Time-of-day discrimination by pigeons, *Columba livia*

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Pigeons were trained to discriminate between four keys. One provided food in the mornings, another provided food in the afternoons, and two never provided food. Three experiments were performed to determine whether pigeons could track food availability over a 24-h period. All the subjects appeared to demonstrate time-place associative learning. A fourth experiment was designed to investigate the mechanisms underlying the timing behavior. Lights-on time was shifted back by 6 h, and no decrease in performance was found during the first session following the phase shift. This suggests that a circadian type of timing mechanism with a self-sustaining oscillator mediates time-place learning over a period of 24 h. Further support for this notion was found in a fifth experiment, in which the subjects were tested in constant dim light. In that experiment, the subjects' continued correct responding provides additional support for a self-sustaining circadian timer.

The ability to represent the temporal structure of experience is essential in order for an animal to base its behavior on what may be predicted to occur. To behave optimally in particular situations, an animal must be able to represent the time of occurrence of events within its daily routine. A natural extension of this is the idea that animals' behavior may be influenced jointly by spatial and temporal control (e.g., Staddon, 1983). The ability of birds to learn associations between time of day and specific spatial locations of food sources has garnered much observational evidence (e.g., Daan, 1981; Daan & Koene, 1981). Several field studies have shown that wild birds are able to adjust their behavior to changing patterns of food availability. For example, oyster catchers seem to be able to anticipate the tidal rhythms that determine mollusk availability (Daan & Koene, 1981). These studies do not, however, demonstrate whether the birds use a time-place association to exploit food, or whether they merely respond directly to changing food availability.

The earliest experimental work in this area was done with invertebrates—namely, bees. Beling (1929) showed that bees can be trained to visit a certain feeding station near the hive at a specific time of day. On test days, when no food was provided, the bees showed peaks of visiting the feeding site just before and during the appropriate time

period. Koltermann (1974) demonstrated that this ability was a robust phenomenon when he trained bees to go to one specific site nine times per day. Early studies on daily feeding schedules and time-place learning were done with several avian species as well, demonstrating that birds can anticipate one or more daily feeding times in both a normal light:dark cycle and under constant-light conditions (starlings, Adler, 1963; finches, Stein, 1951; canaries, Wagner, 1956).

Much of avian and mammalian foraging, however, depends on the animals' ability to associate a specific place with food availability, as opposed to associating one place with different times (e.g., Staddon, 1983). This phenomenon has been studied in several species (e.g., Boulos & Logothetis, 1990). In one such study (Biebach, Gordijn, & Krebs, 1989), garden warblers, *Sylvia borin*, were tested in a chamber consisting of a living area surrounded by four rooms, each with a feeder. Every day, food was available intermittently in a particular room for 3 h. The food was available for 20 sec, after which the bird had to return to the central area for 280 sec before food again became available in the adjacent room. The birds quickly learned to go to the correct room and avoid the incorrect rooms. On test days, although all four feeders were available, the birds continued to visit the appropriate rooms at the proper times.

In another study, it was demonstrated that pigeons can learn time-place associations over a period of 1 h (Wilkie & Willson, 1992). It was shown that the birds could associate a specific pecking key with a particular 15-min interval during a 1-h session. The birds were tested in large Plexiglas chambers with one pecking key and feeder mounted on each of the four walls. They were able to see a variety of spatial cues in the room through the transparent walls of the boxes. The birds received 60-min ses-

This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada. Anita Lee, Piers Samson, and Anna Blasiak assisted with the research. The data reported in this paper comprised part of the first author's MA thesis and were presented at the 1992 and 1993 meetings of the Canadian Society for Brain, Behaviour, and Cognitive Science. Send correspondence concerning this article to D. M. Wilkie, Psychology Department, The University of British Columbia, 2136 West Mall, Vancouver, BC, Canada V6T 1Z4 (e-mail: dwilkie@cortex.psych.ubc.ca).

sions, during which each key provided food rewards for a 15-min period; Key 1 was rewarded for the first 15-min period of the hour, Key 2 was rewarded for the second 15 min, and so on. During probe sessions in which the first and the last 5 min of each 15-min interval were not rewarded, it was demonstrated that the pigeons were tracking food availability over time rather than merely responding to feedings as cues for food availability.

