

**BEING IN THE RIGHT PLACE AT THE RIGHT TIME: TIME OF
DAY DISCRIMINATION BY PIGEONS, *COLUMBA LIVIA*.**

by

LISA MARIE SAKSIDA

B. Sc., The University of Western Ontario, 1991.

**A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF ARTS**

in

THE FACULTY OF GRADUATE STUDIES

(Department of Psychology)

We accept this thesis as conforming to the required standard



THE UNIVERSITY OF BRITISH COLUMBIA

June 1993

© Lisa Marie Saksida, 1993.

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

(Signature)

Department of PSYCHOLOGY

The University of British Columbia
Vancouver, Canada

Date 30 JULY, 1993

ABSTRACT

Pigeons were trained to discriminate between four keys, one of which provided food in the mornings, another which provided food in the afternoons, and two which never provided food. Three experiments were performed to determine if pigeons could track food availability over a 24-hr period. In Experiment 1, food was available at one place (pecking key) in the mornings and at a different place in the afternoons. Although the length of time between sessions was much greater than in previous studies (e.g., Wilkie & Willson, 1992), all subjects appeared to demonstrate time-place associative learning. In order to rule out the possibility of an alternation strategy, in Experiment 2 only morning or only afternoon sessions were given. Subjects maintained well above chance performance, showing that they were not simply alternating between the two rewarded locations. In Experiment 3, the length of time between morning and afternoon sessions was varied. The results indicated an increase in errors as the inter-session interval decreased, which provides further support for a timing as opposed to an alternation mechanism. Experiment 4 was designed to investigate mechanisms underlying the timing behaviour. Lights-on time was shifted back by 6 hr and no decrease in performance was found during the first session following this phase shift. This finding rules out an interval timer and suggests that a circadian type of timing mechanism, with a self-sustaining oscillator, mediates time-place learning over a period of 24 hr. Further support for this notion was found in Experiment 5 in which subjects were tested in constant dim light. In that experiment subjects' continued correct responding provides additional support for a self-sustaining circadian timer.

TABLE OF CONTENTS

ABSTRACT.....	ii
TABLE OF CONTENTS	iii
LIST OF FIGURES	v
ACKNOWLEDGEMENTS.....	vii
INTRODUCTION	1
TIMING WITH A CIRCADIAN MECHANISM.....	2
The Circadian Model.....	6
TIMING WITH AN INTERVAL CLOCK.....	10
Animal Timing Procedures	11
The Internal Clock Model.....	18
The Information-Processing Explanation.....	19
Properties of the Clock	27
The Connectionist Explanation.....	27
The Behavioural Explanation.	29
SUMMARY OF TIMING SYSTEMS	30
TIME-PLACE LEARNING.....	33
Extension of paradigm.....	34
Underlying mechanisms	35
GENERAL METHODS	37
EXPERIMENT 1: TRAINING	38
METHOD	38
RESULTS AND DISCUSSION	39
EXPERIMENT 2: AM ONLY / PM ONLY	44
METHOD	44
RESULTS AND DISCUSSION	45

EXPERIMENT 3: LATE A.M./EARLY P.M.....	48
METHOD	48
RESULTS AND DISCUSSION	48
 EXPERIMENT 4: PHOTOPERIOD	53
METHOD	53
RESULTS AND DISCUSSION	54
 EXPERIMENT 5: DIM LIGHT	61
METHOD	61
RESULTS AND DISCUSSION	62
 GENERAL DISCUSSION.....	65
 REFERENCES	68

LIST OF FIGURES

Figure 1.	An information-processing model of timing.....	20
Figure 2.	Acquisition of the 24-hr time-place task.....	40
Figure 3.	Mean percent of pecks per key during the first and the final block of baseline sessions.....	42
Figure 4.	A.M. Only / P.M. Only: Percent of pecks per key for both sessions following the morning-only probes and the sessions following the afternoon-only probes.....	46
Figure 5.	Late A.M. / Early P.M.: Performance of all subjects in morning sessions as compared to inter-session intervals.....	49
Figure 6.	Late A.M. / Early P.M.: Performance of all subjects in afternoon sessions as compared to inter-session interval.....	51
Figure 7.	Baseline performance of all subjects after being moved from the colony to the new room.....	55
Figure 8.	Percent of pecks per key for each bird on the day immediately following the phase shift.....	57
Figure 9.	Percent of pecks per key for all birds after the phase shift was extended for a period of 6 days.....	59

Figure 10.	Percent of pecks per key for all birds under the dim light condition.....	63
------------	--	----

ACKNOWLEDGEMENTS

First I would like to thank my advisor Don Wilkie for his advice and support over the past two years. I'd also like to thank the other members of my committee, Cathy Rankin and Peter Graf, for their time during a summer that has been extremely hectic for both of them. Finally, I'd like to thank Anita Lee for helping me to figure out the best way to pick up a pigeon, and Piers Samson, Anna Blasiak, and Anita for their invaluable help with testing.

INTRODUCTION

The ability to represent the temporal structure of experience is essential in order for an animal to base its behaviour on what may be predicted to occur. To behave optimally in particular situations, an animal must be able to represent the temporal structure of events that occur within its daily routine. Gallistel (1990) has distinguished two types of timing by coining the term *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 comes 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 that may be stopped, started, and reset by the occurrence of events. In fact, most short-term timing behaviour (less than 1 hr) has been explained by a stopwatch-like mechanism (Church, 1978), whereas most long-term timing (24 hr) has been accounted for by circadian rhythms (Aschoff, 1989).

Time-place learning can be considered to be a special case of timing behaviour combining knowledge of time of day with knowledge of spatial location. Many observational studies (e.g., Daan, 1981; Daan & Koene, 1981) have suggested that animals appear to have the ability to keep track of time of day, that is, to anticipate events which occur on a regular basis, such as restricted feeding. Few researchers, however, have investigated animals' ability to associate a specific place with food availability, let alone the particular timing mechanism that underlies the behaviour.

I will begin this thesis by examining the work that has been done in the area of timing in general; first, timing using circadian rhythms, and second, timing of shorter intervals using an internal clock. Then I will review the research that has been done specifically with respect to time-place learning. In addition, I will present new work relating to the mechanisms underlying time-place learning.

TIMING WITH A CIRCADIAN MECHANISM.

Most animals and plants display activity episodes which reoccur every 24 hr, even under conditions in which all periodically occurring cues are ruled out. In fact, almost all organisms more advanced than bacteria have continuous biological rhythms (e.g., activity/rest, body temperature, evoked responses) which occur within a day (Jacklet, 1985). These daily rhythms seem to be generated from within the organism and are called circadian rhythms.

One example of how ubiquitous circadian mechanisms are results from a study in which the fungus *Neurospora* was included in a space shuttle flight (see Sulzman, Ellman, Fuller, Moor-Ede, & Wasser, 1984). The mission involved circumnavigation of the earth with a periodicity of 1.5 hr for several days. On Earth *Neurospora* cultures produce vegetative spores every 21 to 22 hr. In space, that periodicity was maintained in spite of the fact that the solar day was only 1.5 hr in length. This result strongly suggests that an endogenous circadian pacemaker controls circadian rhythms.

The central pacemaker which controls the rhythms regulates the mechanism by delivering a series of pulses in a consistent pattern. A physiological pacemaker has been located in the mammalian suprachiasmatic nuclei (Moore, 1982; Turek, 1983), the avian pineal organ (see Norgren, 1990), in the optic lobes of certain insects, and in the eyes of some gastropods (Jacklet, 1985). In fact, multicellular organisms contain not just one, but many endogenous oscillators with periods ranging from seconds to years, with all types of intermediate intervals represented (see Aschoff, 1981 and Farner, 1985 for reviews demonstrating endogenous oscillators at each of these periods). Gallistel (1990) suggests that when a system contains a group of oscillators with widely differing periods it can represent times of occurrence of events by recording momentary states, or phases, of the oscillatory processes. This provides us with the physiological grounding of a potential timing mechanism.

In order to be able to anticipate recurrences at the same phases in later cycles the internal cycle must be synchronized with external cycles (e.g., day/night cycle, lunar cycle, tidal cycle). No physical oscillation is perfectly periodic and no two physical oscillations have the same period, so if the external oscillator had no effect on physiological oscillations with similar periods then the two oscillations (external and internal) would not be synchronized. From the phase of the internal oscillator one would not be able to predict the phase of the external oscillator therefore the internal oscillator would be of no use in predicting regular events in the external world. However, endogenous oscillators do respond to some periodically recurring extrinsic events in such a way as to maintain a fixed phase relation between the two processes. This process is called *entrainment*.

The presence of an endogenous self-sustaining oscillatory system allows animals to synchronize their activity with cycles in the environment, as well as with conspecifics, because these oscillators are entrained by signals from extrinsic oscillators or from other oscillators within the same organism. Roberts (1965) performed an experiment which illustrates this phenomenon quite clearly. Using a cockroach as a subject, Roberts made a continuous recording of its movement and then cut that record into 24-hr segments. During the first 20 days of recording, the cockroach showed an abrupt onset of activity shortly after the lights went out every day, which is a normal occurrence in nocturnal animals. Recurring bouts of activity happened throughout the night, and activity was fairly low during the day. At first glance it might appear as though these activities were exogenous, that is, that darkness leads directly to activity and light suppresses it. In the next stage of the experiment, Roberts demonstrated that this was not the case. On Day 20 he painted over the eyes of the cockroach with nail polish so that it could no longer detect light. In spite of this, the roach still showed strong daily variations in activity, but the onset of activity was no longer maintained in a fixed phase relation to the light/dark cycle. Instead, daily activity was determined by an endogenous oscillator with a period of 23.5 hr. Because this period was shorter than that of the extrinsic oscillator (the light/dark

cycle), and because the extrinsic oscillator could no longer entrain the endogenous oscillator, activity began 30 min earlier each day. After 24 days, the onset of activity correlated with lights-on time rather than lights-off. Subjective dusk now corresponded to objective dawn. At this point it was clear that the onset of activity at dusk was not merely a response to the lights being extinguished. On Day 50, Roberts then peeled off the nail polish. During the first eight days after the polish was removed, activity began some time after the lights were turned off. From this, Roberts concluded that onset of activity was still being controlled by the endogenous oscillator, which was running behind the external light/dark cycle. But as soon as the cockroach's sight was returned, the endogenous oscillator again became susceptible to entrainment of the light/dark cycle. From continuous recordings, it could be seen that the onset of activity drift became faster than the free run drift in order to "catch up" with the extrinsic oscillations. From these results, it was obvious that the transition from light to dark was not eliciting and suppressing the activity, but when the transition occurred a few hours too late with respect to the endogenous cycle, it transiently accelerated the endogenous oscillation. In this experiment, daily phase advances gradually brought the internal clock into the correct phase relation -- it caught up with the extrinsic cycle on Day 58. At this point, the endogenously timed activity onset once again coincided with lights out.

Pittendrigh (1980) provided further information about the nature of the oscillations underlying timing behaviour. In this experiment, he used hamsters that were maintained in constant darkness, and he measured running wheel activity. At the beginning of the experiment, activity onset seemed to be controlled by an endogenous oscillator running with a period of 23.8 hr. Continuous recordings showed a steady but slow drift of activity onset. When the free running period had been established, Pittendrigh inserted timing signals consisting of 15-min light pulses at different phases of the endogenous cycle. The first pulse was given early in the nightly activity bout, that is, early in the subjective night, at the phase of the endogenous oscillation that corresponded

with the dark phase of the extrinsic cycle under natural (entrained) conditions. Pittendrigh found that if the pulse was delivered early in the subjective night, it created a phase delay of one-nineteenth of a cycle, that is, during the next 24-hr period activity occurred 1 hr 15 min later than it would have if the pulse hadn't been given. In the days following the phase shift caused by the pulse, the endogenous oscillator continued to drift at the same rate as before the shift, the only difference being that the phase was altered. A second light pulse given later in the subjective night led to a similar delay, but a third pulse, which was given even later, led instead to a small phase advance. The onset of the next activity bout occurred sooner than it would have with no signal. Finally, pulses given farther into the subjective night caused a large phase advance. From these results it can be seen that when the timing signal comes at certain phases of the cycle, it slows down; when it comes during other phases, it speeds up. The responsiveness of the internal oscillator allows it to stay in a fixed phase relation with the external day/night cycle.

In sum, endogenous oscillators can be influenced by extrinsic inputs in two ways. First, transient extrinsic inputs such as timing signals can shift the phase of the oscillator to a different part of the cycle. Second, tonic (slowly changing) extrinsic inputs may modulate the period of the endogenous oscillator. For example, the free-running period of most circadian oscillators can be lengthened by a steady level of environmental illumination. The periodic factors which lead to entrainment are termed *zeitgebers*. The most powerful zeitgeber seems to be the daily transition between light and dark (Aschoff, 1989). Weaker zeitgebers, however, such as temperature (Ostheim, 1992), social cues (Gwinner, 1966; Marimuthu, Subbaraj, & Chandrashekar, 1981), and feeding time (Abe & Sugimoto, 1987; Mistlberger & Rechtschaffen, 1984), have also been demonstrated.

The Circadian Model

The major component of the avian circadian system is the pineal gland, which functions as the main oscillator in the system (Menaker & Zimmerman, 1976). Evidence for another population of oscillators located outside the pineal in the suprachiasmatic nuclei (SCN) has also been found (Takahashi & Menaker, 1979). The basic model that is used to describe these physiological findings was first presented by Gwinner (1978) and suggests that the pineal contains a self-sustaining oscillator that drives a population of weakly coupled, self-sustaining oscillators that in turn control locomotor activity. The avian circadian system seems to be set up in a manner somewhat opposite to the mammalian system. In the rat the principal oscillator is considered to be the SCN. However, the fact that some circadian rhythms persist after the SCN are ablated (e.g., food-anticipatory activity and temperature) has led some researchers to conclude that the SCN may be only one of several pacemakers in a multiple oscillator system, hierarchically organized with the SCN in the dominant position (Rusak, 1977).

The timing signal that holds the oscillator in a fixed phase relation to another oscillator does not have to have the same period as the oscillator that it entrains. Endogenous oscillators with different periods may maintain a fixed phase relation through an exchange of timing signals. For example, many rodents have ultradian (shorter than daily) activity rhythms with a period of 1.5 - 3 hr. In voles the rhythm phase has a fixed relation to the circadian rhythm which is maintained even when the circadian oscillation is free-running (see Gallistel, 1990). It has not been conclusively shown that ultradian rhythms depend on distinct endogenous oscillators. It is possible that each activity bout is triggered when the circadian oscillation reaches a specific phase in its' cycle. However, some evidence has been collected for separate oscillators (Daan & Aschoff, 1981). In some rodents ultradian rhythms are not phase locked to the circadian rhythm (Cowcroft,

1954). If shorter rhythms were produced by trigger points spaced 2.4 hr apart in a circadian oscillation, the rhythm would always be phase locked to that circadian rhythm. If the rhythms were produced by separate oscillators, however, it may or may not be phase locked, depending on whether or not it received an effective timing signal from the circadian oscillator. Even in voles, where the shorter rhythm is obviously phase locked to the longer one, sometimes a drift is seen in the relation between the ultradian and circadian cycles (Aschoff, 1984). This is most readily explained by the presence of two oscillators.

Other evidence for the existence of multiple oscillators is derived from the fact that the period of the short-term rhythm is systematically affected by nutritional factors that have no effect on the period of the circadian oscillation. Factors which increase the amount of food that voles must eat (e.g., lactation or high cellulose in the diet) shorten the period of the ultradian oscillation but not the period of the circadian oscillation (Daan & Aschoff, 1981). This can be easily explained if it is assumed that ultradian rhythms are driven by individual endogenous oscillators. The phenomenon is very difficult to explain, however, by different trigger phases of the same circadian oscillation. Finally, it might appear that the nutritional effect on ultradian rhythms is being driven by filling and emptying of the stomach or some other metabolic cycle but this has been shown not to be the case because the rhythm persists even when the vole has no access to food or water (Daan & Slopsema, 1978).

The most complete conceptual model of circadian rhythmicity which is based on the principle that a multi-oscillator system drives periodic behaviour is that of Gallistel (1990). He suggests that the way in which variables underlying any physical oscillation vary with time make it possible to specify any phase (moment) within a period of oscillation by recording the values of the two variables at that time. If passing time is controlled by an oscillatory process, then specific moments can be marked by two interconnected quantities that describe the state of the oscillatory process at a given time.

