last 5 min of each 15-min period or during the first 5 min of the next period. Thus, food and no-food cues were unavailable to act as signals to switch responding from Key 1 to Key 2, Key 2 to Key 3, and Key 3 to Key 4.

Responding was recorded separately during

each of the 10 components that made up a probe session. Responding during the last 5 min of each 15-min period and the first 5 min of the next was of most interest. Consider the end of Period 1 and the start of Period 2. If pigeons' pecking was controlled jointly by place-time cues, we might expect more responding on Key 1 than on Key 2 in the last 5 min of the first 15-min period and the reverse pattern during the first 5 min of the second 15-min period. Similarly, we would expect more responding on Key 2 than on Key 3 during the last 5 min of the second 15-min period and the reverse pattern during the first 5 min of the third 15-min period. Responding on Keys 3 and 4 should show similar patterns at the end of the third 15-min period and the start of the last 15-min period.

Gandolf received 18 probe sessions interspersed in a quasi-random fashion among 53 additional training sessions; Cindy received 12 probe sessions interspersed among 33 training sessions. In total, then, Gandolf received 85 training sessions, and Cindy received 48.

RESULTS

Figures 3 and 4 show data from all training sessions for both subjects. Data are shown separately for the first and second halves of the training sessions. Responding on the different keys at different points in time is shown in the same format as in Figure 1 in Experiment 1. The front panel shows relative responding on Key 1, the next panel Key 2, and so forth. The curves were smoothed in the same way as in Experiment 1. The corresponding absolute response rates are shown in Table 2.

The pattern of responding on the four keys during the four 15-min periods and during both halves of the training sessions was very similar for both subjects. In general, both subjects responded most often to Key 1 during Period 1, Key 2 during Period 2, Key 3 during Period 3, and Key 4 during Period 4. Responding on Key 1 dropped rapidly after the first period and was all but absent during the last two periods. Responding on Key 4 was all but absent during the first two periods but increased in the third period, suggesting that the subjects were anticipating food availability during the final 15-min period. Apparent anticipation of food availability is also seen in responding on Keys 2 and 3. For example, in the first period subjects responded more to Key

2, and during the second period there was more responding on Key 3 than on Key 4.

The basic requirement of the task in the present experiment was that subjects track the availability of food over the dimensions of space and time. As such, the present procedures resemble to a degree the task of tracking a moving visual target (see McVean & Davieson, 1989; Rilling & LaClaire, 1989; Wilkie, 1986). In tracking procedures, it is possible to count responses that lag the target, hit the target, or lead the target. Such was done with our subjects responding on the two keys (i.e., Keys 2 and 3) on which both "lag" pecks and "lead" pecks were possible. These data, averaged over all training sessions, are shown in Figure 5. Both subjects were very accurate in tracking food availability. For both pigeons, most pecks were "hits" (i.e., were on the reinforcement key). For both subjects, lag pecks (i.e., to the previous reinforcement key) and lead pecks (i.e., to the upcoming reinforcement key) occurred about equally often. For both subjects, however, there was a very small tendency for lag pecks to outnumber lead pecks.