The goal of the present research was twofold. The first objective was to extend Wilkie and Willson's (1992) paradigm over longer periods—namely, morning and afternoon. The second aim was to investigate the timing mechanisms underlying the behavior of visiting certain places at certain times.

Extension of Paradigm

Three experiments were performed to determine whether pigeons could track food availability over a 24-h period. Ultimately, the reason for this was to enable us to discover the mechanisms underlying the timing behavior, but first it had to be established that the birds could time over such an extended period. It had previously been shown that the longest interval over which pigeons could track food availability in an experimental setting was 1 h. For this reason, a demonstration of timing by pigeons over a 24-h period would be an interesting finding in itself. Experiment 1 was performed to determine whether pigeons could actually remember over such an extended period of time in a laboratory setting. In this experiment, food was available at one place (pecking key) in the mornings, and at a different place in the afternoons. In Experiment 2, only morning trials or only afternoon trials were given, in order to rule out the possibility of an alternation strategy. That is, if the birds were alternating their response over trials, then they should peck the afternoon key in the session following the morning session, irrespective of time of day. Thus, elimination of an afternoon session should cause them to peck the inappropriate key during the following morning's session. Finally, in Experiment 3, the length of time between morning and afternoon sessions was varied, again to verify a timing as opposed to an alternation strategy.

Underlying Mechanisms

Gallistel (1990) has distinguished two types of timing by coining the terms *phase sense* to refer to the ability to anticipate events that recur at a fixed time of the day:night cycle, and *interval sense* to describe the ability to respond to something that happens at a fixed amount of time after an event that occurs at varying points within the day:night cycle. Church (1984) assumes that these types of timing are mediated by different mechanisms: Phase sense is governed by endogenous oscillators that run constantly, whereas interval sense is controlled by stopwatch-like timers. In fact, most short-term timing behavior (less than 1 h) has been explained by a stopwatch-like mechanism (Church, 1978), whereas most long-term timing (24 h) has been accounted for by circadian rhythms (Aschoff, 1989).

The main properties of the two potential mechanisms underlying the different types of timing are as follows. The circadian timing system is based on the phase of an endogenous oscillator (Gallistel, 1990), which is continuous, self-sustaining, and entrainable. Because it is self-sustaining, it does not require the presence of external cues for the timing behavior (i.e., learned time-place associations) to be maintained. The role of external cues in this type of system is to act as "zeitgebers," which entrain the oscillator. In other words, if a circadian system is at work, the behavior will persist in the absence of zeitgebers. Over time, however, it may not adhere to a 24-h period or schedule. Interval (stopwatch) timers, on the other hand, are discrete and can be stopped, started, reset, or restarted by various external events (e.g., Gibbon & Church, 1984; Roberts, 1981). Because stopwatch timers are greatly influenced by external events, alterations in these cues will immediately affect any type of behavior associated with the interval clock. For example, a stopwatch timing mechanism is reset every day by the lights coming on. This ensures that the animal will start timing daily events from the same point every day. If the lights-on time is shifted, however, the stopwatch clock is reset for a different time, and events will be predicted to occur on the basis of the new starting point. Accordingly, if a stopwatch timer is used, then the routine behavior of the bird should be shifted to correspond with the new reset time.

One approach to empirically distinguish these two possibilities is to manipulate the external cue and observe the effects on behavior. In a natural environment, the daily light:dark cycle provides a fairly stable reference for animals. Many laboratory studies have confirmed that this seems to be an extremely salient timing cue (see Aschoff, 1981). Following from this, in Experiment 4 the light:dark cycle was manipulated with an advance of the time of lights on. More specifically, lights-on time was shifted back by 6 h, and performance was observed the following day. If the birds' learned time-place associations are being controlled by an interval timing mechanism that is set by lights on, then an immediate shift in behavior should be observed. However, if the behavior is controlled by a self-sustaining oscillator, then the shift should have a minimal effect on the next day's performance, although over time the birds' behavior should become entrained to the new schedule.

In Experiment 5, a further test of an underlying circadian timing mechanism was performed. The birds were held in constant dim light, and their performance on the time-place learning task was measured. If the birds use an interval timer, the elimination of lights on and lights off should cause errors in performance on the task because the major cue for resetting the internal clock would be missing. If the birds use a circadian mechanism, however, performance should continue as usual (at least for some time) because this timing system is based on a self-sustaining oscillator that is relatively independent of changes in external cues.