This system only works over the period of one oscillation. If the sine and cosine values of the oscillation are being used to specify time, then they are unique only for time intervals that are integer multiples of the period of oscillation. As a result, memory for moments based on the recorded values of components of oscillations does not distinguish between corresponding moments in different periods of the longest oscillation contributing to the record. This may not matter to some animals. The honeybee, for example, has a life span of 3 weeks in the summer and thus may not need to distinguish between days. Longer lived animals, however, do have the ability to distinguish days. Birds can recognize something that happens every second day (Causiens & Edwards, unpublished manuscript; see Gallistel, 1990). Also, endogenous oscillators with a period of a year have been shown (Gwinner, 1981; Farner, 1985). This suggests that the animal's temporal record must incorporate coordinates that come from a slower oscillation whose period encompasses several cycles of the faster oscillation.

Based on the above theory, only one oscillatory process with a long enough period is necessary to record all potential time coordinates. In reality, however, it is not likely that the mechanism which reads time records will be able to distinguish reliably between similar recorded quantities. In other words, the system will not be able to distinguish moments separated by seconds if it records moments by storing circannual oscillatory values. Thus a system based on several different oscillators with different orders of magnitude is necessary in order to span a large interval but also record moments in the realm of seconds.

When entrained to 24 hr, circadian rhythms can potentially be used as a clock that is essential for many animal behaviours such as synchronization of activities among individuals, adjustment of activities to environmental conditions, and the measurement of temporal intervals (Aschoff, 1989). One type of behaviour whose dependence on circadian rhythms is well documented is the phenomenon of food-anticipatory activity (FAA), which is apparent in many animals when they are put on a restricted feeding

schedule. When animals are limited to one meal at a fixed time of day, increased arousal during the hours before feeding is usually observed. This has been detected in many paradigms, including wheel-running (Bolles & deLorge, 1962; Richter, 1922), unreinforced lever pressing (Boulos & Terman, 1980), activity directed toward an empty feeding dish (Birch, Burnstein, & Russell, 1958; Mistlberger & Rusak, 1988), and generalized cage activity (Mistlberger & Rechtschaffen, 1984). Explanations based on external cues triggering FAA have been ruled out because rats and other species demonstrate the same behaviour in artificial environments in which there is no variation in light, temperature, or sound that could be a signal for immediate food access.

The main piece of evidence for circadian rhythms being involved in the control of FAA comes from a study which showed that rats fail to anticipate daily meals that are separated by 19 hr or 29 hr (Bolles & deLorge, 1962). This demonstrates that when feeding schedules differ greatly from 24 hr anticipatory activity does not occur, and suggests that FAA is not based on interval timers that can be reset to any arbitrary interval. It also coordinates with the idea of entrainment, which allows only for minor modifications of the timing mechanism by external cues. Physical oscillators are limited as far as the maximum phase shift that can occur in one cycle is concerned.

A second bit of evidence involves food deprivation. FAA can last for a week when previously restricted rats are fed ad libitum (Edmonds & Adler, 1977; Aschoff, von Goetz, & Honma, 1983; Honma, von Goetz, & Aschoff, 1983; Gibbs, 1979; Stephan, 1983) however, usually it disappears by the second day after the switch (Gibbs, 1979; Coleman, Harper, Clarke, & Armstrong, 1982; Rosenwasser, Pelchat, & Adler, 1984; Stephan, Swann, & Sisk, 1979). On the other hand, if a rat demonstrating FAA is food deprived for at least 2 days FAA persists (Bolles & Moot, 1973; Stephan et al., 1979; Clark & Coleman, 1986; Ottenweller, Tapp, & Natelson, 1990; Mistlberger, 1992b). If 3-7 day blocks of food deprivation are repeated after one or more weeks of ad libitum feeding, FAA reappears at the usual time of day, even 50 days after the last feeding schedule

(Bolles & Moot, 1973; Stephan et al., 1979; Coleman et al., 1982; Clarke & Coleman, 1986; Ottenweller et al., 1990). These observations are incompatible with an interval type of timer, but can work with an entrainable oscillator model if the coupling between the food-entrained oscillator and behaviour is gated by the animal's motivational state.

A third example of how FAA fits in with a food-entrainable oscillator model involves succeeding activity. Some rats who demonstrate FAA on 24 hr restricted feeding show a second bout of activity about 3-6 hr after mealtime (Aschoff et al., 1983; Honma et al., 1983; Stephan et al., 1979). This succeeding activity can be explained in the oscillator model as the trailing end of the active phase of the food-entrained oscillator. This is further supported by the observation that durations of FAA and succeeding activity are negatively correlated across days and feeding cycles of different periodicities so that the combined daily duration is preserved (Aschoff et al., 1983; Honma et al., 1983).

This area has been extensively researched and I have mentioned only a few of the studies that have been done. Although the exact mechanisms underlying FAA are still a matter of debate (see Mistlberger, in preparation, for a full review), it provides a good example of how one behaviour may be controlled by a circadian mechanism.

TIMING WITH AN INTERVAL CLOCK

Many instances of temporal discrimination of short intervals have been demonstrated in animals. Stubbs (1968) showed that pigeons can be trained to make one response if a particular stimulus is longer than a criterion, and another response if the stimulus is shorter than the criterion. When the results were plotted, it could be seen that the percentage of responses of one kind varied as a function of stimulus duration. In addition to being sensitive to duration of the stimulus, animals are also sensitive to duration of the response. In 1973, Platt, Kuch, and Bitgood demonstrated that response duration can be altered by differential reinforcement. When a rat receives food if it pushes

a lever longer than a criterion duration, the median response duration increases as a power function of the duration of the criterion. Other examples of timing of short intervals include: If reinforcement is available only if the animal withholds responding longer than a criterion time, the distribution of inter-response times (IRTs) is closely related to the minimum reinforced IRT (Kramer & Rilling, 1970), an aversive event presented at regular intervals produces temporal conditioning (LaBarbera & Church, 1974), and when food is presented a fixed amount of time after signal onset, the animal's response rate increases as the time to the next reinforcement approaches (Pavlov, 1927). The results of these, and many other studies (see Anger, 1963; Gibbon, 1972; Libby & Church, 1974; Dews, 1970) suggest that animals can learn to adjust their behaviour to a specific time interval. From these basic results, it became quite clear that some sort of *internal clock* was regulating animal timing behaviour. This term began as a metaphor, but as research moved forward characteristics of the clock were discovered, and now the concept is no longer thought of as a metaphor, but as something that truly exists (Church, 1978). A great deal of the work that has been done in this area is the contribution of Church, Gibbon, Meck, and Roberts. They have collaborated on a series of experiments using various procedures geared toward developing a model of how elapsed intervals are estimated, remembered, and compared.

Animal Timing Procedures

The peak procedure. This was originally described by Catania (1970), but has more recently been used by Church, Miller, Gibbon, and Meck (1988). During a peak procedure session, a rat is placed in a lever box and exposed to two trial types; food and nonfood. During a food (training) trial, the rat is exposed to a white noise signal. The first lever response after 20 s is followed by food, and subsequently the end of the signal. The critical trials are the non-food trials, during which the rat receives the white noise

signal for 120 s but never receives food. The time of each response beginning from stimulus onset is recorded throughout the session, and this gives an indication of when the rat is expecting food, based on the training trials.

The data in this paradigm are obtained from the nonrewarded trials. During these trials, the mean probability of response increases to a maximum near the time that food is sometimes received, and then decreases in a fairly symmetrical fashion. The peak in latency of responding usually differs from the rewarded latency by a multiplicative factor, the value of which varies between animals but is constant within an individual. This finding led to the development of *scalar timing theory* (Gibbon, 1977; also see Gibbon, 1991) which states that the remembered duration of an elapsed interval consists of the experienced duration multiplied by a scalar factor, which varies between animals. A second observation is that performance on individual trials, unlike the mean functions, is characterized by an abrupt change from a state of low responding to one of high responding and finally to another state of low responding. This is typically known as the "break-run-break" pattern of response on a single trial (Schneider, 1969). Finally, the mean functions of different times of reinforcement (e.g., if time of reward is changed from 20 s to 12 s after noise onset) are very similar when time is shown as a proportion of time of reinforcement. This highlights the fact that the animal's rate of responding is determined by the ratio between the remembered reward latency and its measure of the interval so far elapsed in the current trial. In sum, what determines the rat's rate of responding is its *memory* of the elapsed interval before the reward, not the interval that was actually experienced (Church & Broadbent, 1990).

Generalization. In a generalization experiment (e.g., Church & Gibbon, 1982), a stimulus is turned on for a variable duration which is to be judged by the animal. If the stimulus is on for the correct (rewarded) duration, a response leads to food. Otherwise, no reward is obtained. Results from generalization experiments show that the probability of response

varies as a function of the duration of the signal, that is, there is a peak in response at the rewarded duration. This paradigm provides additional support for the scalar properties of timing because the probability of response is determined by the ratio between the signal duration and the remembered duration of rewarded signals .

Bisection. During a bisection experiment (see Church & Deluty, 1976; 1977) the animal hears or sees a signal of variable duration, as in the previous generalization procedure, but two levers are inserted into the box at the end of the signal. Pressing on one of the levers is rewarded if the signal was the shortest in the range of signals used, pressing on the other lever is rewarded if the signal was the longest, and there is no reward if the signal was of intermediate duration. The data consist of the probability of responding on the "long" lever as a function of the duration of the prereponse signal. Experiments using this paradigm have shown that responding is based on duration ratios, as opposed to differences in the subjective temporal quantities, because the point of indifference (intermediate signal duration at which the long lever is chosen on half of the trials) is the logarithmic midpoint between the shortest and the longest intervals.

Estimation. A typical estimation procedure involves a delayed symbolic matching-to-sample (DSMTS) task (e.g., Spetch, 1987; Spetch & Rusak, 1989; Spetch & Wilkie, 1983). In this task, pigeons are reinforced for pecking at one stimulus (e.g., a red key) after a short (e.g., 2 s) sample presentation and at another stimulus (e.g., a green key) after a longer presentation of the same stimulus (e.g., 10 s). Retention of the length of the sample is tested by varying the delay between the beginning of the sample and the presentation of the choice stimuli. Results from this procedure have shown that pigeons do store duration information analogically, as opposed to simply a categorical coding of long or short. Spetch and Sinha (1989) concluded that pigeons retain an analogical, and not a categorical, memory of the temporal properties of the sample in a DSMTS task.

Pigeons do seem to use different temporal coding strategies, however, depending on the task. In a successive matching-to-sample task, there are 2 different test stimuli but only one is presented following the sample on each trial. Pecks to one of the test stimuli are reinforced for a short duration, whereas pecks to the other are only reinforced for a long duration. Grant and Spetch (1981) used this type of task and found that pigeons employed a prospective, categorical strategy.

Subdivision. Another question regarding timing is whether animals deal with the interval to be timed as a whole, or do they subdivide it into parts? Rhythmic behaviours during a timing session are often observed (Church, 1978) and there is potential that the behaviour could be some sort of oscillator used to drive the internal clock. Deluty and Church (1976; see Church, 1978) performed an experiment to discover if this was indeed the case. A loud white noise was pulsed during the light signal to be timed. It was assumed that the animal would have trouble maintaining a rhythm different from the pulse rate. Using an estimation procedure, rats were trained to press the left lever when the light stimulus had a duration of 2 s, and the right lever if the light duration was longer (2.5, 3.0, 3.5, 4.0 s). Half of the stimuli were delivered at the standard 2 s duration, and the other half were presented at one of the comparison durations. During different phases of the experiment, the noise pulses were given either at regular 0.5 s intervals, random 0.5 s intervals, or no noise was presented at all. The results provided no evidence that the pulses increased, or that the random noise interfered with, the accuracy of timing. In other words, it seems as though rats do not subdivide when timing an interval.

Time-left. In this paradigm, the animal has to judge from moment to moment which of two response options will pay off in a shorter amount of time (see Gibbon & Church, 1981). At the start of a trial one option will pay off sooner than the other one but at some point this reverses. In the pigeon version of the task, a trial begins with the illumination of

two response keys (red and white). Continuous responding on the red key leads to a reward at time $T + 30$ s. This 30 s interval is known as the standard interval (S). T is randomly determined from trial to trial by choosing with equal likelihood from 6 alternatives ranging from $1/6$ of S (5 s) to $11/6$ of S (55 s). If the bird only pecks at the red key, it realizes that T for a given trial has timed out when one peck turns the key green. At that point, the bird loses the option of responding on the white key (it goes blank) so it must finish the trial on the red key and it gets a reward 30 s later. The white key, on the other hand, provides a reward at $60 - T$ s where 60 s is the comparison interval (C). If the bird only pecks the white key then it realizes that T is timed out when one peck extinguishes the red key and thus white becomes the only option. The bird must finish the trial on this key, and wait $60 - T$ s before it is rewarded. Whether the bird must finish on the red or the white key is determined by which key it pecks first after T has timed out.

The best approach to take in this situation would be to peck the red key for the first 30 s because if T times out while the bird is pecking red it will receive a reward after 30 s. If the bird was pecking white, the reward would be obtained after $60 - T$ s, which is a longer wait than 30 s as long as the time elapsed (T) is less than 30 s. When more than 30 s have elapsed, however, the best approach would be to switch to the white key because the reward would occur in a shorter amount of time. Basically, in order to perform well on this task, the animal must compute the difference between the remembered duration which corresponds to C and the time elapsed since trial onset. Both pigeons and rats are able to do this. The probability of responding to white starts low and rises during the trial whereas the probability of responding to red starts high and ends low. The point of indifference (latency at which the probability of responding white is equal to responding red) is a linear function of the difference between C and S.

Timing with interruptions. Church and Roberts, in a series of two studies, looked at the concept of stopping the timing mechanism (Church & Roberts, 1975; Roberts & Church,

1978). In the first experiment (Church & Roberts, 1975) rats were trained to press a lever on a discrete 1-min fixed interval schedule. The lever was inserted into the box, and food became available with the first press after 1 min had passed. By the end of training, a steep temporal gradient was developed, that is, the response rate increased as the time of the next reinforcement approached. In the critical part of the study, the fixed intervals were periodically interrupted by a 15 s break, during which the lever was withdrawn and white noise was played. The rationale was that if they continued timing during the break, the clock setting would increase during that period of time, whereas if the clock stopped during the break, then the clock setting would remain the same. The rats were divided into two groups -- a run group, for whom time ran during the break (if there were 40 s before food priming when the break began, there would be 25s to the next priming when the break ended), and a stop group (if 40 s were left before food priming when the break began, there would be 40 s to the next priming when the break ended). The final results demonstrated that the two groups were indistinguishable before the break, but differed afterward. Initially, all subjects stopped their clocks during the break. Eventually, however, subjects in the run group learned to run their clocks during the interval. This provides strong evidence for flexibility of timing, depending on the situation.

Absolute timing units. Two studies by Roberts and Church (1978) suggested that timing units are absolute and that the internal clock times "up". In this study, rats were trained on a discrete 30 s FI schedule and a 60 s FI schedule, with a light signalling the shorter interval and a noise indicating the longer interval. In the critical part of the test, the rats continued to receive the same types of trials. In addition, however, on one-third of the trials the 30 s light signal was shifted to the 60 s noise signal. The shift could occur 6, 12, 18, 24, or 30 s after trial onset. On shifted trials, food was primed at a time appropriate for an absolute up timer for half of the rats (absolute group), and for a proportional up timer for the remaining rats (proportional group). The rationale was that if rats used the

same internal clock to time the light and the noise, whether they were timing in absolute or proportional units, and whether they were timing up or timing down could be inferred from the response rate during the trials which were shifted to the 60 s noise signal. As an example, consider the case in which, after 12 s of light (30 s signal) the light would be extinguished and replaced by noise (60 s signal). There are four possible responses, and four corresponding timing mechanisms, that could occur with this type of trial. If the rat was using *absolute up* timing, 12 s have passed so performance would be equivalent to that of a rat on plain FI 60 after 12 s. If an *absolute down* timer was being used, 18 s would be left on the timer therefore performance would be similar to that of a rat on FI 60 after 42 s. A third possible mechanism would be a *proportional up* timer, and in this case 40% of the total time has passed, so the rat would perform as though 24 s (40%) of the FI60 schedule had passed. Finally, using a *proportional down* timer, 60% of the total time would be left, consequently the rat would behave as though 36 s were left. The question here is: Does the performance of a rat switched from a FI 30 schedule to a FI 60 schedule after 12 s correspond to the behaviour of a rat on FI 60 after 12, 24, or 42 s?