Table 3 shows data for each subject during the probe sessions. As with the training phase data, results are shown separately for the first and second halves of the probe sessions. The data are the average number of pecks made in the six critical 5-min components during the probe sessions. In general, the subjects accurately discriminated the end of one 15-min period and the start of the next. Responding on the reinforcement key for the last 5 min of a 15-min period was generally higher than responding on this same key during the first 5 min of the next 15-min period. Responding on the key that would provide reinforcement in the next 15-min period was generally lower during the last 5 min of the current period than during the first 5 min of the next period. Responding on keys not involved in a reinforcement transition from one key to another was generally low. For example, consider the transition from Key 1 reinforcement to Key 2 reinforcement for Gandolf during the first half of the probe sessions. Consider the first two rows of Table 3. The mean number of pecks made on Key 1 during the last 5 min of the first 15-min period was 17; the mean number of pecks made during the first 5 min of the next 15-min period (when Key 1 no longer provided reinforcement during training ses-
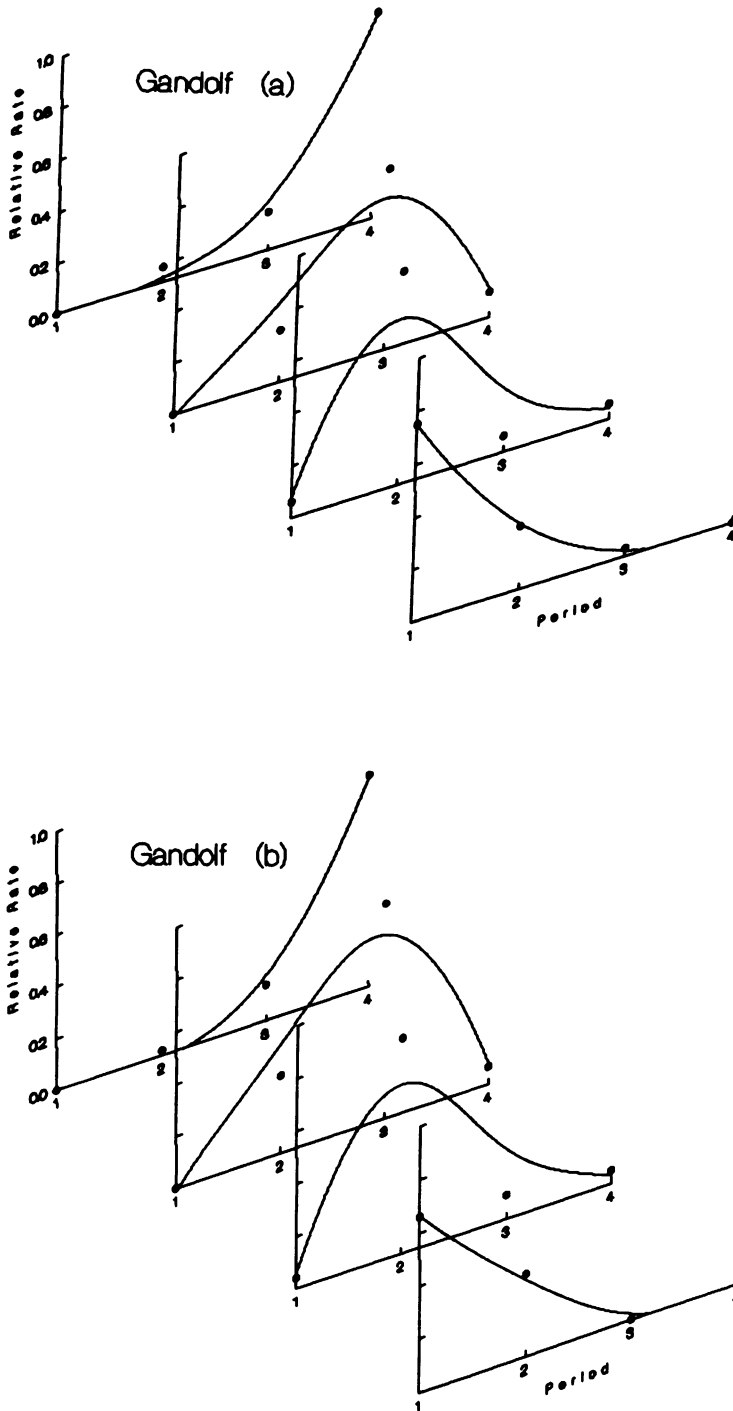
Fig. 3. Relative response rate across periods on the four response keys (Key 1 front, Key 4 rear) for Gandolf. Data are taken from training sessions, with panel (a) showing data from the first half of the training sessions and panel (b) those from the second half. Details about fitted curves are in the text.
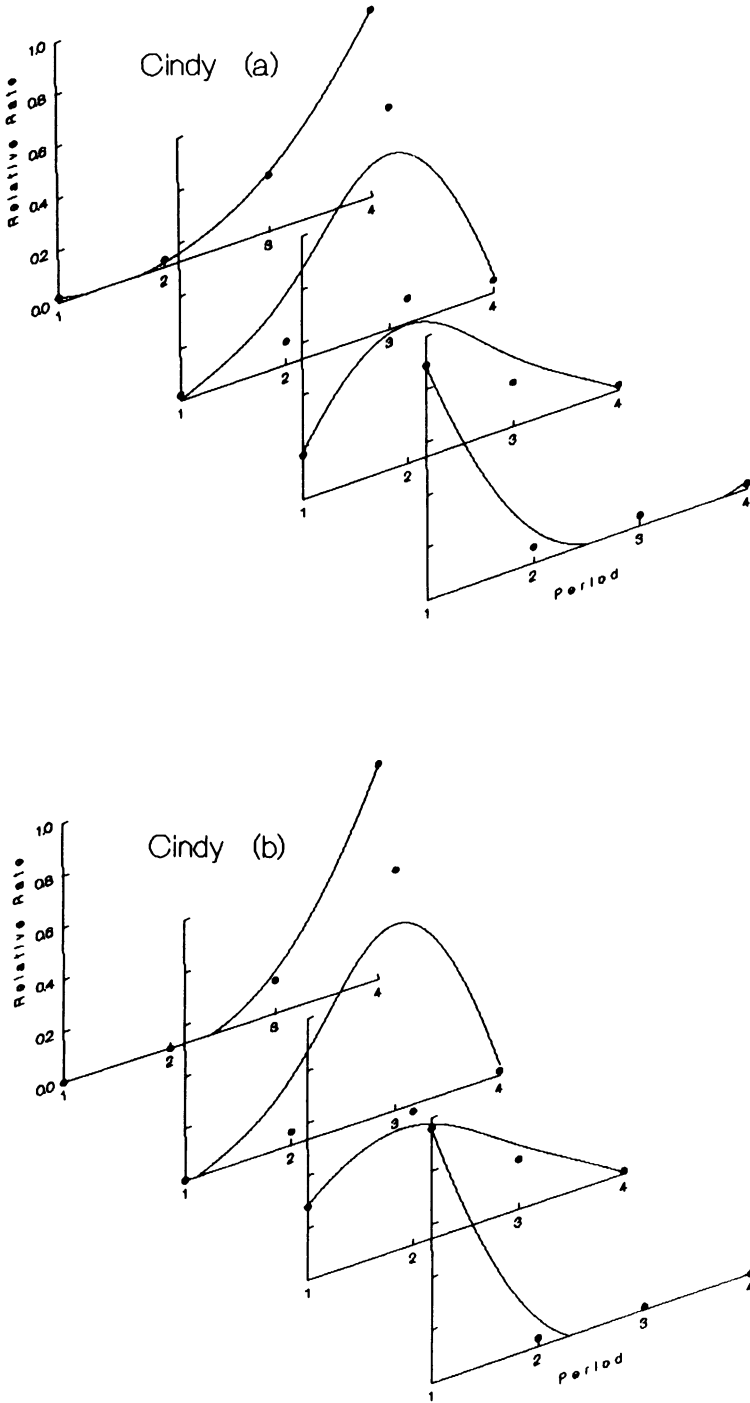
Fig. 4. Relative response rate across periods on the four response keys for Cindy. Details are the same as for Figure 3.