GENERAL METHOD

Subjects

The subjects were 1 White King (Allanon) and 3 Silver King (Silvercloak, Johann, and Jack) pigeons. The birds were maintained at approximately 90% of their free-feeding weights with a grain mixture that was available both during and after the testing sessions. All extrasession feedings were given at various times after testing was completed for the day. The subjects were also fed at irregular times on days on which they were not tested (weekends). Approximately half of their daily food intake was obtained during testing, and the other half was provided by extra feeding.

The birds lived in large plastic-coated, wire-mesh cages with ad-lib access to grit, oyster shells, and vitamin-fortified water. The colony was climate controlled (20°C) and had a light:dark cycle matched to natural sunrise and sunset times. Times of lights on and lights off in the colony were changed continuously every 2 to 3 days. Luminance in the colony was approximately 82 cd/m². Data collection occurred between January 3, 1992 and September 15, 1992. Sunrise times ranged from 05:50 to 08:08, and sunset times ranged between 16:24 and 20:52 during this period. (Data were provided by the Atmospheric Environment Service of Environment Canada.) All the subjects were experienced with pecking keys for food reinforcement, but were naive with respect to this experimental procedure.

Apparatus

The apparatus was identical to that used by Wilkie and Willson (1992). Briefly, the pigeons were tested in a large Plexiglas Skinner box with one 3.5-cm-diam pecking key on the center of each of the four walls. Behind each key was a microswitch that recorded pecks that had a force greater than 0.15 N. The keys were illuminated with a 28-V dc No. 313 light that was covered with a red gelatin filter, and each key was mounted above a standard grain feeder. The box was located in a small (2×2 m) well-lit (150 cd/m²) testing room. The subjects were able to see a variety of room cues (window, door, posters, etc.) through the transparent walls of the chamber. Data collection and experimental control were carried out by the MANX programming language (Gilbert & Rice, 1979) running on a minicomputer.

Procedure

All the subjects had had previous keypecking experience; therefore, no preliminary training was required. Trials began with the illumination of all four keys in the box and were initialized by the first peck made by a subject. After initialization, each trial lasted for 17 min. During the first minute of the test, pecks to each key were recorded but did not produce a food reward. Responses during this nonrewarded period were the primary data analyzed in the experiment. During the remainder of the trial, 5-sec access to mixed grain was available on a variable-interval 1-min schedule for pecking the appropriate key (e.g., Key 1 in the morning and Key 3 in the afternoon).

EXPERIMENT 1

Training

Method

The initial question that we addressed was whether the pigeons could learn a time-place association over a long interval (24 h). The subjects were exposed to a discrete-trial procedure in which pecks to one of four keys in a large Plexiglas Skinner box was rewarded, depending on the time of day. Response-initiated trials lasted for 17 min and were presented twice per day—once in the morning (starting between 9:00 and 10:00) and once in the afternoon (starting between 15:30 and 16:30), 5 days per week. Altogether, each subject received 40 sessions of baseline training. Each bird had a different pair of keys that provided food at different times

in order to control for possible key preferences due to previous experience with the present apparatus (Silvercloak—morning Key 1, afternoon Key 3; Johann—morning Key 2, afternoon Key 4; Jack—morning Key 3, afternoon Key 1; Allanon—morning Key 4, afternoon Key 2). All keys were lit in each session, instead of only the two that were rewarded for each bird, so that we could measure potentially different types of error in later experiments.

Results and Discussion

Figure 1 illustrates pecks to the appropriate key for each bird for both morning and afternoon sessions during the first 8 weeks of the experiment. A discrimination ratio was calculated by comparing the number of pecks to the appropriate key with the total number of pecks made during the first nonrewarded minute of the session, and this ratio was converted to a percentage. Each point on the graph represents the mean of discrimination ratios for each 5-day block during the 8-week period. It is important to emphasize that food cues to indicate the correct key were not available during this period.