The results of their study led them to the conclusion that the response ratio in the 60 s signal was a function of the time since the trial began. It did not matter if the trial began with a 60 s signal, or if it was shifted after 6, 12, 18, or 24 s. To predict response ratio in the 60 s signal, they needed to know only the time since the trial began; it did not matter how much of the total time was comprised of either the 30 s or the 60 s signal.

Roberts and Church (1978) concluded four things about the nature of the internal clock from this study. First, it provides evidence for a single clock. If separate clocks were used to keep track of the 30 s visual signal and the 60 s auditory signal, then the length of time that the animal spent exposed to the visual signal prior to the shift should have no effect on behaviour. If one clock was used, then the response ratio in the 60 s signal should be related to the time spent in the 30 s signal, and it was. This conclusion has since been modified (see Meck & Church, 1984). Second, the clock advances as a

function of absolute, not proportional, time. In this case, the response ratio was a function of the duration of the total signal. Since it did not matter what proportion of the combined signal was the 30s signal, this study provides no evidence for differential rates of timing. Third, the clock times up. The curves after a shift and the curves of trials in which a shift had not occurred were very similar. A rat shifted from FI 30 to FI 60 after 12 s has a response ratio similar to that of a rat having had an FI 60 schedule for 12 s. If the clock was timing down as a function of time, the clock would not be explained by a simple shift in criterion. Finally, when the experiment was extended for 40 3hr sessions, the rats in the absolute timing group continued to act in the same manner, whereas the rats in the proportional group shifted their behaviour. By the end of the experiment, they learned to deal with time in proportional units. This provides evidence for flexibility of timing behaviour, which will be discussed in more detail later.

The Internal Clock Model

The above studies have led to the more rigorous development of an internal clock model. An internal clock advances as a function of time from or during a well-defined event, and the animal adopts a temporal criterion and response rate which relates the probability of a particular response to the clock setting and the criterion (Church, 1978). In an estimation procedure (e.g., generalization or estimation), the signal starts the clock. When the signal terminates, the pigeon reads the value of the clock and makes a decision to respond either on the short or the long lever based on the relationship between the clock setting and the criterion. If the clock setting is less than the criterion, then the pigeon chooses short, whereas if the clock setting is longer than the criterion, the pigeon chooses long (Spetch & Sinha, 1989). In a production procedure (e.g., peak procedure), the signal starts the clock and the animal continually makes decisions about whether or not to respond, again based on the clock setting and the criterion (Church et al., 1988).

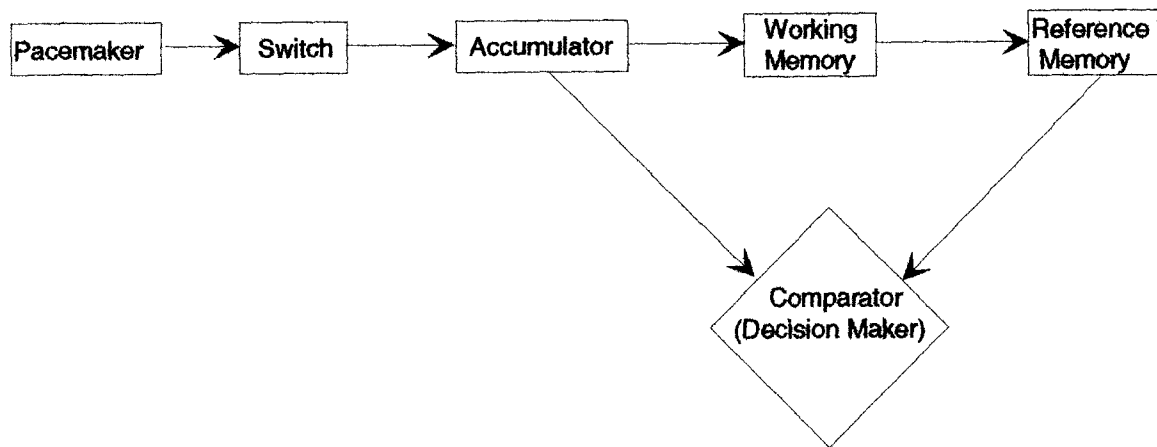
The Information-Processing Explanation

The idea of treating humans as "information-processing machines" began with Broadbent (1958). He suggested that the machine consists of modules and their interconnections, and that the task of the researcher is to reverse-engineer the system. Based on observations of the input and the resulting output, inferences can be made about how the machine works. His basic model was made up of a selective filter, limited channel and a long-term store where the parts were connected serially such that information moved from the senses into central processing and eventually to motor output.

The information processing idea has been extended to animal cognition and traditionally has been used to account for the various properties of the internal clock. Gibbon, Church, and Meck (1984) present a theory in which the basic parts of the model include a pacemaker, a switch, an accumulator, working memory, reference memory, and a comparator (see Fig. 1).

Pacemaker. The pacemaker is an internal mechanism that generates pulses. The mean rate of the pacemaker seems to be able to be controlled by drug, dietary, or environmental manipulations. For example, methamphetamine has been shown to produce a leftward shift in the psychophysical function that relates the probability of a "long" response to signal duration (Maricq, Roberts, & Church, 1981; Meck, 1983). In other words, in this psychological model methamphetamine increases the speed of the pacemaker. Haloperidol, on the other hand, causes a rightward shift in the same function (Maricq & Church, 1983) and thus seems to decrease pacemaker speed. These findings suggest that the pacemaker rate varies with the effective level of dopamine in the system, because drugs that increase the release or decrease reuptake of dopamine cause a leftward shift in

Figure 1: An information-processing model of timing.



the function, whereas drugs that inhibit dopamine lead to a rightward shift in the same function.

Diet also has been shown to affect pacemaker speed. A typical rat diet is high in carbohydrates. Prefeeding with sucrose, however, seems to decrease pacemaker speed whereas prefeeding with protein increases speed (Meck & Church, 1983).

Finally, environmental stimuli can affect pacemaker speed. Wilkie (1987) showed that the perceived duration of a dim light was shorter than that of a bright light of equal length. This suggests that stimulus intensity can affect pacemaker speed. Also, Meck (1983) showed that stress resulting from footshock tended to increase the speed of the pacemaker.

It is interesting that the pacemaker can be influenced by so many variables because in order to discriminate small time differences the pacemaker should be relatively rapid and stable. Gibbon and his colleagues (1984) account for this fact by suggesting that the measurement of the pacemaker and temporal judgement should be affected by the same manipulations by an equivalent amount, and moment-to-moment variation in the measurement of the pacemaker should correlate with moment-to-moment variation in temporal judgement.

Switch. The function of the switch is to gate pulses from the pacemaker to the accumulator. Its main property is that it can operate in various modes. For example, consider a stimulus that is on for a duration a , off for b , and on for c . In this situation, the switch can gate pulses in different ways, depending on the mode. If the system is in "run" mode, the duration of pulses is $a+b+c$ (the interval is timed from signal onset to the end of the trial). If the system is in "stop" mode, however, the duration of pulses is only $a+c$ (duration is timed only when the stimulus is on). As mentioned previously, rats initially adopt stop mode (Church & Roberts, 1975; Roberts & Church, 1978). In this case, the pacemaker puts pulses into the accumulator during the first stimulus segment, it pauses

during the gap, and then adds pulses again after the gap. This has been shown in both the bisection procedure (Church, 1978; Roberts & Church, 1978) and the peak procedure (Roberts, 1981; Meck, Church, & Olton, 1984).

The switch can also operate in "event" mode, where the switch is closed for some short, fixed period of time after each stimulus onset. In this case, the animal uses its internal clock as a counter (Meck & Church, 1983; Church & Meck, 1982). Even when temporal cues are controlled, the animal can classify a stimulus sequence by number of elements (Meck & Church, 1983; Fernandes & Church, 1982; Davis & Memmot, 1982).

In sum, when a signal is composed of several stimuli, the switch can close at the onset of a stimulus and open at either the beginning of each stimulus (event mode), the end of each stimulus (stop mode), or the end of the trial (run mode). With differential reinforcement, the animal seems to be able to use any mode and the switch mode can be transferred from one modality to another (Church & Meck, 1984; Meck & Church, 1982; Gibbon & Church, 1981; Roberts, 1982).

Accumulator. The purpose of the accumulator is to hold the sum of the pulses: It is an "up" counter that increments in arithmetic units in an absolute manner. Evidence from the time-left procedure suggests that when the time left in an elapsing interval is equal to the standard interval, that animals are indifferent in choosing between the intervals (Gibbon & Church, 1981).

Working Memory. Working memory, as defined for this particular model, stores information about the current trial in the absence of the signal. One property of working memory is that it can be reset quickly. For example, in the bisection procedure rats are trained to make a right response after a 2 s signal and a left response after an 8 s signal. On test trials, a preset signal is presented after which comes an interval with no chance to respond, which in turn is followed by another signal duration. The animal can learn to use

the second signal without interference from the first signal (Church, 1980). Working memory is used only if there is an interval between the end of the stimulus and the chance to respond; otherwise the sensory store (accumulator) is used. When there is a retention interval between time of exposure and opportunity to respond, there is a decrement in performance that can be attributed to decay in working memory (Church, 1980; Kraemer, 1985). Church (1980) suggests that this decay is on a dimension orthogonal to time. This view has been challenged, however, by Spetch and Wilkie (1983) who provide evidence for an analogical encoding of the temporal properties of a sample. They further suggest that subjective shortening in working memory may be due to a gradual resetting of the internal clock, which argues against Church's (1980) suggestion that working memory can be reset quickly. Further evidence against a quickly resettable working memory component of the internal clock is provided by Wilkie (1988). This study found proactive effects (produced by intertrial manipulations) in pigeons' timing behaviour. In other words, new information presented between trials was carried over to a succeeding trial where it then influenced classification of event duration. This implies that working memory is not cleared at the end of each trial, and therefore that a decay type of process is more likely to control the emptying of working memory

Reference Memory. Reference memory permanently stores information about previous trials and their consequences. Various drugs and lesions can affect this memory constant. For example, physostigmine produces a leftward shift and atropine produces a rightward shift (Meck, 1983). Thus it seems that the level of acetylcholine affects the memory constant. In addition, lesions of the frontal cortex produce a rightward shift in the function or, in other words, increase the remembered time of reinforcement (Maricq, 1978). Diet also contributes -- choline administered prior to a testing session leads to a leftward shift in the response function (Meck & Church, 1983).

Comparator. The comparator determines the response on the basis of a decision rule which involves a comparison between a value in the accumulator or working memory with a value from reference memory. As a result, it must contain two time values and a response rule.

Simultaneous Temporal Processing. One additional property of this timing system that should be mentioned is the fact that animals must have more than a single timing process even though initially it appeared as though there was only one clock because the same clock could be used for different modalities (Meck, Church, & Olton, 1984; Church & Meck, 1982; Meck & Church, 1983; Church & Meck, 1981; Meck & Church, 1982a; Meck & Church, 1982b; Roberts, 1982). More recently, however, rats have been shown to time two signals simultaneously without interference. Meck & Church (1984) put rats on a 50-s peak procedure signalled by light, with a 1-s noise signal presented every 10 s (except at the 50 s point). The resulting performance of subjects fit into a scalar model in which the same model was used for the 50-s and the 10-s timing process and the same parameter values were used for the 50-s function whether or not the 10-s signal was present. Rats have also been shown to time and count simultaneously without interference (Meck & Church, 1983). These results suggest that animals must have many switch-accumulator parts to handle all of these tasks.

In sum, there are several components making up the psychological process used for timing intervals, each with various properties.

- (1) Pacemaker: Mean rate can be manipulated by drugs, diet, or stress.
- (2) Switch: Has a latency to operate and can work in several modes: Run, stop, and reset.
- (3) Accumulator: Times up, in absolute arithmetic units.

- (4) Working Memory: Can be reset by events or after lesions in the fimbria fornix when there is a gap in the signal.
- (5) Reference Memory: Transfer from accumulator to reference memory is done with a multiplicative constant which is affected by drugs, lesions, and individual differences.
- (6) Comparator: Uses the ratio between the value in the accumulator (or working memory) and reference memory.

The number of pulses in the accumulator is equivalent to the rate of pulses per second multiplied by the number of seconds that the switch from pacemaker to accumulator has been closed. The number of pulses in reference memory on a single trial equals the number of pulses in the accumulator at the time of reinforcement times a memory constant. Finally, reference memory consists of distributions of such values. Decisions are based on the similarity of the value in the accumulator to a random sample of a single value from reference memory. On some trials, the animal may attend to the stimulus and this information processing model will apply, whereas on other trials the animal may not attend to the stimulus and will respond at some fixed level (Church & Gibbon, 1982; Heineman, Avin, Sullivan, & Chase, 1969). This model allows you to identify the effects of individual variables. For example, the operation of the switch can be changed by differential reinforcement; during a gap in the signal it can be made to stay closed or remain open (Church, 1978). This accounts for the "run" and the "stop" mode, where the value in the accumulator either continues to increase or stops during the interval. Finally, this internal clock model can operate in either event mode, where a relatively fixed value is added to the accumulator when a signal of variable duration is begun (Meck & Church, 1983), or in reset mode, where the value in the accumulator is initialized to zero at signal onset (Church, 1978).

Properties of the Clock

Sundials, stopwatches, digital watches and computer clocks have many different properties, but at the same time they have only one commonality -- they change with time in a regular way. Clocks may operate at different rates, some are more accurate than others, some are continuous and some are discrete, some are cyclical and some only change in one direction, some are driven by a specific external event, and some depend on an internal mechanism, and finally, some time up and some time down.

Results from the studies discussed above suggest that the properties of the internal clock correspond closely to those of a stopwatch. Some of the properties of a stopwatch are:

- (1) Initializable.
- (2) Can start timing at a constant rate.
- (3) If stopped, can hold a constant value indefinitely.
- (4) Can be restarted from the constant value or
- (5) Can be restarted from the initial value.
- (6) Can be read while timing or when stopped.

Most often, this is the analogy that is used to understand the properties of the internal clock.

The Connectionist Explanation

Recently it has been suggested by Church and Broadbent (1990) that there are several problems with the information-processing model that may be better explained with a connectionist interpretation. They discuss three main problems, all based on the fact that the model invokes some cognitive abilities that are difficult to interpret with known biological mechanisms. First, there is no known biological correlate for the accumulation

of time, retention of a distribution of values, or random sampling from memory. The second problem has to do with capacity. Storing information learned on successive trials requires storing an increasingly large number of values. As a result, the hardware must either be replicated, or previous values must be forgotten as new ones are added. Third, in order to remember different times, multiple distributions of values must be maintained and kept separate. However, animals do not seem to have any trouble handling many trials or differential times of reinforcement, nor do they appear to lose all past training (Meck & Church, 1984).

These problems with the information-processing approach have led to the development of a basic connectionist model of timing (Church & Broadbent, 1990). The connectionist model is similar to the information-processing model in that the main characteristics of the system are still derived from the relationship between input and output. The main differences, however, are that many processes can occur simultaneously, and the representations are not dependent on the state of any particular element. Advantages of this type of model include the fact that it is characteristic of the nervous system of animals, the same system of elements can contain information about different events, and performance is less likely to be disrupted by modification of the internal components.

The structure of the model is very similar to that of the information-processing model with three main differences. The *pacemaker* is expanded into a set of pacemakers, or oscillators, with different periods. The *accumulator* is replaced by a set of *status indicators*, one for each oscillator. These record not just the number of cycles as the accumulator would, but also the phase of the oscillator. Finally, the sample distributions that make up working and reference memory in the information-processing model are replaced by matrices of connection weights such that any given time is stored throughout the matrix, instead of being held as a scalar number. This is an advantage because a distributed memory matrix can store information about an infinite number of samples of a

value whereas a distribution of values must increase in size to accommodate more samples. Mathematically, times are represented as vectors and memories as matrices of connection strengths between units of the time vectors.

The connectionist variation on the information-processing theme does add to the model both in terms of biological feasibility and correlation with other theories of timing and time-place learning. For example, the idea of multiple storage pacemakers supports Gallistel's (1990) theory that timing is controlled through the interaction of many physiological oscillators. Also, the idea that working memory operates as a matrix of connection weights eliminates the problem of infinite capacity. Finally, computer simulations using the connectionist model produce very realistic data. This version of the model is still new and preliminary, but seems to be a viable path for future research.