Table 2

Mean number of responses on each of the four keys during each of the four 15-min periods that comprised a session in Experiment 2. Data are shown separately for the first and second halves of the training sessions. Gandolf received a total of 85 training session tests, Cindy 48.

	Period			
	1	2	3	4
Gandolf—first half				
Key 1	102	32	4	1
Key 2	12	158	11	11
Key 3	1	37	128	19
Key 4	0	9	24	132
Gandolf—second half				
Key 1	91	42	2	2
Key 2	11	223	25	13
Key 3	0	34	308	27
Key 4	0	6	49	283
Cindy—first half				
Key 1	547	34	23	12
Key 2	98	366	100	13
Key 3	9	57	515	28
Key 4	9	16	110	370
Cindy—second half				
Key 1	716	23	8	0
Key 2	190	346	131	10
Key 3	3	45	809	18
Key 4	2	3	98	609

sions) dropped to 7. Pecking on Key 2 increased from 32 to 37 during the same periods. As another example, consider the second and third rows of the same table, which show responding on Key 2 dropping (48 to 22) and responding on Key 3 increasing (from 18 to 29) during the 10-min period in which food reward availability normally switched from Key 2 to Key 3.

Figure 6 summarizes how responding changed during probe sessions for each subject. This figure shows relative difference scores for each of the pairs of keys involved in a transition from pecks on one key being reinforced to pecks on another key being reinforced (i.e., Keys 1 and 2, Keys 2 and 3, Keys 3 and 4). Table 3 shows relative responding (in parentheses) on keys involved in a transition. For example, for the transition from Key 1 to 2 for Gandolf, the proportion of responding on Key 1 was .71 in the last 5 min of the first 15-min period and .29 during the first 5 min of the second period. For Key 2 the proportions were .46 and .54. Thus, relative responding decreased on Key 1 and increased on Key 2. These proportions
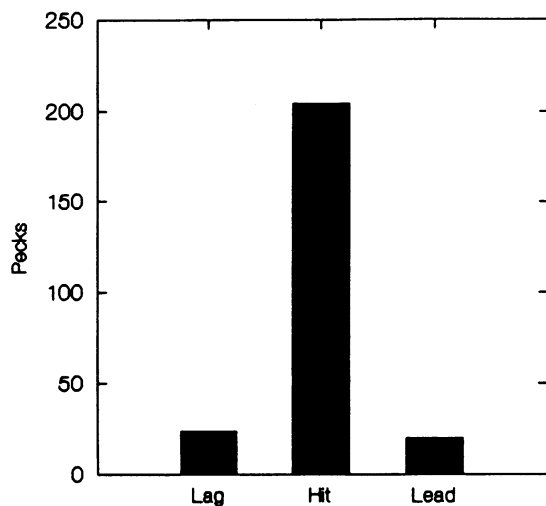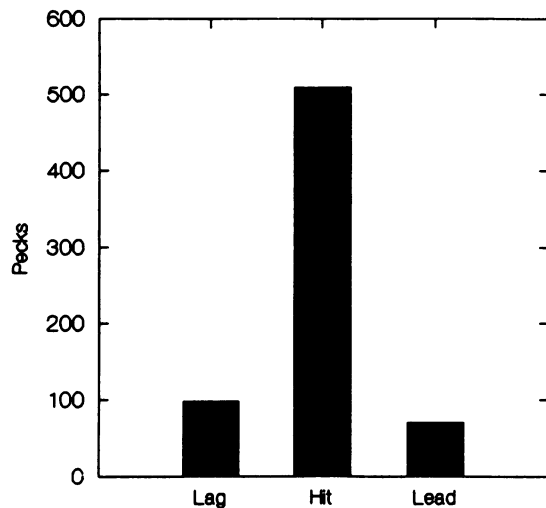
Fig. 5. Average number of responses to the key associated with reinforcement in the previous 15-min period (Lag), to the key currently associated with reinforcement (Hit), and to the key associated with reinforcement in the next 15-min period (Lead). Data are averaged across training sessions and the three transitions that occurred in each session.

Table 3

Data for Gandolf and Cindy from probe sessions of Experiment 2. The data are average total number of pecks during the six critical 5-min test periods in the probe sessions—the last 5 min of the first 15-min period (pecks on Key 1 reinforced), the first 5 min and the last 5 min of the second 15-min period (pecks on Key 2 reinforced), the first 5 min and the last 5 min of the third 15-min period (pecks on Key 3 reinforced), and the first 5 min of the last 15-min period (pecks on Key 4 reinforced). Data in parentheses are proportions of pecks on the two keys involved in the first and second 5-min intervals involved in a transition. For example, during the first transition .71 of responding on Key 1 occurred in the last 5 min of the first 15-min period and .29 in the first 5 min of the second 15-min period. Gandolf received a total of 18 probe tests, Cindy 12.