If a subject did not discriminate, but simply responded randomly, performance would be 25% at the beginning of training (one out of four keys is rewarded). Over time, because pecks to only two keys are rewarded, chance would be closer to 50%. The slope of the lines indicates that 3 of the birds began with a score at chance level, but by the end of the training session they were performing well above even a 50% chance level, in the range of 80% to 95% correct. One bird, Jack, seemed to have some problems with the task during the morning sessions. Initially he acquired the task at a rate similar to the rest of the subjects, but around the fourth week his performance suddenly dropped back to 50% correct. In the afternoon, however, Jack reached a level of 80% correct by the eighth week.

Figure 2 summarizes the percentage of pecks per key in the first minute of each session during both the first and final blocks of baseline sessions. Pecks to all four keys are represented. "Correct" bars represent the percentage of pecks made to the appropriate key for the session, "alternate" bars represent the percentage of pecks made to the key appropriate for the alternate session, and "error" bars represent pecks made to the other two keys in the box.

An examination of the data in this figure suggests that the birds were indeed capable of acquiring the morning/afternoon task. That is, all the subjects seemed quite capable of responding to the appropriate key at the proper time of day. A one-way repeated measures analysis of variance indicated a significant effect of blocks on percent correct for both morning [$F(28) = 2.804, p < .05$] and afternoon [$F(28) = 4.244, p < .01$] acquisitions. Also, a one-sample t test comparing final baseline with a conservative estimate of chance (50%) was significant [$t(7) = 4.22, p < .005$].

All the subjects appeared to demonstrate time-place associative learning, even though the length of time between trials was much greater than in previous studies illustrating this phenomenon in pigeons (e.g., 1 h in Wilkie & Willson, 1992). The birds responded at different places at different times; they learned that one out of four keys provided food in the mornings, and a different key pro-

Figure 1. Percentage of pecks to the appropriate key for both morning (top panel) and afternoon (bottom panel) sessions for all subjects. Data are shown in blocks of five sessions.

vided food in the afternoons. At first glance, this seems to indicate that the pigeons had kept track of time of day in order to determine which was the appropriate key. However, there are other potential explanations for this ability—for instance, a simple alternation strategy is a possibility. Consider the subject Allanon. For every second trial Key 4 provides food, whereas for the alternate trials Key 2 is rewarded. He may simply have used an “every other trial, Key 2 is good” type of rule to determine which key would provide him with a reward. In order to rule out this possibility, several probe trials were conducted in Experiment 2.

EXPERIMENT 2 A.M. Only/P.M. Only

Method

In an attempt to eliminate the possibility of an alternation type of strategy, trials in which only the morning session was presented were inserted twice per week between baseline days. Thus, in one 4-week period, the birds were given 8 morning-only sessions and 12 baseline sessions. If the birds were merely alternating their response over trials, then they should automatically peck the afternoon key in the session following the morning session, regardless

of the time of day. Thus, elimination of any afternoon session should cause them to peck the wrong key during the following morning's session. Following these morning-only probes, a similar type of test was conducted in which 8 morning sessions were eliminated over a 4-week period. Again, these afternoon-only sessions were given twice per week and were alternated with 12 baseline sessions. The rationale was the same: Missing the morning session should cause the birds to go to the inappropriate key during the afternoon session of the same day, if alternation was being used.

Results and Discussion

Figure 3 illustrates percentage of pecks per key for the sessions following the morning-only probes and the sessions following the afternoon-only probes. This graph has the same format as Figure 2 (i.e., pecks to all four keys are represented). All of the birds, with the possible exception of Jack in the morning, seemed to peck the appropriate key in spite of the elimination of the previous session. The subjects seemed to do slightly better in the mornings, with an average of 80% of responses to the appropriate key, compared with 75% correct responses in the afternoon.

Thus, all the subjects showed evidence of using a timing strategy as opposed to alternation. The subjects responded

Figure 2. Mean percentage of pecks per key during the first (top panel) and the final (bottom panel) block of baseline sessions. "Correct" bars represent pecks made to the appropriate key for the session, "alternate" bars represent pecks made to the key appropriate for the alternate session, and "error" bars represent unrewarded pecks to the two other keys.

to the appropriate key in both the mornings and afternoons, in spite of the fact that the previous session had been eliminated. If a bird received rewards for pecking Key 2 in the mornings, Key 4 in the afternoons, and Key 2 again, an alternation strategy would suggest a high degree of error if one of the sessions was eliminated. The low error rate and high degree of response to the appropriate key suggest that this was not the case. In order to further strengthen this finding, however, a second type of probe trial was conducted in Experiment 3.