The Behavioural Explanation

Although most of the literature focus on the internal clock model, one major alternative model has been developed by Killeen and Fetterman (1988). They suggest that behaviour is the mediator of temporal control. Animals do not make temporal judgements, that is, they do not separate stimuli to be timed from other events in their environment and then compare them in some way. Instead, the stimuli within timing experiments elicit various behaviours, called adjunctive behaviours, and they do so in terms of the stimulus's average temporal proximity to reinforcement. When a temporal judgement is necessary, the animal makes different responses depending on the adjunctive behaviour they were engaged in at that time. For example, if an animal was pacing when a choice was called for, it would choose the response "short"; if it was pecking the wall it would choose "long"; and if it was doing neither of those things it would select the alternative that was most often associated with reward in the context of the ongoing behaviour. They suggest that this is a model of an uncomplicated organism that merely

responds in one way if it is interrupted while doing one thing, and in another way if it is doing some other thing. Their model does not require a representation in memory because the animal is just making simple conditional discriminations. The only essential factor is that adjunctive behaviours correlated with the response increase in a cumulative manner over time.

According to Killeen and Fetterman, transitions between adjunctive behaviours are caused by pulses from a biological oscillator within an internal clock system. The counter consists of the animal's ability to use action states (behaviours such as pacing the side wall) that are correlated with various successive states. They have some observational support for this idea. In a study by Church, Getty, and Lerner (1976) they noticed that the stereotyped behaviours of the two subjects that were better at the discrimination were more rapid than those of the subjects with poorer discrimination. Also, the behaviour during the signal was the same as the behaviour during the ITI only for the subjects with poorer discrimination. Time will tell if this will be an effective computation for the internal clock model.

SUMMARY OF TIMING SYSTEMS

Two basic timing systems have been postulated: One based on circadian mechanisms, and the other based on an interval clock model. Usually circadian mechanisms are used to explain timing over the course of a day, whereas interval models are used to explain timing of intervals on the order of seconds or minutes. Although they have been discussed separately, my intention is not to pit them against each other. It is most likely, in fact, that these systems work together. Both timers could be part of one multiple oscillator system, the difference being that they are each working at different levels. This multiplicity of timing systems within a single organism may account for the flexibility that seems to be inherent in the timing behaviour of many animals.

The flexibility in timing systems suggests that animals have the capacity to adjust to a changing environment, and predict the likelihood of future events, which is essential in order to survive. One of the ways in which animals may be predicting these events is connected to classical conditioning. A theoretical connection between timing and classical conditioning has been established (Gibbon & Balsam, 1981; Roberts, 1983; Roberts & Holder, 1984a), and in turn classical conditioning has been postulated to be essential for the optimum fitness of an animal (Hollis, 1982). Initially it was suggested that the mechanism used for time discrimination is identical to that used for classical conditioning (Gibbon & Balsam, 1981). Other researchers (Roberts, 1983; Roberts & Holder, 1984a) suggested that the mechanisms of classical conditioning and timing have similar functions; both help the animal to predict future events. Classical conditioning predicts what will happen, whereas timing predicts when it will happen.

The empirical connection between timing and classical conditioning was established by Roberts and Holder (1984b, 1985), when they showed that treatments that were meant to change the associative strength (signal value) of a stimulus (a classical conditioning procedure) also changed the effective duration of the stimulus when measured with a time discrimination procedure. Duration was measured using various tasks, light or sound was used as the conditioned stimulus (CS) and food was used as the unconditioned stimulus (US). Their work contributed three main findings. First, after CS-alone (extinction) trials, forward-pairing trials increased the effective duration of the CS. Second, after forward-pairing trials, extinction trials decreased the effective duration of the CS. Third, when one stimulus (CS+) was followed by food and another (CS-) was not, the effective duration of the CS+ was greater than the effective duration of the CS-. These changes in effective duration seemed to be due to changes in timing of the stimulus by the internal clock. This suggests that a decision is made whether or not to time a stimulus and that decision depends on the same variables that determine signal value, that is, the same variables that determine the strength of conditional response.

Further experiments (Holder & Roberts, 1985) provided a more direct measure of signal value to determine whether changes in timing and signal value could be explained with the same mechanisms. Their study suggested that indeed there is a common mechanism for signal value and timing because under various treatments the two variables changed in the same direction, were near zero at the same times, and had similar time courses. Their proposed common mechanism is essentially a decision-maker which decides if a stimulus has signal value. The decision about signal value then influences the timing that is used in the time discrimination. The selectivity of timing in these studies provides excellent support for the idea that the function of the time discrimination mechanism is to help the animal predict when important events will happen. In order to predict when food will be available, the animal must be able to time signals for food and at the same time not time stimuli that are not signals, evidence for which is suggested by this research.

Further support for this idea is provided by Hollis (1982, 1984) who establishes a biological function for classical conditioning. Signaled presentations of food, rivals, predators, and mates can lead to anticipatory behaviour (Farris, 1967; Hearst & Jenkins, 1971). Hollis (1982) suggests that the function of the conditioned response is to allow the animal to better deal with the forthcoming unconditioned stimulus. The CR is a preparatory response which Hollis calls *prefiguring*. These anticipatory CRs function to optimize the individual's interactions with predators, rivals, mates, and food. Empirical evidence for this idea is presented in Hollis (1984) where it is demonstrated that the signaled presence of territory intruders leads to a conditioned response consisting of anticipatory aggressive behaviour in adult male blue gouramis. In a natural habitat, this classical conditioning may give the individual territorial male means with which to increase his likelihood of successful territorial defense, which ultimately confers a reproductive advantage on that individual.

TIME-PLACE LEARNING

The utility of possessing a timing mechanism becomes apparent when one looks at the behaviour, and survival tactics, of animals in natural settings. Usually, timing is used in conjunction with spatial memory in order to predict when and where food sources are likely to be most plentiful. Accordingly, animals' behaviour tends to 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 naturalistic studies have shown that wild birds are able to adjust their behaviour to changing patterns of food availability. These studies do not, however, demonstrate whether the birds are using a time-place association to exploit food, or whether they are merely responding directly to changing food availability.

Most experimental work in this area has been done with invertebrates, namely bees. In an early study, 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 in anticipation of 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 19 times per day.

Few researchers, however, have investigated animals' ability to associate a specific place with food availability, as opposed to associating one place with different times. In one such investigation, Biebach, Gordijn, and Krebs (1989) tested garden warblers, *Sylvia borin*, 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 hr. Food was available for 20 s, after which the bird had to return to the central area for 280 s, 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.

A second study, which used pigeons as subjects, demonstrated that these birds can learn time-place associations over periods of 1 hr (Wilkie & Willson, 1992). In their study it was shown that the birds could associate a specific pecking key with a particular 15-min interval during a 1-hr session. The birds were tested in large Plexiglas chambers with one pecking key and feeder mounted on each of the four walls. Subjects were able to see a variety of spatial cues in the room through the transparent walls of the boxes. Subjects received 60 min sessions during which each key provided food rewards for a 15-min period. In other words, 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 is two-fold. The first objective is to extend the Wilkie and Willson (1992) paradigm over longer periods, namely morning and afternoon. The second aim is to investigate the timing mechanisms underlying the behaviour of visiting certain places at certain times of the day.

Extension of paradigm

Three experiments were performed to determine if pigeons could track food availability over a 24-hr period. Ultimately, the reason for this was to enable us to get at the question of mechanisms underlying the timing behaviour, but first it had to be established that the birds could time over such an extended period. Previously, the longest interval over which pigeons have been shown to track food availability in an experimental setting was 1 hr. For this reason, a demonstration of pigeons timing over a 24-hr period in the laboratory would be a remarkable 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 that 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

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). This oscillator is continuous, self-sustaining, and entrainable. Because it is self-sustaining, it does not require the presence of external cues for the timing behaviour (i.e., learned time-place associations) to be maintained. The role of external cues is to act as "zeitgebers" which entrain the oscillator. In other words, if a circadian system is at work, the behaviour will persist in the absence of zeitgebers. Over time, however, it may not adhere to a 24-hr period or schedule. Interval (stopwatch) timing, on the other hand, has been intensely investigated in the timing of short intervals (e.g., Gibbon & Church, 1984; S. Roberts, 1981). Basically, these timers are discrete and can be stopped, started, reset, or restarted by various external events. Since stopwatch timers are greatly influenced by external events, alterations in these cues will immediately affect any type of behaviour 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 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 being used then the routine behaviour of the bird should be shifted to correspond with the new reset time.

One approach to empirically distinguishing these two possibilities is to manipulate the external cue, or zeitgeber, and observe the effects on behaviour. According to work in the field of circadian rhythms, possible zeitgebers include temperature changes, social signals, and feeding. However, the most salient zeitgeber to which a cycle may be entrained is the light-dark cycle (Aschoff, 1989). Following from this, in Experiment 4 the light-dark cycle was manipulated with a phase shift. More specifically, lights-on time was shifted back by 6 hr, and performance was observed the following day. If the birds' learned time-place associations are being controlled by an interval timing mechanism then an immediate shift in behaviour should be observed. However, if the behaviour is controlled by a self-sustaining oscillator, then the shift should have a minimal effect on the phase of the following cycle, that is, on the next day's performance.

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 a bird is using an interval timer, 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 bird is using a circadian mechanism, however, performance should continue as usual since this timing system is based on a self-sustaining oscillator which is relatively independent of changes in external cues.

GENERAL METHODS

Subjects

The subjects were one White King (Allanon) and three Silver King (Silvercloak, Johann, and Jack) pigeons. The birds were maintained at approximately 90% of free-feeding body weight with a grain mixture obtained during testing sessions as well as post-session feedings. Subjects lived in large plastic coated wire mesh cages with ad libitum access to grit, oyster shells, and vitamin fortified water. The colony was climate controlled (20^o C) and had a light/dark cycle matched to natural sunrise/sunset times. Luminance in the colony was approximately 82 cd/m². Data collection occurred between 3 January 1992 and 15 September 1992. Sunrise times ranged from 05:50 to 08:08 and sunset times ranged between 16:24 and 20:52 during this period. (Data provided by the Atmospheric Environment Service of Environment Canada).

All subjects had previous experience 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, pigeons were tested in one of two large, clear Plexiglas Skinner boxes with one 3.5 cm diameter pecking key on the centre of each of the four walls. The floor area of the first box was 3600 cm² (Silvercloak and Jack) and the floor area of the second box was 2025 cm² (Johann and Allanon). Behind each key was a microswitch, which recorded pecks having a force greater than 0.15 N. The keys were illuminated with a 28VDC #313 light covered with a red gelatin filter, and each key was mounted above a standard grain feeder. The box was located in a small (2m x 2m) well lit testing room. 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.

General Procedure

All subjects had previous key pecking 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. During the remainder of the trial, 5-s 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 I addressed was whether the pigeons could learn a time-place association over a long interval (24 hr). Subjects were exposed to a discrete trial procedure in which 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 2 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 to the total number of pecks made during the first non-rewarded 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 emphasise that food cues were not available to indicate which key was correct.

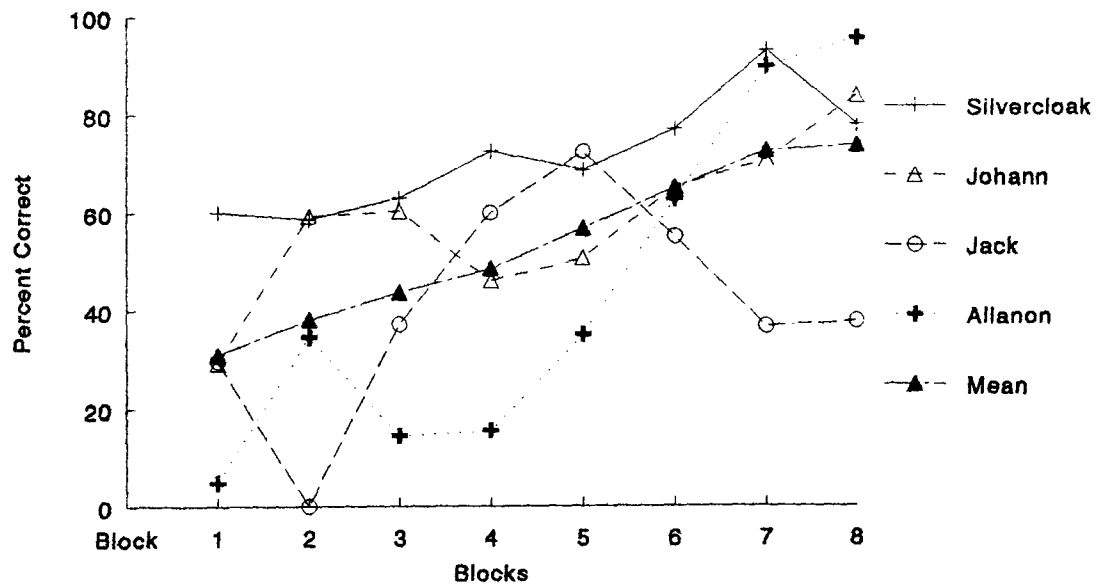
If the subject did not discriminate and simply responded randomly performance would be 25% (one out of four keys is rewarded). The slope of the lines indicates that three of the birds began with a score at a chance or slightly above chance level, but by the end of the training session they were performing well above chance in the range of 80 to 95 % correct. One bird, Jack, seemed to have some problems with the task during 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 3 summarizes the percent of pecks per key in the first minute of each session during both the first block and the final block of baseline sessions. Pecks to all four keys are represented: "Correct" bars represent the percent of pecks made to the appropriate key for the session, "alternate" bars represent the percent 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 subjects seemed quite

Figure 2: Acquisition of the 24-hr time-place learning task. This graph shows percent of pecks to the appropriate key for both morning and afternoon sessions for all subjects.

Morning Acquisition



Afternoon Acquisition

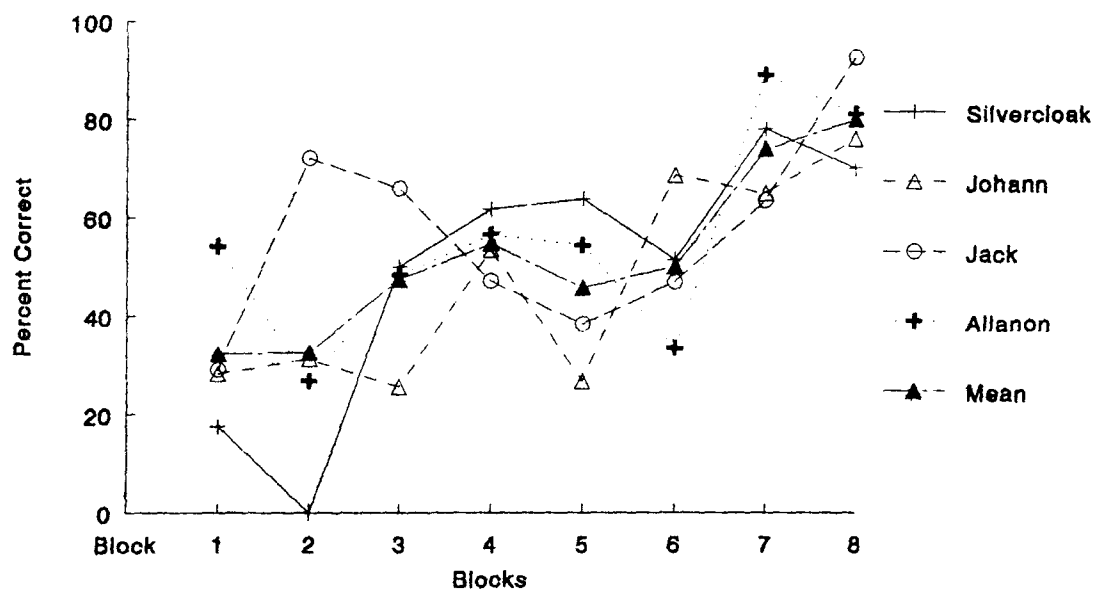
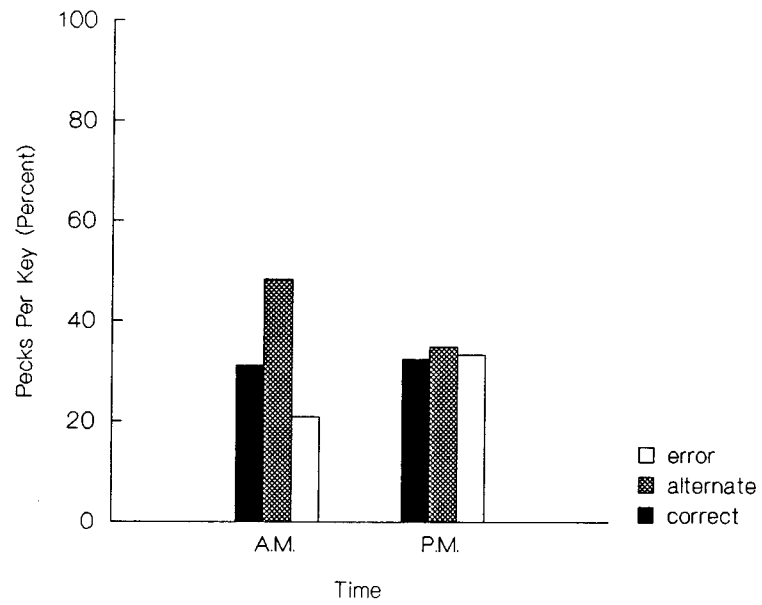
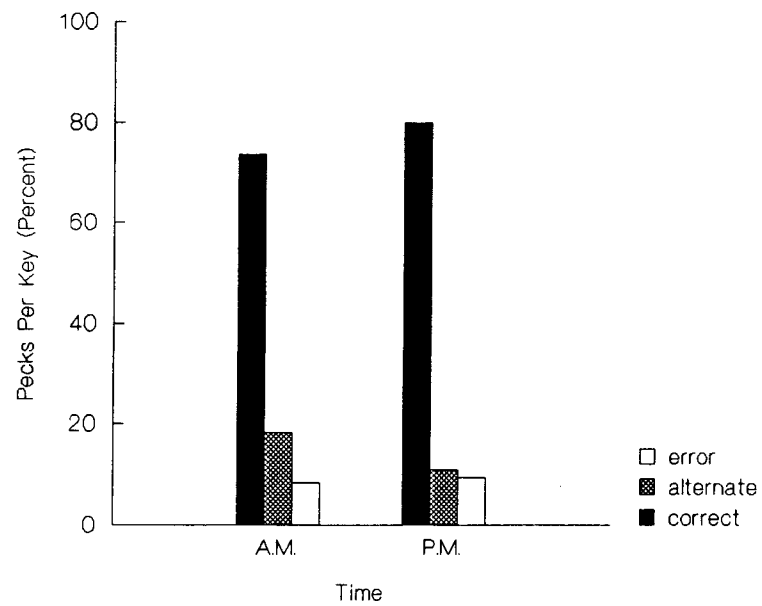


Figure 3: Mean percent of pecks per key during the first and the final block of baseline sessions. "Correct" bars represent pecks made to the appropriate key for the session, "alternate" bars represent pecks made to the key appropriate for the alternate session, and "error" bars represent pecks made to the 2 keys which are never rewarded.