| Key	Last 5 of first 15	First 5 of second 15	Last 5 of second 15	First 5 of third 15	Last 5 of third 15	First 5 of fourth 15
Gandolf—first half						
1	17 (.71)	7 (.29)	0	1	0	0
2	32 (.46)	37 (.54)	48 (.69)	22 (.31)	5	4
3	5	23	18 (.38)	29 (.62)	63 (.83)	19 (.17)
4	1	2	4	3	11 (.31)	25 (.69)
Gandolf—second half						
1	10 (.77)	3 (.23)	0	0	0	0
2	40 (.38)	64 (.62)	46 (.65)	25 (.35)	2	3
3	4	20	32 (.32)	68 (.68)	87 (.73)	32 (.27)
4	1	0	4	13	24 (.36)	42 (.64)
Cindy—first half						
1	137 (.72)	53 (.28)	12	9	1	11
2	50 (.60)	34 (.40)	131 (.70)	59 (.30)	15	7
3	20	67	66 (.40)	101 (.60)	178 (.88)	26 (.12)
4	3	48	16	33	47 (.28)	120 (.71)
Cindy—second half						
1	244 (.73)	90 (.27)	13	20	2	11
2	10 (.12)	73 (.88)	160 (.77)	48 (.23)	6	9
3	5	56	85 (.44)	110 (.56)	286 (.72)	110 (.28)
4	0	5	4	26	15 (.11)	124 (.89)

were subtracted from each other to yield the difference scores plotted in Figure 6. If responding was under the joint control of place and time cues, the first difference score for each transition should be negative (responding on reinforcement key dropping; e.g., .29 − .71 = −.42 for Key 1 for first transition for Gandolf), whereas the second difference score should be positive (responding increasing on the key that will be reinforced next; e.g., .54 − .46 = .08 for Key 2 for the first transition for Gandolf). This was the pattern for both subjects at all transitions except one, in both the first and second halves of the probe sessions. The one exception was that Cindy's responding did not increase on Key 2 at the start of the second 15-min period during the first half of the probe sessions. (We suspect that there may have been some feeder malfunctions associated with Key 2 during the early sessions that may account for this anomaly.)

The results of the probe session tests show that the subjects moved from one key location to the next at the appropriate time. These results suggest that moving to a certain location was under the control of temporal cues rather than cues such as cumulated reinforcers or periods of nonreinforcement. Additional analyses of training session data bolster this conclusion. In each training session we kept a record of how many reinforcers each subject obtained in each of the 15-min periods. These data were used in a correlational analysis in which we correlated relative responding at the "correct" key (e.g., Key 2 during Period 2) with the number of reinforcers obtained in the *previous* 15-min period (the first 15-min period in the present example). Because the number of reinforcers obtained on a variable-interval schedule will vary depending upon the rate of pecking and vagaries of random interval generation by the controlling computer, the num-
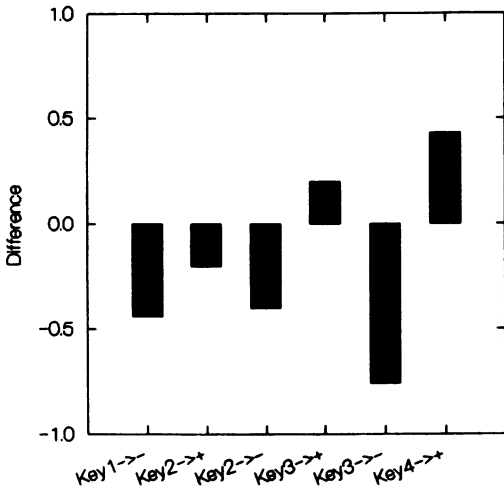
Gandolf First Half
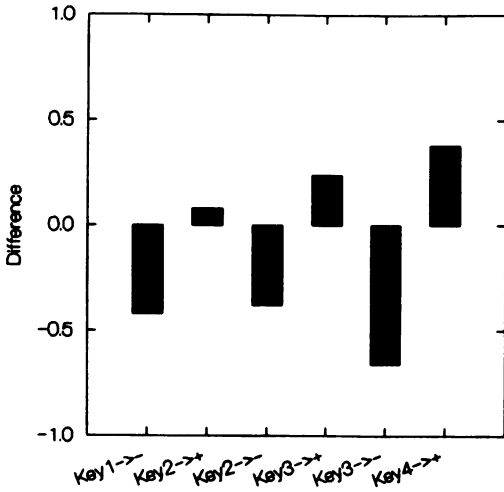
Gandolf Second Half
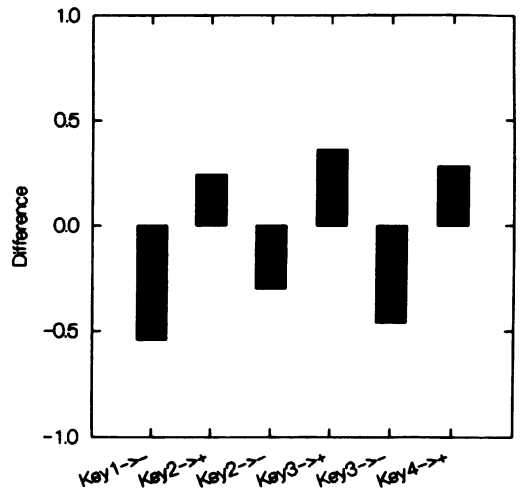
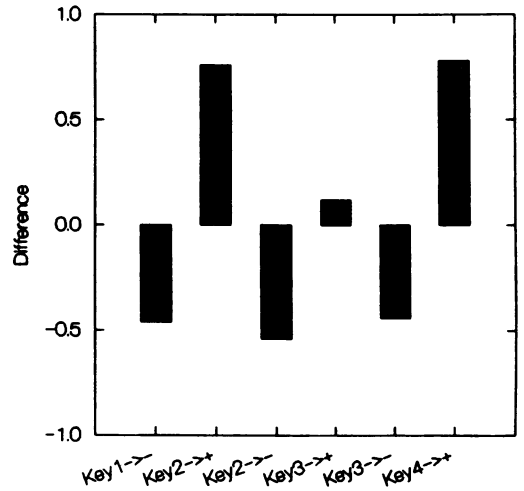Cindy First Half