EXPERIMENT 3 Late A.M./Early P.M.

Method

A second way of ensuring that a timing strategy was being used was to change the spacing between morning and afternoon sessions. If an alternation strategy was being used, then the error rate should be the same as that in the baseline sessions, or perhaps less because of the shortened retention interval between the 2 sessions. If a timing strategy was being used, however, the error rate should increase in relation to how far the probe session deviates from the

Figure 3. Percentage of pecks per key for the sessions following the morning-only probes and the sessions following the afternoon-only probes.

baseline time of session. Time of baseline sessions was approximately 09:30 for the morning sessions and 16:00 for the afternoon sessions. Two separate probe trials were conducted (6 sessions each): Probe 1 (first session at 11:00 and second session at 15:00) and Probe 2 (first session at 12:30 and second session at 14:00). Thus, the intersession intervals varied between 6.5 h (baseline), 4.5 h (Probe 1), and 1.5 h (Probe 2). Each week, 2 probe trials were alternated with 3 baseline sessions, for a total of 12 probes and 18 baseline sessions.

Results and Discussion

Performance on Probe 1, Probe 2, and baseline for morning sessions is illustrated in Figure 4. Two of the birds (Silvercloak and Allanon) tended to perform worse than baseline on both types of probe, as would be expected if they were using the phase of a circadian oscillator as a timer. The other 2 birds, however, showed different patterns. Johann showed slightly better performance on Probe 1 than on baseline, and Jack was better at both probes than baseline. Jack's aberrant results are likely due to the fact that his typical morning baseline performance was far below average, as mentioned in Experiment 1.

The results for the afternoon session are much clearer (see Figure 4, bottom panel).

Between 80% and 99% of the variance in percent correct could be accounted for by intersession interval (Silvercloak, $r^2 = .992$; Johann, $r^2 = .801$; Jack, $r = .797$; Allanon, $r^2 = .895$). As predicted, this suggests that a decline of performance depended on how far the probe testing times deviated from the original testing times, thereby providing further evidence for a timing strategy, as opposed to alternation.

One reason for the variable results for the birds during the morning session may be the fact that the actual difference in times for the two probe trials (2.5–4.5 h) was not very large in relation to the total amount of time that the bird was timing (24 h). As will be seen later, the subjects' timing systems seem to be somewhat flexible; animals must be able to adapt to changes in their environment. Consequently, the birds' timing systems seemed to be able to accommodate slight discrepancies in time of trial presentation. All three types of probes in both Experiments 2 and 3 provide strong evidence that the birds

Figure 4. Performance of all subjects in morning (top panel) and afternoon (bottom panel) sessions as compared with intersession interval (baseline, 6.5 h; Probe 1, 4.5 h; Probe 2, 1.5 h).

had used a timing strategy, so we moved on in Experiment 4 to look at the possible underlying mechanisms.

EXPERIMENT 4 Photoperiod

Method

Once it was established that the birds had used a timing strategy, the next step was to look at the mechanisms underlying the behavior. One possibility was that the birds used an interval, or stopwatch, timer. A second possibility was that they used a circadian timing mechanism. A main feature of a circadian system is that it is self-sustaining; therefore, after a sudden shift in time of lights on, be-

havior will continue as usual—at least for the first cycle following the shift. However, with extended exposure to the new photoperiod, the circadian cycle will gradually become entrained to the new light:dark cycle, and timing behavior will shift accordingly. In contrast, an interval timer can be reset daily by lights-on time. Any behavior that is based on timing will not persist, but instead will immediately shift in accordance with the new schedule.

In Experiment 4, the 4 birds were moved from the colony to a new room so that their light:dark cycle could be shifted without affecting the other birds in the colony. A new baseline measure was taken in order to ensure that the move did not cause a change in their performance. Luminance in the new room approximated that of the colony (95 cd/m²). After 15 days of adjustment to the new room, lights-on time was shifted back 6 h (from 06:00 to

24:00). The subjects were tested, as usual, for baseline sessions on the day immediately following the shift (around 09:30 and 16:00) and then for 6 days following the shift.