Mean Baseline (Block 1)



Mean Baseline (Block 8)



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 acquisition ($F(28)=2.804, p<.05$) and afternoon acquisition ($F(28)=4.244, p<.01$). Also, a one sample t-test comparing final baseline to chance (25%) was significant for both morning ($t(3)=3.88, p<.05$) and afternoon ($t(3)=11.39, p<.001$).

All 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 hr 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 provided food in the afternoons. At first glance, this seems to indicate that the pigeons were keeping 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 be using an 'every-other-trial-key 2-is-good' type of rule to determine which key will provide him with a reward. In order to rule out this possibility, several probe trials were conducted in Experiment 2.

EXPERIMENT 2: AM ONLY / PM ONLY

METHOD

In an attempt to eliminate the possibility of an alternation type of strategy, eight trials in which only the morning session was presented were inserted twice per week between baseline days. Thus, in one 4 week period 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 eight 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, in the case that alternation is being used.

RESULTS AND DISCUSSION

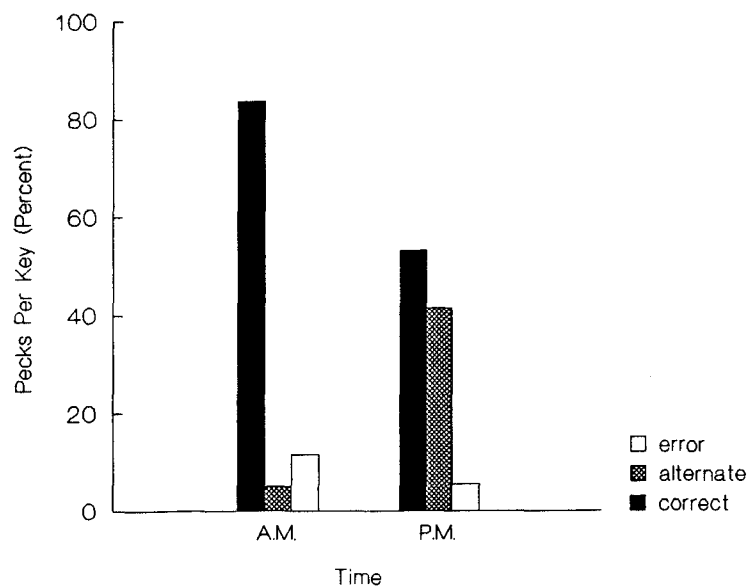
Figure 4 illustrates percent of pecks per key for both the sessions following the morning-only probes and the sessions following the afternoon-only probes. This graph has the same format as Figure 3, (i.e., pecks to all four keys are represented).

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. Subjects seemed to do slightly better in the mornings, with an average of 80 % of responses to the appropriate key, whereas in the afternoon about 75 % of responses were to the correct key.

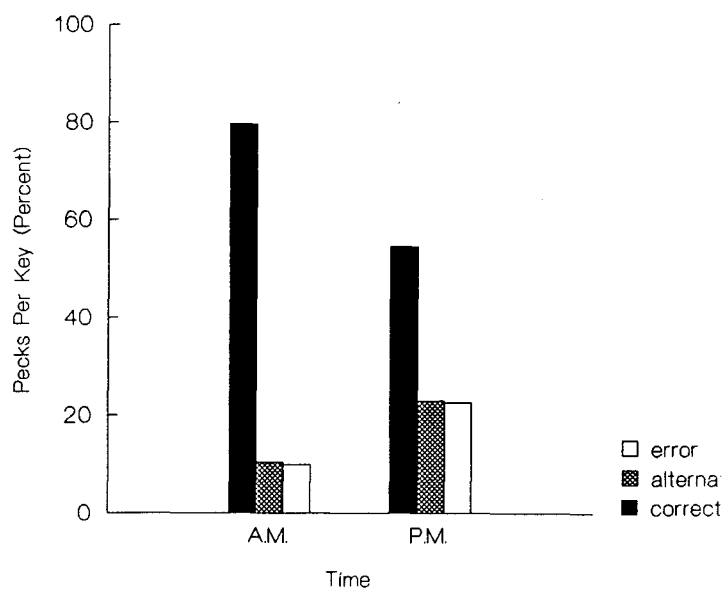
Thus, all subjects showed evidence of using a timing as opposed to an alternation strategy. The subjects responded to the appropriate key in both the mornings and the afternoons, in spite of the fact that the previous session had been eliminated. If a bird was receiving rewards for pecking Key 2 in the mornings and Key 4 in the afternoons, then 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.

Figure 4: Percent of pecks per key for both sessions following the morning-only probes and the sessions following the afternoon-only probes.

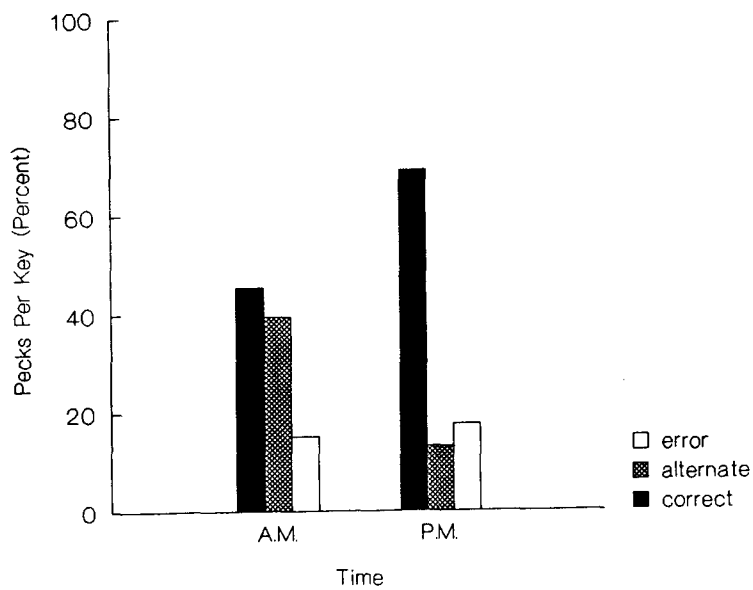
Silvercloak -- AM Only / PM Only



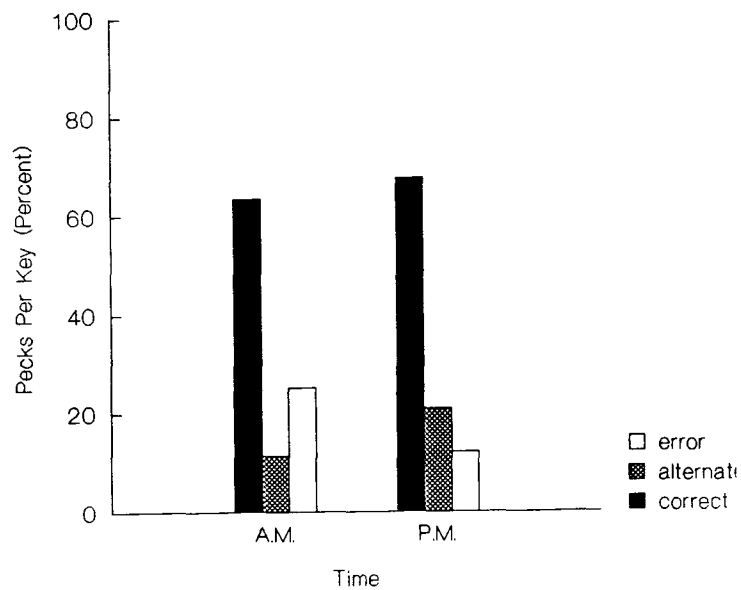
Johann -- AM Only / PM Only



Jack -- AM Only / PM Only



Allanon -- AM Only / PM Only



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 is being used, then the error rate should be the same as in the baseline sessions, or perhaps less because of the shortened retention interval between the two sessions. If a timing strategy is being used, however, the error rate should increase in relation to how far the probe session deviates from the baseline time of session. Baseline time of sessions was approximately 09:30 for the morning sessions and 16:00 for the afternoon sessions. Two separate probe trials were conducted (six 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 inter-session intervals varied between 6.5 hr (baseline), 4.5 hr (Probe 1) and 1.5 hr (Probe 2).

RESULTS AND DISCUSSION

Performance on Probe 1, Probe 2, and Baseline for morning sessions is illustrated in Figure 5.

Two of the birds (Silvercloak and Allanon) tended to perform worse than baseline on both types of probe, as expected if subjects were using the phase of a circadian oscillator as a timer. The other two birds, however, showed different patterns. Johann showed slightly better performance on Probe 2 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 6).

Figure 5: Performance of all subjects in morning sessions as compared to inter-session intervals.(Baseline, 6.5 hr; Probe 1, 4.5 hr; Probe 2, 1.5 hr).

A.M. Performance versus Inter-Session Interval

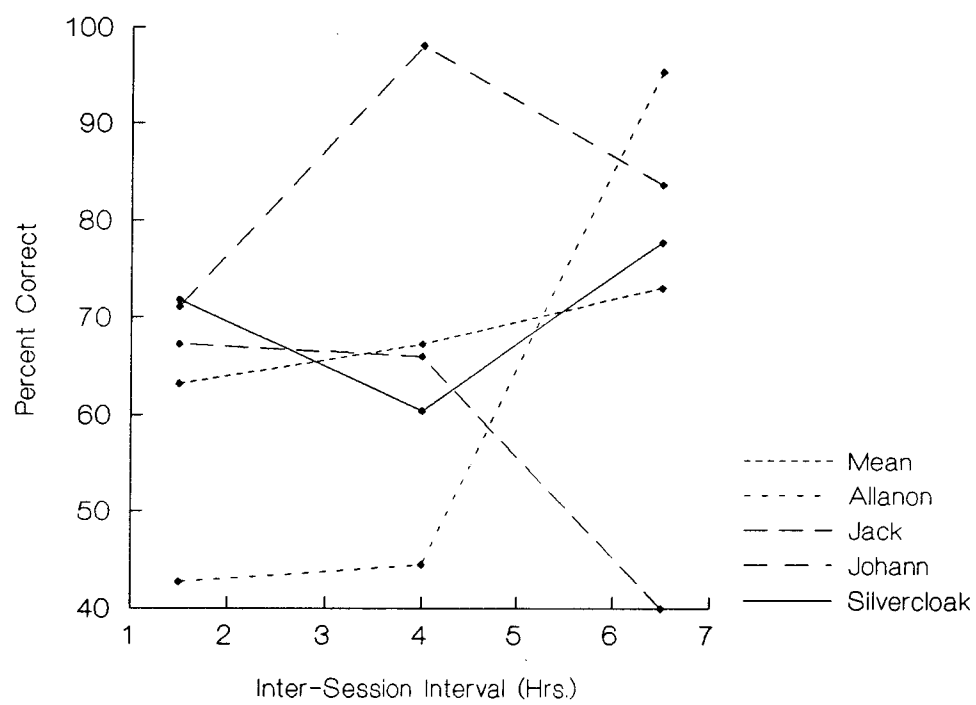
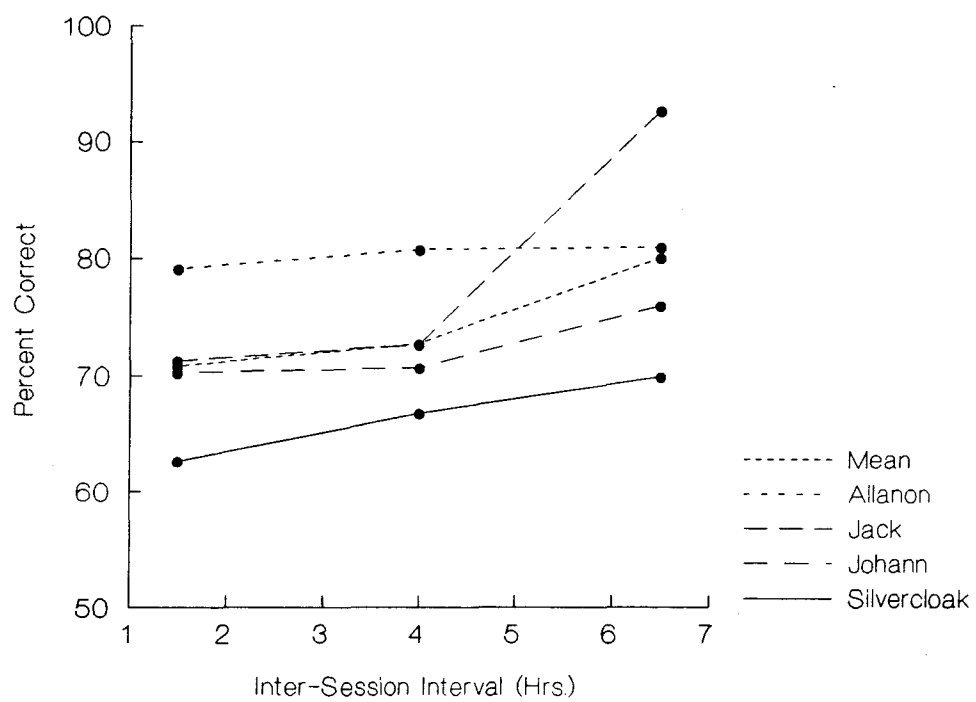


Figure 6: Performance of all subjects in afternoon sessions as compared to inter-session interval (Baseline, 6.5 hr; Probe 1, 4.5 hr; Probe 2, 1.5 hr).

P.M. Performance versus Inter-Session Interval



Between 80% and 99% of the variance in percent correct could be accounted for by inter-session interval (Silvercloak $r^2 = .992$; Johann $r^2 = .801$; Jack $r^2 = .797$; Allanon $r^2 = .895$). As predicted, this suggests that performance was worse depending on how far the interval between testing times deviated from the original testing times, thereby providing further evidence for a timing strategy.

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 hours) was not very large in relation to the total amount of time that the bird was representing (24 hours). As mentioned previously, the subjects' timing systems seem to be somewhat flexible. Animals must be able to adapt to changes in their environment. Consequently, their timing systems seem to be able to accommodate slight discrepancies in time of trial presentation. All three types of probes in both Experiment 2 and Experiment 3 provide strong evidence that the birds were using a timing strategy, so we moved on to looking at the possible underlying mechanisms in Experiment 4.