Cindy Second Half

Fig. 6. Differences between relative response rates on a key in probe sessions across changes in the key normally associated with reinforcement. Each of the three pairs of bars (reading from left to right) in each frame illustrates changes that occurred on adjacent keys at times when reinforcement availability usually moved (during training sessions) from key n to key $n + 1$. The value for each bar represents the change in relative response rate on a key during the 5 min after the normal time of change in reinforcement availability. Data are presented separately for the first half of training and the second half of training for each subject. Other details are in the text.
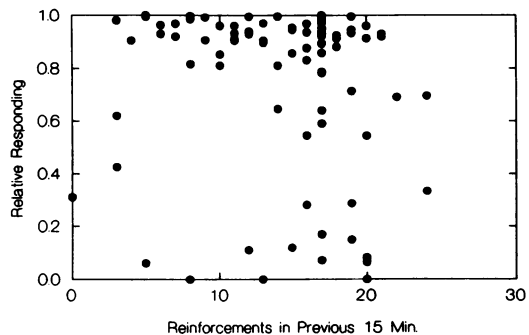
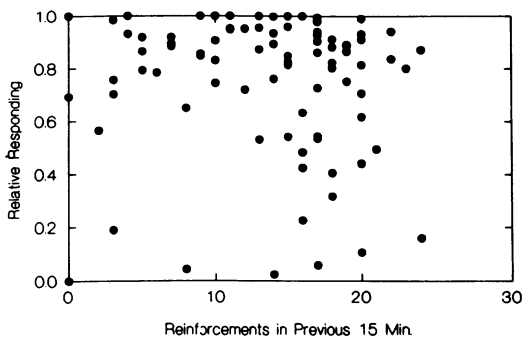Key 2   Key 3
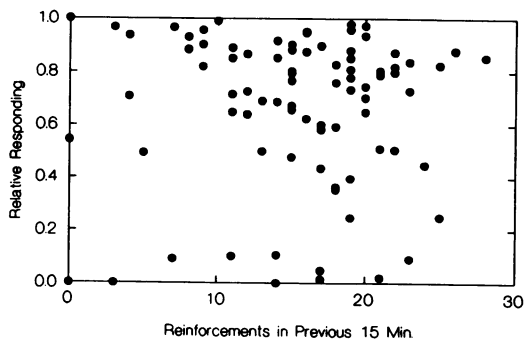
Key 4