Results and Discussion

Figure 5 shows that the birds were not affected by the change in rooms; consequently, the advance in lights-on time was performed. Figure 6 illustrates the performance of each bird on the day immediately following the phase shift. Each of the 4 birds continued to respond to the appropriate key at above chance (Silvercloak, 70%; Johann, 98%; Jack, 65%; Allanon, 100%). It is interesting to note that for most of the birds, correct response actually increased after the advance. The subjects' behavior was not deleteriously affected by the advance, so these data are consistent with a circadian-based timing system.

All 4 of the birds maintained their performance in the session following the shift in lights on. This provides evidence for a circadian, and not a stopwatch, timing system. A clock that is based on an interval system would

be reset by a major external cue, such as a phase shift. A circadian system, on the other hand, is run by a self-sustaining oscillator, and therefore it would not be expected to lead to a change in behavior immediately following a phase shift.

Finally, Figure 7 shows performance of the birds when the phase shift was extended for a period of 6 days. The data for individual birds are considerably different. Both Johann and Allanon performed at an above-chance level, although their scores did drop noticeably. Silvercloak, however, fell to a level that was basically at chance. The number of pecks that he made to keys that were never rewarded was approximately equal to the number of pecks made to both the correct and alternate keys. Jack's scores were also greatly influenced by the continued phase shift, but his strategy was quite different from Silvercloak's. Although his performance in the morning was still extremely high, performance in the afternoon for the correct key was actually below chance. Pecks to the morning-appropriate key in the afternoon, however, approached 80%. This

Figure 5. Baseline performance of all subjects after being moved from the colony to the new room.

Figure 6. Percentage of pecks per key for each bird on the day immediately following the phase shift.

suggests that Jack used the strategy of pecking at one key, both in the mornings and the afternoons, thereby indicating that he was no longer timing appropriately.

The finding that 2 of the birds were able to continue to respond appropriately for up to 6 days provides further evidence for a circadian-based system, as opposed to an interval-based system. Also, the fact that these birds' scores dropped quite a bit from their performance during the first session following the shift, in combination with the poor performance by the other 2 subjects after 6 days, provides evidence that they did not use an alternation type of strategy. If they had, then performance would have either remained the same or improved over the 6-day period. Although this experiment provides strong evidence for a circadian-based timing mechanism, we performed one more test, in Experiment 5, to confirm it.

EXPERIMENT 5

Method

A second way of testing a circadian timing mechanism is, instead of shifting lights-on time, to eliminate it altogether. As in the previous experiment, the absence of the daily lights-on cue should not affect timing behavior, at least for the first cycle after the transition to dim light, if it is based on a self-sustaining mechanism.

In this experiment, the birds were maintained in constant dim light (14 cd/m^2) and then were tested as usual for baseline sessions (09:30 and 16:00) for 4 days following the move to dim light.

Results and Discussion

Three subjects (Johann, Jack, and Allanon) performed extremely well in the dim-light condition (see Figure 8). For each of these birds, percentage of pecks to the correct key were well above chance, and did not differ from baseline scores. This strongly supports a self-sustaining, circadian-based timing system. Silvercloak, on the other hand, performed above chance in the morning sessions but did not peck accurately in the afternoons, thus demonstrating a general decline in performance because he made many errors but few "alternate" responses. Silvercloak's performance in this experiment illustrates the fact that different subjects may use different strategies, depending on the situation.

GENERAL DISCUSSION

The first goal of this research was to determine whether pigeons are capable of timing, in the laboratory, over intervals as long as 24 h. Previous work has demonstrated timing capabilities in the order of seconds (e.g., Gibbon

Figure 7. Percentage of pecks per key for all birds after the phase shift was extended for a period of 6 days.

& Church, 1984; Roberts, 1981) or over 1 h (Wilkie & Willson, 1992). The present work suggests that pigeons are indeed capable of timing over 24 h and that they appear to use a true timing strategy, as opposed to a learned pattern such as alternation. When required to peck at a key that provided food only in the mornings and a different key that provided food only in the afternoons, the pigeons learned this discrimination. When either the morning or afternoon session was omitted, the birds maintained their level of responding. Finally, when the amount of time between sessions was altered, the birds' error level increased. These three findings suggest that pigeons can time over an extended period. This ability is important in the natural environment because resources may be variably available over the course of a day or even longer periods—not merely over the course of an hour. An organism must be able to integrate timing and behavior in order to optimally gain resources in a natural environment.