EXPERIMENT 4: PHOTOPERIOD

METHOD

Once it is established that the birds are using a timing strategy, the next step is to look at the mechanisms underlying the behaviour. One possibility is that the birds are using an interval or stopwatch timer. A second possibility is that the birds are using a circadian timing mechanism. A main feature of a circadian system is that it is self-sustaining. Therefore, after a sudden shift in photoperiod behaviour 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 behaviour will shift accordingly. In contrast, an interval timer is

reset daily by lights-on time. Any behaviour based on timing will not persist but instead will immediately shift in accordance with the new photoperiod.

In this experiment the four birds in the study 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 the birds' performance. Illuminance in the new room approximated that of the colony (95 cd/m^2). After 15 days of adjustment to the new room, lights-on time was shifted backward by six hours (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) for 6 days following the shift.

RESULTS AND DISCUSSION

Figure 7 shows that the birds were not affected by the change in rooms; consequently the shift in light-dark cycle was performed.

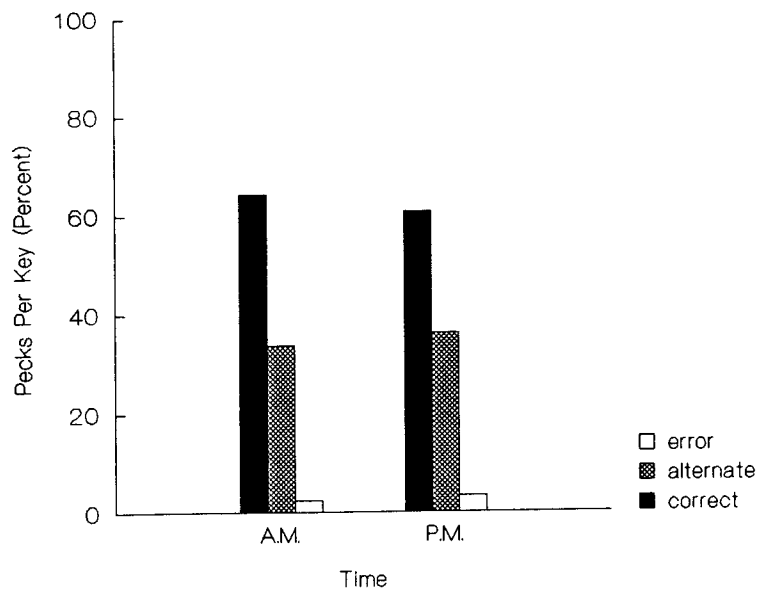
Figure 8 illustrates the performance of each bird on the day immediately following the phase shift. Each of the four birds continued to respond at above chance to the appropriate key (Silvercloak, 70%; Johann, 98%; Jack, 65%; Allanon, 100%). It is interesting to note that for most birds, correct response actually increased after the phase shift. Since subjects' behaviour was not deleteriously affected by the phase shift, these data are consistent with a circadian based timing system.

All four birds maintained their performance in the session following the phase shift. This provides evidence for a circadian, not a stopwatch, timing system. A clock 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 would not be expected initially to lead to a change in behaviour following a phase shift.

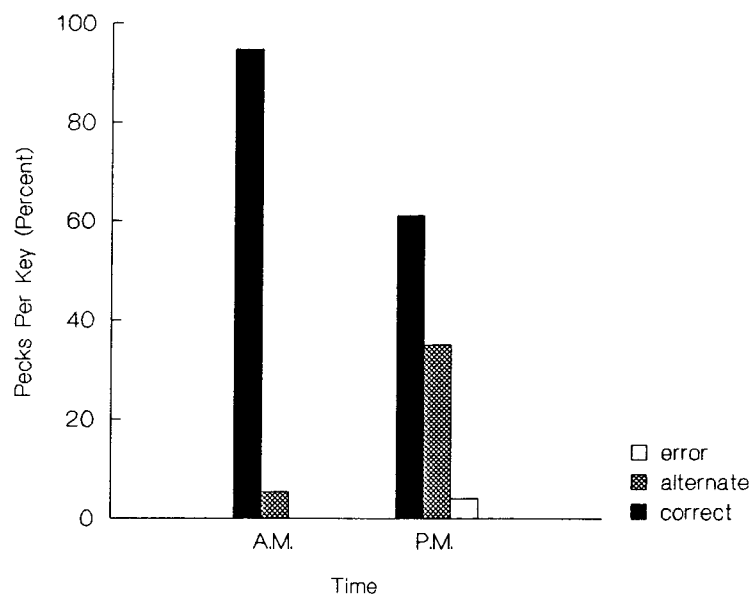
Finally, Figure 9 shows performance of the birds when the phase shift was extended for a period of 6 days. The data for individual birds are considerably different.

Figure 7: Baseline performance of all subjects after being moved from the colony to the new room.

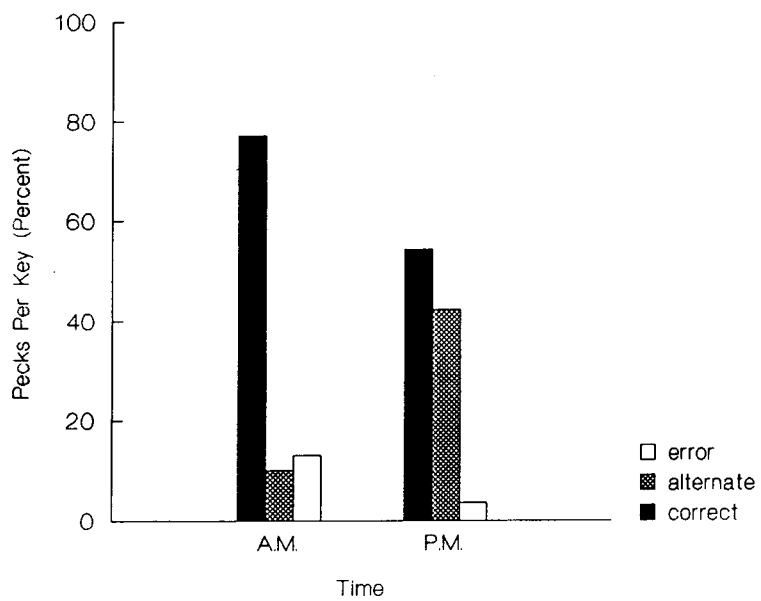
Silvercloak -- New Baseline



Johann -- New Baseline



Jack -- New Baseline



Allanon -- New Baseline

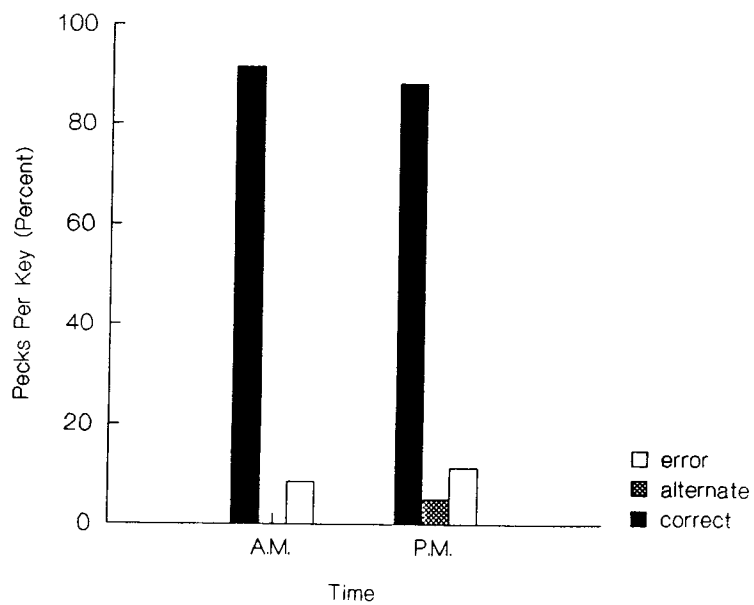
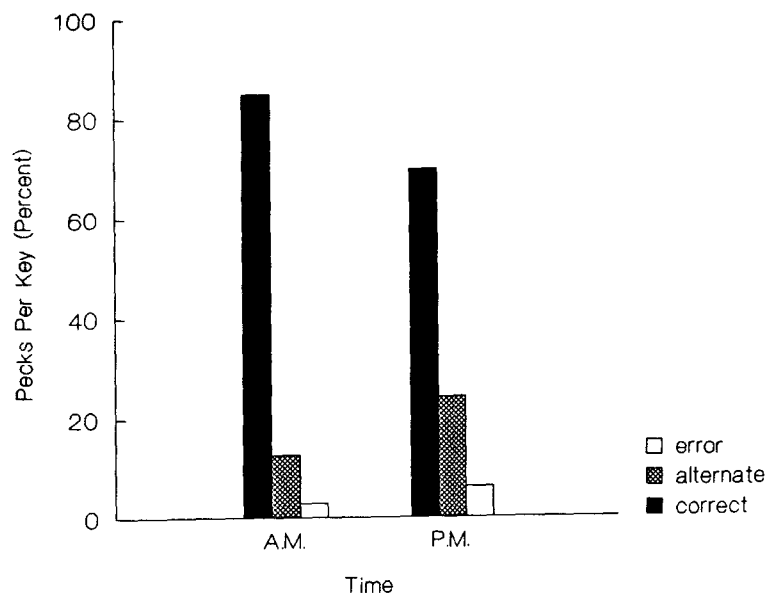
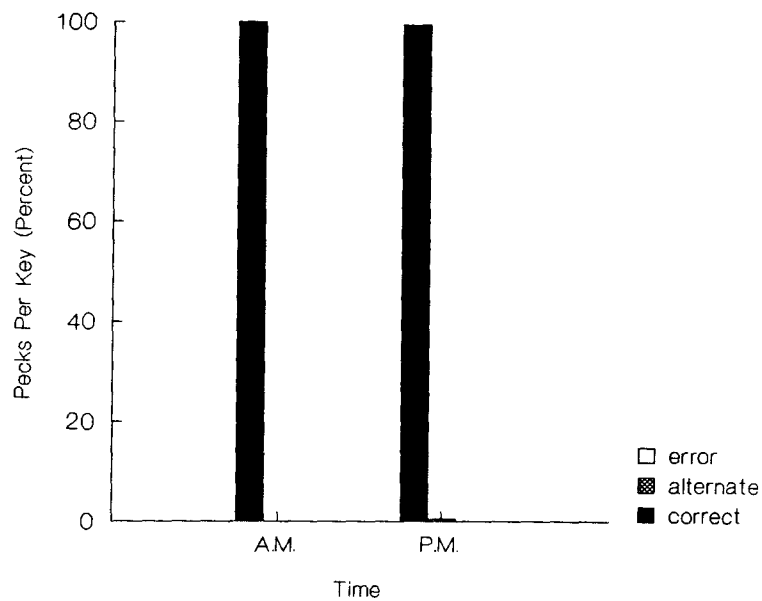


Figure 8: Percent of pecks per key for each bird on the day immediately following the phase shift.

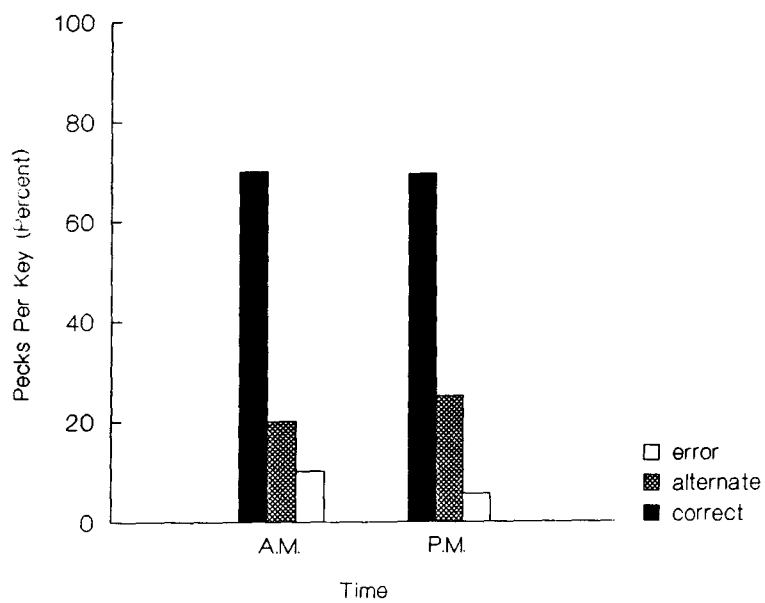
Silvercloak -- Session Following Phase Shift



Johann -- Session Following Phase Shift



Jack -- Session Following Phase Shift



Allanon -- Session Following Phase Shift

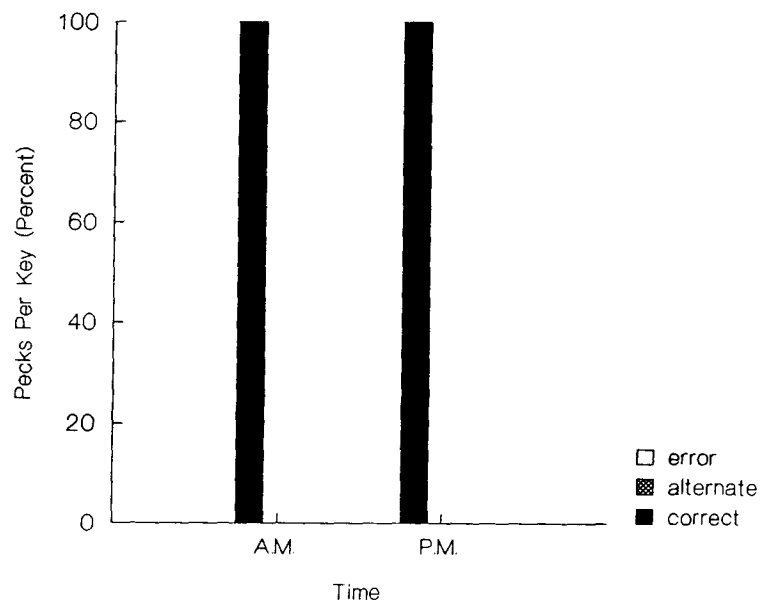
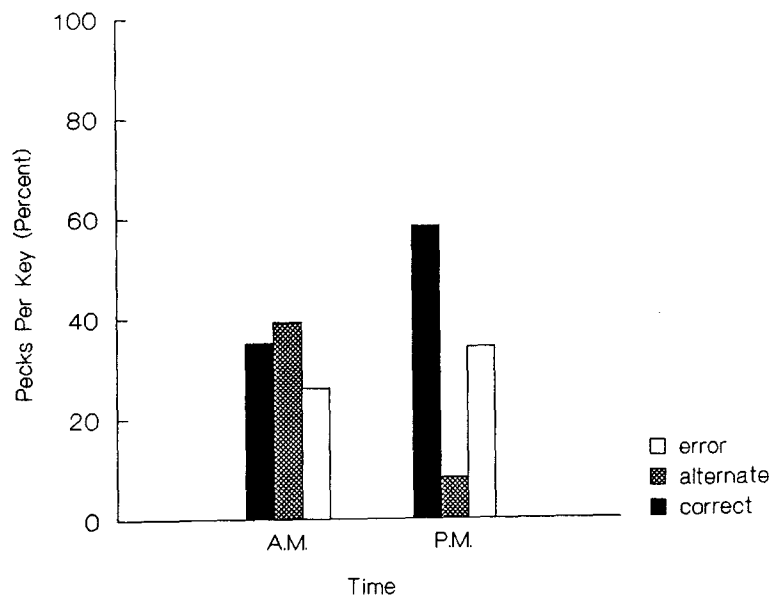
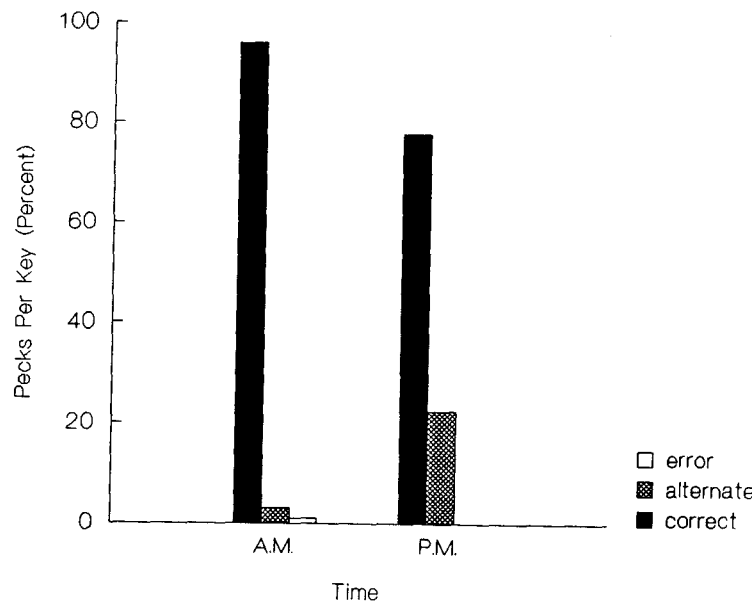


Figure 9: Percent of pecks per key for all birds after the phase shift was extended for a period of 6 days.