Fig. 7.   Scatterplot of relative rates of responding during training sessions on Keys 2, 3, and 4 over number of reinforcers delivered in the previous 15 min.

ber of reinforcers should vary around a certain mean. If control of pecking location is under the control of reinforcement, we would expect a strong correlation between correct responding at a certain key and the number of reinforcers obtained in the previous 15-min period. For example, assume that subjects typically obtain 20 reinforcers in Period 1. If number of previous reinforcements controls switching to Key 2, we would expect accurate Key 2 responding on days when the subject obtained about 20 reinforcers and less accurate responding on Key 2 on days when many fewer (or many more) reinforcers were obtained.

Plots of relative responding on Keys 2, 3, and 4 as a function of the reinforcement density in the previous 15-min period are shown for Gandolf and Cindy in Figures 7 and 8, respectively. The top left panel for each subject shows relative responding on Key 2 during Period 2 (pecks to Key 2 divided by the total

of pecks to all four keys) as a function of the number of reinforcers obtained in Period 1. The top right panel shows relative responding on Key 3 as a function of the number of reinforcers obtained in Period 2. Similarly, the bottom panel shows relative responding on Key 4 as a function of the number of reinforcers obtained in Period 3. Data for all training sessions are shown. The striking feature of these plots is that there is not the least hint of a relationship between the two variables. The Pearson correlation coefficients for the top left, top right, and bottom panels for Gandolf were −.09, .02, −.05, and were .03, .07, and .27 for Cindy.

DISCUSSION

The results of this experiment, in conjunction with those in Experiment 1, suggest that pigeons can learn time-place relationships. A
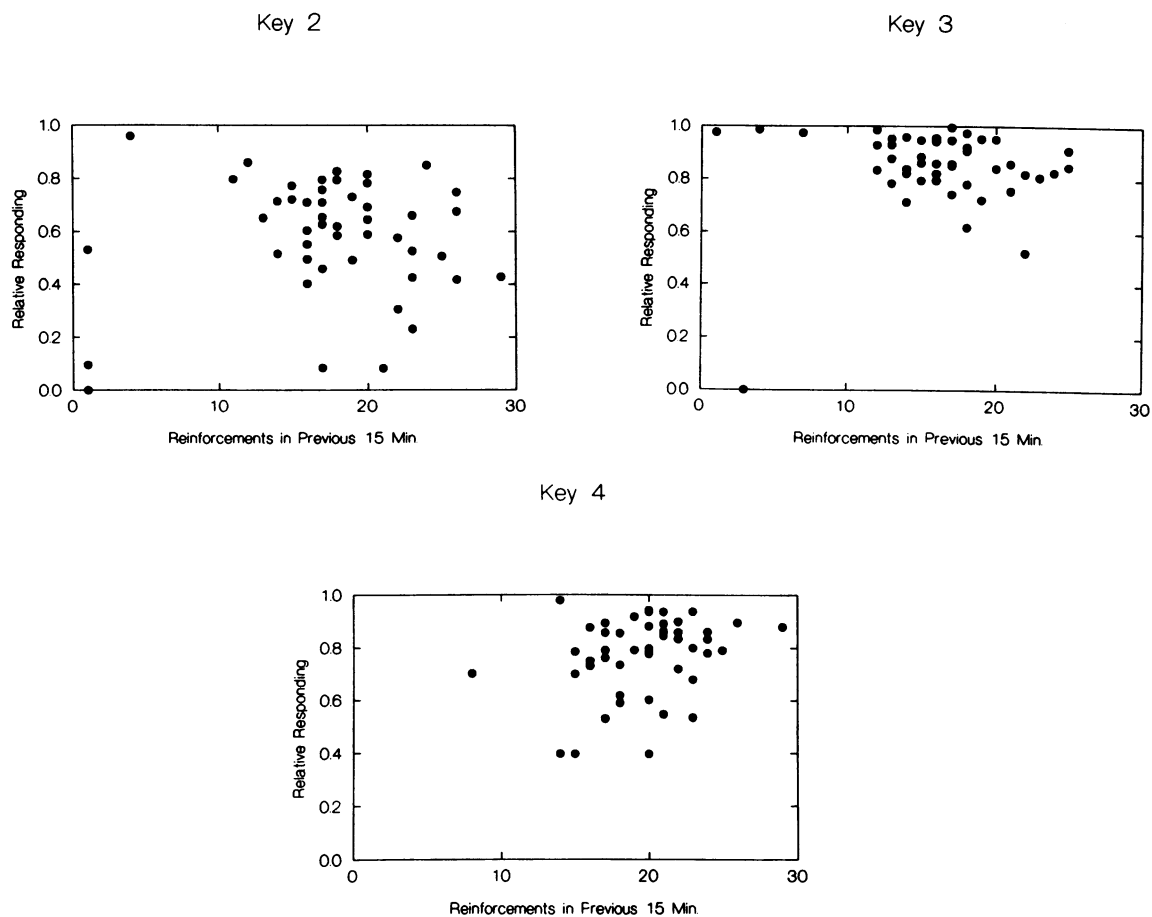
Key 2