Once it was established that the subjects were capable of timing over an extended period, we were interested in the mechanism underlying the behavior. The results from Experiments 4 and 5 suggest that this long-term timing is mediated by a circadian clock as opposed to an interval timer. When their lights-on time was shifted back by 6 h, the birds' performance on the day following the shift remained high. In addition, when the birds were kept in constant dim light, performance in the subsequent testing sessions was comparable to baseline performance. This suggests that their timing involved some sort of self-sustaining oscillator that would allow for the maintenance of appropriate behavior in spite of significantly altered external cues. If they had used a stopwatch mechanism, then a substantial decrease in performance would be expected because the clock should be reset by the change in lights-on time, and subsequent behavior should correspond with that shift.

Figure 8. Percentage of pecks per key for all birds under the dim-light condition.

The fact that the birds' performance remained high during both the lights-on advance and the constant-light condition could potentially be attributed to a food-entrained, as opposed to a light-entrained, oscillator (see Boulous & Logothetis, 1990; Rosenwasser & Adler, 1986; Stephan, 1986a, 1986b, 1984; Stephan & Becker, 1989). On baseline days, food was obtained twice per day at about the same time each day; thus, it seems possible that the birds' cycles could be entrained to feeding times. However, feeding was quite irregular on probe days. The first two types of probe sessions involved either a missing session or a session that occurred at a time other than baseline. Also, extra feedings in all types of sessions, along with weekend feedings, were purposely varied and thus occurred at many different times. Thus, one reason that it does not seem likely that food was the sole zeitgeber is that food was not always regularly available. In addition, although in rats feeding times are only a minor zeitgeber for the light-entrainable oscillator, in pigeons feeding schedules have entrained the free-running rhythms (Abe & Sugimoto, 1987). This suggests that pigeons may

have a single oscillator that is entrainable by both light and food, or that the two oscillators are more strongly coupled than those in rats (see Boulous & Logothetis, 1990). This makes the two possible zeitgebers difficult to separate. In this research we did not specifically address the possibility of a food-entrainable oscillator; the main issue was the distinction between an interval mechanism and any type of circadian mechanism. In future work it would be interesting to look at the possibility of a separate food-entrainable oscillator.

Another possibility that has not been addressed is that responding may have been controlled by exogenous cues, as opposed to internal timing cues. Potential exogenous cues include temperature, social signals, and noise from outside the colony and testing chamber. Temperature was maintained at a constant level of 20°C. Potential signals resulting from the experimenter's patterns of entry into the colony were minimized by conscious attempts to vary the times of feeding and maintenance that required access to the colony. Also, during Experiments 4 and 5, the pigeons were in a private room with very little traffic

except for extrasession feedings (which were varied). The fact that their performance was unaltered after the move from the colony to the new room suggests that they did not use social signals that could have been available while they were living in the colony. Finally, there is the possibility that noise from the hallway could have cued the birds as to whether it was morning or afternoon. However, this seems to be unlikely because both the colony and the private room are located in areas that do not have a lot of traffic. Also, the pigeon colony is quite noisy during the day, and it is difficult to hear noise from the hallway once inside the room. Finally, the testing sessions occurred at times during the regular weekday, when the number of people in the laboratory, and thus the noise level, is fairly consistent. These controls do not conclusively eliminate the possibility that exogenous cues were responsible for the timing behavior, but they do make it seem quite unlikely.

The present findings correspond to Biebach, Falk, and Krebs's (1991) work on garden warblers, in which it was also found that a circadian mechanism best explained learning on a time-place task when four 3-h periods were timed. They do not correspond, however, to a finding of stopwatch-like timing in a 1-h time-place paradigm in pigeons (Wilkie, Saksida, Samson, & Lee, 1994). This suggests that the interval between sessions is the most important determinant of the timing system used, and not some additional factor such as a species difference between garden warblers and pigeons. In addition, this supports the idea that pigeons can be flexible in their use of timing systems: Pigeons appear to use a stopwatch-like system for relatively short intervals and a circadian-based system for longer intervals.

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(Manuscript received April 23, 1993;
revision accepted for publication September 8, 1993.)