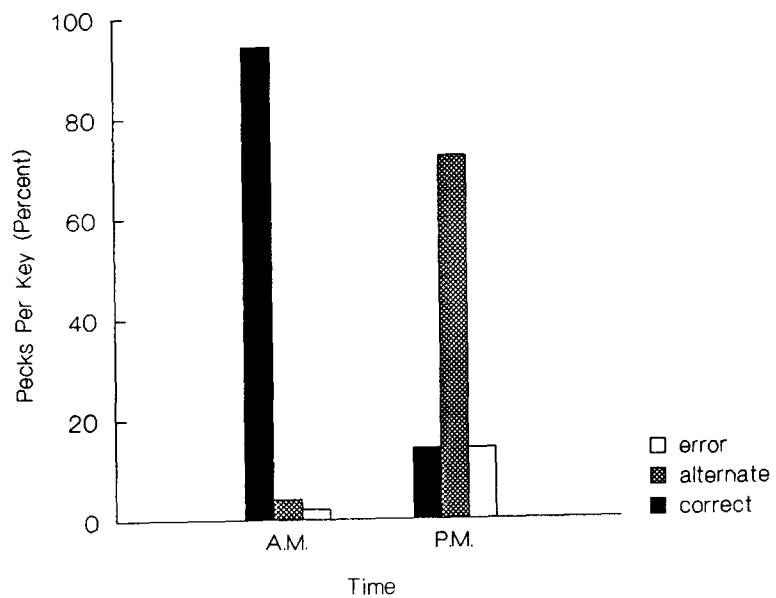
Silvercloak -- Phase Shift



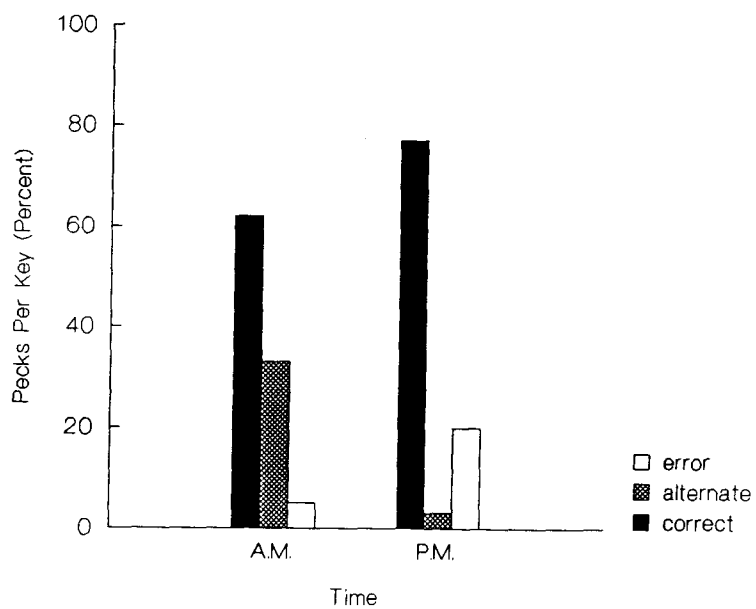
Johann -- Phase Shift



Jack -- Phase Shift



Allanon -- Phase Shift



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. He seemed to peck every key equally, including those for which he was never rewarded. Jack's scores were also greatly influenced by the continued phase shift, but his strategy was quite different from Silvercloak's. While 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 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 two of the birds were able to continue to respond appropriately for up to 6 days provided further evidence for a circadian based system. First, two of the birds were able to continue to respond appropriately for up to 6 days, thereby providing further evidence for a circadian 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 two subjects after six days, provides strong evidence that they are not using an alternation type of strategy. If they were alternating, then performance should either remain the same or improve over the course of 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 that this is the case.

EXPERIMENT 5: DIM LIGHT

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, absence of the daily

lights-on cue should not affect timing behaviour, 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 (9:30 and 16:00) for 4 days following the move to dim light.

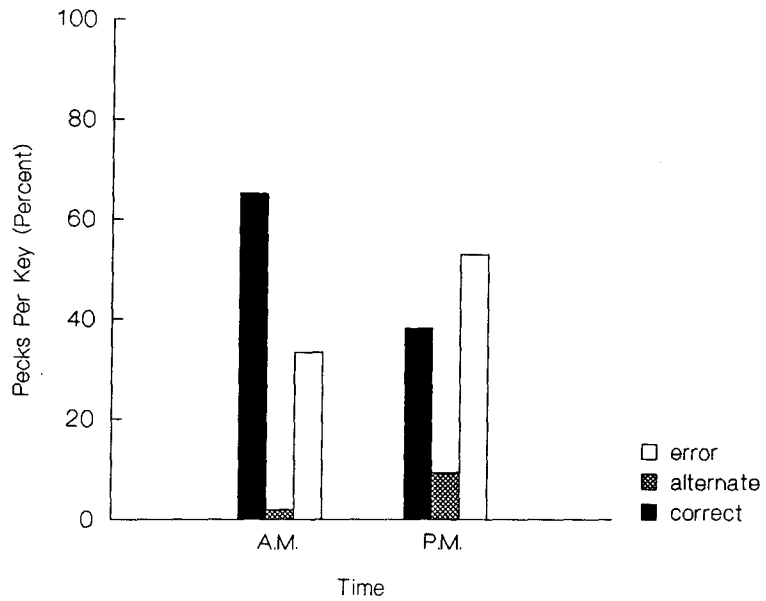
RESULTS AND DISCUSSION

Performance on the first day of the dim light condition is shown in Figure 10. Three subjects (Johann, Jack, and Allanon) performed extremely well.

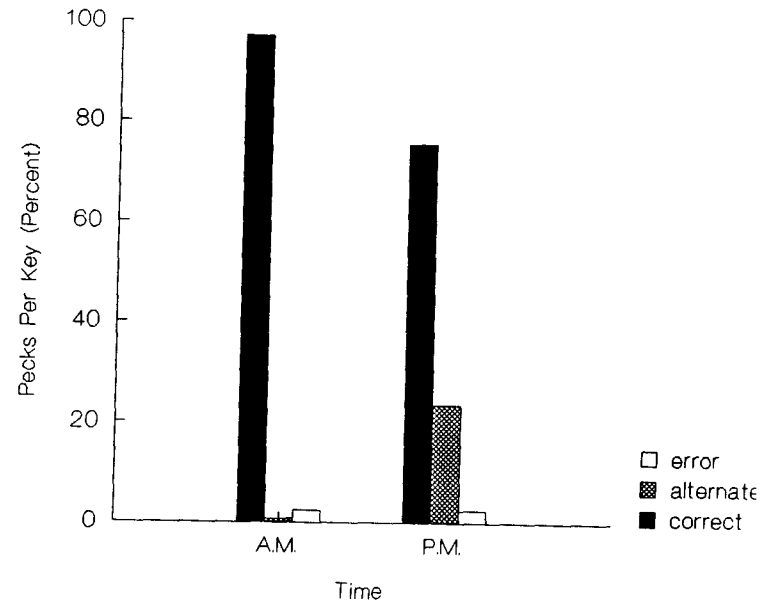
For each of these birds percent of pecks to the correct key were well above chance, and did not differ from baseline scores. This strongly supports a self-sustaining, circadian-based timing system. Silvercloak, on the other hand, performed above chance in morning sessions but did not peck accurately in the afternoons, thereby suggesting that he may have been using an alternate timing strategy. Silvercloak's performance in this experiment illustrates the fact that different individuals may use different strategies depending on the situation.

Figure 10: Percent of pecks per key for all birds under the dim light condition.

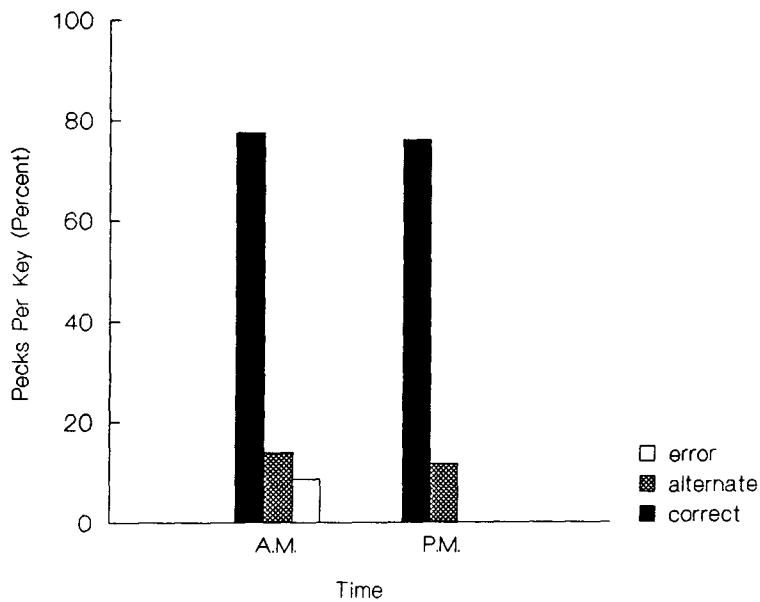
Silvercloak -- Dim Light



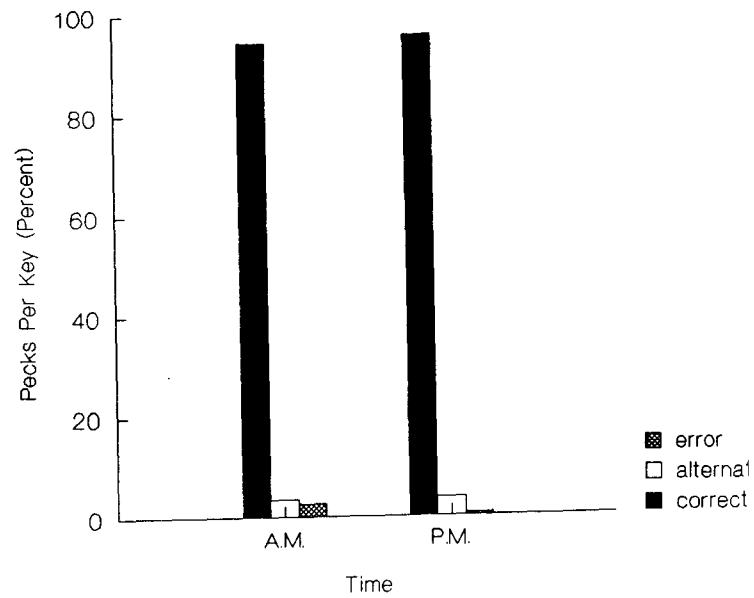
Johann -- Dim Light



Jack -- Dim Light



Allanon -- Dim Light



GENERAL DISCUSSION

The first goal of this research was to determine whether pigeons are capable, in the laboratory, of timing over intervals as long as 24 hr. Previous work has demonstrated timing capabilities in the order of seconds (e.g., Gibbon & Church, 1984; S. Roberts, 1981) or over 1 hr (Wilkie & Willson, 1992). The present work suggests that pigeons are indeed capable of timing over 24 hr and that they appear to be using a true timing strategy, as opposed to a learned pattern such as alternation. When required to peck at a key that was reinforced only in the mornings and a different key which was providing food only in the afternoons, the pigeons learned this discrimination up to at least 80% correct. When either morning or afternoon sessions were 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 as resources may be variably available over the course of a day or a week, not merely over the course of an hour. An organism must be able to integrate timing and behaviour in order to gain optimal resources in the real world.

Once it was established that subjects were capable of timing over an extended period I was interested in the mechanism underlying the behaviour. The results from Experiment 4 and 5 suggest that this long term timing is mediated by a circadian clock as opposed to an interval timer. When their light-dark cycle was shifted back by 6 hr the birds' performance on the day following the shift remained high. In addition, when 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 which would allow for the maintenance of appropriate behaviour in spite of significantly altered external cues. If a stopwatch mechanism was being used then a substantial decrease in performance would be expected because the clock should be

reset by the change in lights-on time, and subsequent behaviour should correspond with that shift. This finding corresponds with Biebach et al.'s (1989) work on garden warblers, where it was also found that a circadian mechanism best explained learning on a time-place task in which four 3-hr periods were timed. It does not correspond, however, with a finding of stopwatch-like timing in a one hour time-place paradigm in pigeons (Wilkie, Saksida, Samson & Lee; in press). This suggests that session duration, not species difference, is the most important determinant of the timing system used. 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.

Further evidence for flexibility of timing was found in the last part of Experiment 4. In this part of the experiment, the phase shift was extended for a period of six days. Each bird appeared to use a different strategy to cope with the change in light-dark cycle. This suggests that although pigeons may generally use particular strategies to time over different intervals, they seem to be able to adapt their individual strategies depending on the situation.

Individual differences in timing strategies is a thread that runs through several of the experiments in this thesis. In the first 3 experiments, the birds had very comparable data, with the exception of Jack in the mornings. His accurate performance during afternoon sessions, however, suggested that he was learning the task and was not using a non-timing strategy such as alternation. His performance in the mornings did improve over the course of the research, however, which again suggests that he was not using a different strategy but was just slower in learning the task. Experiments 4 and 5, which were designed to investigate the mechanisms underlying the time-place learning behaviour, showed some individual differences that appear to be more likely due to differing strategies as opposed to differences in acquisition time. The obvious example of this occurs in Experiment 4 when the phase shift was extended for a period of several days.

Initially, when the phase shift occurred, all four subjects adopted the same circadian-based timing strategy. Their performance on the task was not affected by the major change in light-dark cycle. However, after several days of the lights-on cue not corresponding with reward, all of the birds' behaviour began to change. Two of the subjects, Johann and Allanon, were still going to the keys that had been rewarded before the phase shift. A considerable amount of error ("trying out" other keys), however, did begin to creep into their data. Silvercloak, on the other hand, started to peck at all keys equally, even those for which he had never been rewarded. Jack took a completely different approach to the problem. He pecked consistently at one key, both in the morning and in the afternoon, thus he did very well during morning sessions but failed miserably in the afternoons. These differences in the data do not suggest that the birds were using different timing strategies, because in this part of the experiment none of the birds were timing appropriately for the rewards that were available to them. Instead, they were using different strategies to solve the problem that although their self-sustaining timing mechanism was still running, the rewards that they had been getting previously were no longer available. In other words, although a circadian timing mechanism is not governed by external events, it is still affected by them, and will gradually become entrained (synchronised) with the light-dark cycle (see Aschoff, 1989). An interesting follow up to Experiment 4 would be to extend the phase shift for several weeks, and determine whether the birds could eventually all return to baseline performance, in spite of the different strategies that they might use to get there.

REFERENCES

- Abe, H. & Sugimoto, S. (1987). Food anticipatory response to restricted food access based on the pigeon's biological clock. *Animal Learning & Behavior*, **15**, 353-359.
- Anger, D. (1963). The role of temporal discriminations in the reinforcement of Sidman avoidance behavior. *Journal of the Experimental Analysis of Behavior*, **6**, 477-506.
- Aschoff, J. (1989). Temporal orientation: Circadian clocks in animals and humans. *Animal Behaviour*, **37**, 881-896.
- Aschoff, J. (1984). Circadian timing. In: J. Gibbon & L. Allan (Eds.), *Timing and time perception*, (pp. 442-468). New York: New York Academy of Sciences.
- Aschoff, J. (Ed.). (1981). *Biological rhythms, handbook of behavioural neurobiology*, **4**. New York: Plenum Press.
- Aschoff, J., von Goetz, C., & Honma, K. (1983). Restricted feeding in rats: Effects of varying feeding cycles. *Zeitschrift fur Tierpsychologie*, **63**, 91-111.
- Aschoff, J., Daan, S., & Groos, G. (Eds.). (1982). *Vertebrate circadian systems: Structure and physiology*. Berlin: Springer-Verlag.
- Beling, I. (1929). Uber das Zeitgedachtnis der Bienen. *Zeitschrift fur vergleichende Physiologie*, **9**, 259-238.
- Biebach, H., Falk, H. & Krebs, J.R. (1991). The effect of constant light and phase shifts on a learned time-place association in garden warblers (*Sylvia Borin*): Hourglass or circadian clock? *Journal of Biological Rhythms*, **6**, 353-365.
- Birch, D., Burnstein, E., & Clark, R. (1958). Response strength as a function of hours of food deprivation under a controlled maintenance schedule. *Journal of Comparative Physiology and Psychology*, 350-354.
- Bolles, R.C., & deLorge, J. (1962). The rat's adjustment to a diurnal feeding cycle. *Journal of Comparative Physiology and Psychology*, **55**, 760-762.