Key 3

Key 4

Fig. 8. Scatterplot of relative rates of responding during training sessions on Keys 2, 3, and 4 over the number of reinforcers delivered in the previous 15 min.

large body of previous literature has shown that pigeons' and other animals' behavior is sensitive to control by spatial and temporal cues. Our results, along with those of Biebach et al. (1989), show that these two cues can jointly control behavior. Our results may be somewhat surprising in light of results reported by Bowe and Green (1988), who studied pigeons (and rats) in a situation in which both the time of food availability and the place of food availability were unpredictable. They permitted their subjects to respond on keys that produced cues indicating either when food was going to be available ("now" or "later") or when it was going to be available ("here" or "there"). These subjects learned to respond on keys producing temporal information but not spatial information. The fact that these subjects responded for temporal but not spatial cues may have been due to the fact that the two locations at which food was produced were

quite close together relative to our four locations. It is interesting to note that we found less clear evidence of joint temporal-spatial control in Experiment 1 when three food locations (i.e., keys) were also spatially quite close together.

Another novel result of our Experiment 2 and the experiment of Biebach et al. (1989) was that behavior was controlled by temporal cues that were much longer than those used in previous studies of temporal control. In contrast to the vast majority of studies in which temporal cues have varied over a range of several seconds, our subjects and those of Biebach et al. tracked food availability over periods ranging over several minutes and several hours. In future research it will be important to attempt to determine if the underlying mechanism(s) of temporal control are the same or different when responding is controlled by short and long durations. What seems clear now,

however, is that at least some animals appear capable of discriminating temporal intervals on the scale of several minutes or hours.

The fact that animals can apparently learn place-time relations has two important implications. First, it provides some empirical validation to Staddon and Dale's (e.g., Staddon, 1983) hypothesis that animals use joint place-time memory codes on spatial tasks and to Gallistel's (1990) notion that place-time information may be used to organize memory. Although there is extensive evidence that animals' behavior is readily controlled by spatial and temporal cues, direct experimental evidence for the possibility that these cues may jointly control behavior comes from the results of Biebach et al. (1989) and the present experiments. Second, place-time learning may be, as Biebach et al. pointed out, an important mechanism in foraging behavior. For example, consider a common local bird, the northwestern crow (*Thais lamellosa*). In Vancouver this bird can frequently be seen collecting mussels (which are often dropped on nearby rocks or pavement to crack open) at low tides. Because of the tides, this source of food is available at different parts of the day and, because of different shore depths, different places will be exposed at different times. Time-place learning may be an important mechanism in determining where these birds forage at different times during the day. Indeed, time-place learning may be an important mechanism controlling the behavior of all foragers who live in environments in which resources vary with temporal and spatial regularity.

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