- Boulos, Z., & Terman, M. (1980). Food availability and daily biological rhythms. *Neuroscience and Biobehaviour Review*, *4*, 119-131.
- Broadbent, D.E. (1958). *Perception and communication*. New York: Pergamon Press.
- Caccamise, D.F., & Morrison, D.W. (1986). Avian communal roosting: Implications for diurnal activity centers. *American Naturalist*, *128*, 191-198.
- Catania, A.C. (1970). Reinforcement schedules and psychophysical judgements: A study of some temporal properties of behavior. In: W.N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1-42). New York: Appleton-Century-Crofts.
- Church, R.M. (1984). Properties of the internal clock. In: J. Gibbon and L. Allan (Eds.), *Timing and time perception*, (pp. 567-582). New York: New York Academy of Sciences.
- Church, R.M. (1980). Short-term memory for time intervals. *Learning and Motivation*, *11*, 208-219.
- Church, R.M. (1978). The internal clock. In: Hulse, S.H., Fowler, H. & Honig, W.K. (Eds.) *Cognitive processes in animal behavior*. (pp. 277-310) New Jersey: Erlbaum.
- Church, R.M., & Broadbent, H.A. (1990). Alternative representations of time, number, and rate. *Cognition*, *37*, 55-81.
- Church, R.M., & Deluty, M.Z. (1977). The bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behaviour Processes*, *3*, 216-228.
- Church, R.M., & Deluty, M.Z. (1976). *Scaling of time by rats*. Paper presented at the Annual Meeting of the Psychonomic Society, St. Louis, Missouri.
- Church, R.M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 165-186.
- Church, R.M., Miller, K.D., Gibbon, J., & Meck, W.H. (1988). *Symmetrical and asymmetrical sources of variance in temporal generalization*. Paper presented at the Annual Meeting of the Psychonomic Society, Chicago, November, 1988.

- Church, R.M., & Meck, W.H. (1984). The numerical attributes of stimuli. In: H.L. Roitblat, T.G. Bever, & H.S. Terrace (Eds.) *Animal cognition* (pp. 445-464). Hillsdale, NJ: Erlbaum.
- Church, R.M., & Roberts, S. (1975). *Control of an internal clock*. Paper presented at the Annual Meeting of the Psychonomic Society, Denver, Colorado.
- Cowcroft, P. (1954). The daily cycle of activity in British shrews. *Proceedings of the Zoological Society* (London), **123**, 715-729.
- Daan, S. (1981). Adaptive daily strategies in behavior. In: J. Aschoff (Ed.), *Biological rhythms*, (pp. 275-298). New York: Plenum.
- Daan, S., & Aschoff, J. (1981). Short-term rhythms in activity. In: J. Aschoff (Ed.), *Biological rhythms* (pp. 491-499). New York: Plenum.
- Daan, S., & Koene, P. (1981). On the timing of foraging flights by oystercatchers, *Haematopus ostralegus*, on tidal mudflats. *Netherlands Journal of Sea Research*, **15**, 1-22.
- Daan, S., & Slopeema, S. (1978). Short term rhythms in foraging behavior of the common vole, *Microtus avarilis*. *Journal of Comparative Physiology*, **127**, 215-227.
- Davis, H., & Memmot, J. (1982). Counting behavior in animals: A critical evaluation. *Psychological Bulletin*, **92**, 547-591.
- Dews, P.B. (1970). The theory of fixed-interval responding. In W.N. Schoenfeld (Ed.) *The theory of reinforcement schedules* (pp. 43-61). New York: Appleton-Century-Crofts.
- Edmonds, S.C. & Adler, N.T. (1977). Food and light as entrainers of circadian running activity in the rat. *Physiology & Behavior*, **18**, 915-919.
- Eiserer, L.A. (1984). Communal roosting in birds. *Bird Behaviour*, **5**, 61-80.
- Farner, D.S. (1985). Annual rhythms. *Annual Review of Physiology*, **47**, 65-82.

- Farris, H.E. (1967). Classical conditioning of courting behavior in the Japanese quail, *Coturnix coturnix japonica*. *Journal of the Experimental Analysis of Behavior*, **10**, 213-217.
- Fernandes, D.M., & Church, R.M. (1982). Discrimination of number and sequential events by rats. *Animal Learning & Behavior*, **10**, 171-176.
- Gallistel, C.R. (1990). *The organization of learning*. Cambridge, Mass: MIT Press.
- Gibbon, J. (1991). Origins of scalar timing. *Learning and Motivation*, **22**, 3-38.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's Law in animal timing. *Psychological Review*, **84**, 279-325.
- Gibbon, J. (1972). Timing and discrimination of shock density in avoidance. *Psychological Review*, **79**, 68-92.
- Gibbon, J., & Balsam, P.D. (1981). Spreading association in time. In: C.M. Locurto, H.S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 219-253). New York: Academic Press.
- Gibbon, J., & Church, R.M. (1984). Sources of variance in an information processing theory of timing. In: H.L. Roitblat, T.G. Bever, & H.S. Terrence (Eds.) *Animal cognition* (pp. 465-488). Hillsdale, N.J. : Erlbaum.
- Gibbon, J., & Church, R.M. (1981). Time left: Linear versus logarithmic subjective time. *Journal of Experimental Psychology: Animal Behavior Processes*, **7**, 87-107.
- Gibbon, J., Church, R.M., & Meck, W.H. (1984). Scalar timing in memory. In: J. Gibbon & L. Allan (Eds.), *Timing and time tprception* (pp. 52-77). New York Academy of Sciences.
- Gilbert, S.G., & Rice, D.C. (1979). NOVA SKED II: A behavioural notation language utilizing the Data General Corporation real-time disk operating system. *Behavioral Research Methods & Instrumentation*, **11**, 71-73.

- Grant, D.S., & Spetch, M.L. (1981). Pigeons' memory for event duration: Differences between choice and successive matching tasks. *Learning and Motivation*, **22**, 180-199.
- Gwinner, E. (1981). Circannual systems. In: J. Aschoff (Ed.), *Biological rhythms*, (pp. 391-410). New York: Plenum.
- Gwinner, E. (1978). Effects of pinealectomy on circadian locomotor activity rhythms in European starlings, *Sturnus vulgaris*. *Journal of Comparative Physiology*, **126**, 123-129.
- Gwinner, E. (1966). Entrainment of a circadian rhythm in birds by species-specific song cycles (Aves, Fringillidae: *Carduelis spinus*, *Serinus serinus*). *Experientia*, **22**, 765.
- Hearst, E., & Jenkins, H.M. (1974). *Sign tracking: The stimulus reinforcer relation and directed action*. Austin, Texas: Psychonomic Society.
- Heineman, E.G., Avin, E., Sullivan, M.A., & Chase, S. (1969). Analysis of stimulus generalization with a psychophysical method. *Journal of Experimental Psychology*, **80**, 215-224.
- Hoffman, K. (1960). Experimental manipulation of the orientational clock in birds. *Cold Spring Harbour Symposium on Quantitative Biology*, **25**, 379-387.
- Holder, M.D., & Roberts, S. (1985). Comparison of timing and classical conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 172-193.
- Hollis, K.L. (1984). The biological function of Pavlovian conditioning: The best defense is a good offense. *Journal of Experimental psychology: Animal Behavior Processes*, **10**, 413-425.
- Hollis, K.L. (1982). Pavlovian conditioning of signal-centered action patterns and autonomic behavior: A biological analysis of function. *Advances in the Study of Behavior*, **112**, 1-64.

- Honma, K., von Goetz, C., & Aschoff, J. (1983). Effects of restricted daily feeding on freerunning circadian rhythms in rats. *Physiology and behaviour*, **30**, 905-913.
- Jacklet, J.W. (1985). Neurobiology of circadian rhythm generators. *Trends in Neurosciences*, **8**, 69-73.
- Killeen, P.R., & Fetterman, J.G. (1988). A behavioral theory of timing. *Psychological Review*, **95**, 274-295.
- Kleber, E. (1935). Hat das Zeitgedachtnis der Bienen biologische Bedeutung? *Z. vergl. Physiol.*, **22**, 221-262.
- Koltermann, R. (1974). Periodicity in the activity and learning performance of the honey bee. In: L.B. Browne (Ed.) *The experimental analysis of insect behavior*. (pp. 218-226). Berlin: Springer.
- Kramer, T.J., & Rilling, M. (1970). Differential reinforcement of low rates: A selective critique. *Psychological Bulletin*, **74**, 224-254.
- LaBarbera, J.D., & Church, R.M. (1974). Magnitude of fear as a function of expected time to an aversive event. *Animal Learning & Behavior*, **2**, 199-202.
- Lang, J.W. (1976). Amphibious behavior of *Alligator mississippiensis*: Roles of a circadian rhythm and light. *Science*, **191**, 575-577.
- Libby, M.E., & Church, R.M. (1974). Timing of avoidance responses by rats. *Journal of the Experimental Analysis of Behavior*, **22**, 513-517.
- Maricq, A.V., & Church, R.M. (1983). The differential effects of haloperidol and methamphetamine on time estimation in the rat. *Psychopharmacology*, **79**, 10-15.
- Maricq, A.V., Roberts, S., & Church, R.M. (1981). Methamphetamine and time estimation. *Journal of Experimental Psychology: Animal Behavior Processes*, **7**, 18-30.
- Maricq, A.V. (1978). Some effects of lesions on the prefrontal cortex on timing behavior in the rat. Unpublished honours thesis, Brown University.

- Marimuthu, G., Subbaraj, R., & Chandrashekar, M.K. (1981). Social entrainment of the circadian rhythm in the flight activity of the microchiropteran bat *Hipposideros speoris*. *Behavioural Ecology and Sociobiology*, **8**, 147-150.
- Meck, W.H. (1983). Selective adjustment of the speed of internal clock and memory processes. *Journal of Experimental Psychology: Animal Behavior Processes*, **9**, 171-201.
- Meck, W.H., & Church, R.M. (1984). Simultaneous temporal processing. *Journal of Experimental Psychology: Animal Behavior Processes*, **10**, 1-29.
- Meck, W.H., Church, R.M., & Olton, D.S. (1984). Hippocampus, time, and memory. *Behavioral Neuroscience*, **98**, 3-22.
- Meck, W.H., & Church, R.M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes*, **9**, 320-334.
- Meck, W.H., & Church, R.M. (1982a). Abstraction of temporal attributes. *Journal of Experimental Psychology: Animal Behavior Processes*, **8**, 226-243.
- Meck, W.H., & Church, R.M. (1982b). Discrimination of intertrial intervals in cross-modal transfer of duration. *Bulletin of the Psychonomic Society*, **19**, 234-236.
- Menaker, M., & Zimmerman, N. (1976). Role of the pineal in the circadian system of birds. *American Zoologist*, **16**, 45-55.
- Mistlberger, R. (1993, in prep.). Circadian food-anticipatory activity: Formal models and psychological mechanisms.
- Mistlberger, R. E., & Rusak, B. (1988). Food-anticipatory circadian rhythms in rats with paraventricular and lateral hypothalamic ablations. *Journal of Biological Rhythms*, **3**, 277-291.
- Mistlberger, R. E., & Rechtschaffen, A. (1984). Recovery of anticipatory activity to restricted feeding in rats with ventromedial hypothalamic lesions. *Physiology & Behaviour*, **33**, 227-235.

- Moore, R.Y. (1982). The suprachiasmatic nucleus and the organization of a circadian system. *Trends in Neurosciences*, **5**, 404-407.
- Norgren, R.B. (1990). Neural basis of avian circadian rhythms. *Bird Behaviour*, **8**, 57-66.
- Ostheim, J. (1992). Coping with food-limited conditions: Feeding behavior, temperature preference, and nocturnal hypothermia in pigeons. *Physiology & Behavior*, **51**, 353-361.
- Pavlov, I.P. (1927). *Conditioned reflexes* (translated by G.V. Anrep). London: Oxford University Press.
- Pittendrigh, C.S. (1980). Some functional aspects of circadian pacemakers. In M. Suda, O. Hayaishi, & H. Nakagawa (Ed.), *Biological rhythms and their central mechanism* (pp. 3-12). New York: Elsevier.
- Pittendrigh, C.S. (1954). On temperature independence in the clock system controlling emergence time in *Drosophila*. *Proceedings of the National Academy of Science U.S.A.*, **40**, 1018-1029.
- Platt, J.R., Kuch, D.O., & Bitgood, S.C. (1973). Rats' lever-press duration as psychophysical judgements of time. *Journal of the Experimental Analysis of Behavior*, **19**, 239-250.
- Richter, C.P. (1922). A behaviouristic study of the activity of the rat. *Comparative Psychology Monographs*, **1**, 1-55.
- Roberts, S. (1983). Properties and function of an internal clock. In: R.L. Mellgren (Ed.), *Animal cognition and behavior* (pp. 345-397). Amsterdam: North-Holland.
- Roberts, S. (1982). Cross-modal use of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, **8**, 2-22.
- Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, **7**, 242-268.

- Roberts, S., & Church, R.M. (1978). Control of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, **4**, 318-337.
- Roberts, S., & Holder, M.D. (1985). Effect of classical conditioning on an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 194-214.
- Roberts, S., & Holder, M.D. (1984a). The function of time discrimination and classical conditioning. In: J. Gibbon and L. Allan (Eds.), *Timing and time perception* (pp. 228-241). New York: New York Academy of Sciences.
- Roberts, S., & Holder, M.D. (1984b). What starts an internal clock? *Journal of Experimental Psychology: Animal Behavior Processes*, **10**, 273-296.
- Roberts, S.K. (1965). Photoreception and entrainment of cockroach activity rhythms. *Science*, **148**, 958-960.
- Rusak, B. (1977). The role of the suprachiasmatic nuclei in the generation of circadian rhythms in the golden hamster, *Mesocricetus auratus*. *Journal of Comparative Physiology*, **118**, 145-164.
- Schneider, B.A. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior*, **12**, 677-687.
- Spetch, M.L. (1987). Systematic errors in pigeons' memory for event duration: Interaction between training and test delay. *Animal Learning & Behavior*, **15**, 1-5.
- Spetch, M.L., & Rusak, B. (1989). Pigeons' memory for event duration: Intertrial interval and delay effects. *Animal Learning & Behavior*, **17**, 147-156.
- Spetch, M.L., & Sinha, S.S. (1989). Proactive effects in pigeons' memory for event duration: Evidence for analogical retention. *Journal of Experimental Psychology: Animal Behavior Processes*, **15**, 347-357.

- Spetch, M.L., & Wilkie, D.M. (1983). Subjective shortening: A model of pigeons' memory for event duration. *Journal of Experimental Psychology: Animal Behavior Processes*, **9**, 14-30.
- Staddon, J. E. R. (1983). *Adaptive behavior and learning*. Cambridge: Cambridge University Press.
- Stubbs, D.A. (1968). The discrimination of stimulus duration by pigeons. *Journal of the Experimental Analysis of Behavior*, **11**, 223-238.
- Sulzman, F., Ellman, D., Fuller, C., Moore-Ede, M., & Wasser, G. (1984). *Neurospora* circadian rhythms in space: A reexamination of the endogenous-exogenous question. *Science*, **225**, 232-234.
- Takahashi, J.S., & Menaker, M. (1979). Brain mechanisms in avian circadian systems. In: M. Suda, O. Hayaishi, & H. Nakagawa (Eds.) *Biological rhythms and their central mechanism*. (pp. 95-109). Amsterdam: Elsevier.
- Turek, F.W. (1983). Neurobiology of circadian rhythms in mammals, *Bioscience*, **33**, 439-444.
- Wilkie, D.M. (1988). Proactive effects in pigeons' timing behavior: Implications for an internal-clock model. *Animal Learning & Behavior*, **16**, 132-136.
- Wilkie, D.M. (1987). Stimulus intensity affects pigeons' timing behavior: Implications for an internal clock model. *Animal Learning & Behavior*, **15**, 35-39.
- Wilkie, D.M., Saksida, L.M., Samson, P., & Lee, A. (In press). Properties of time-place learning by pigeons, *Columba livia*.
- Wilkie, D.M., & Willson, R.J. (1992). Time-place learning by pigeons, *Columba livia*. *Journal of the Experimental Analysis of Behavior*, **57**, 145-158.