

Timing

Most organisms must learn and store information about space and time in order to survive. The preceding chapter dealt with spatial cognition, and this chapter discusses temporal cognition. Most people have made observations that suggest that animals have a sense of time. Cats howl at feeding time each day, and dogs seem to wait expectantly at the door at about the time the mailman arrives. Wild animals are often reported to hunt at the time of day when their prey is most likely to make an appearance. Beyond casual observation, however, there is extensive experimental evidence to support the impression that animals are indeed sensitive to time of day.

TIME-PLACE LEARNING

Time of Day

If wild animals seek food in different places at different times of day, it should be possible to test this ability in the laboratory. Biebach, Gordijn, and Krebs (1985) carried out just such an experiment with garden warblers. A bird was housed in an experimental chamber that consisted of a central living room and four feeding rooms, any one of which could be entered from the living room (see Figure 8.1). Although all four feeding rooms contained feeders, only one feeder could be opened at a given time. If a warbler went to the correct room, it was allowed to open the feeder and eat from it for 20 seconds. After visiting a feeding room, a bird always had to return to the living room and stay there for 280 seconds before it could enter another feeding room. Access to food was allowed in different rooms at different times of day. Food was available in Room 1 from 0600 to 0900 hours, in Room 2 from 0900 to 1200 hours, in Room 3 from 1200 to 1500 hours, and in Room 4 from 1500 to 1800 hours.

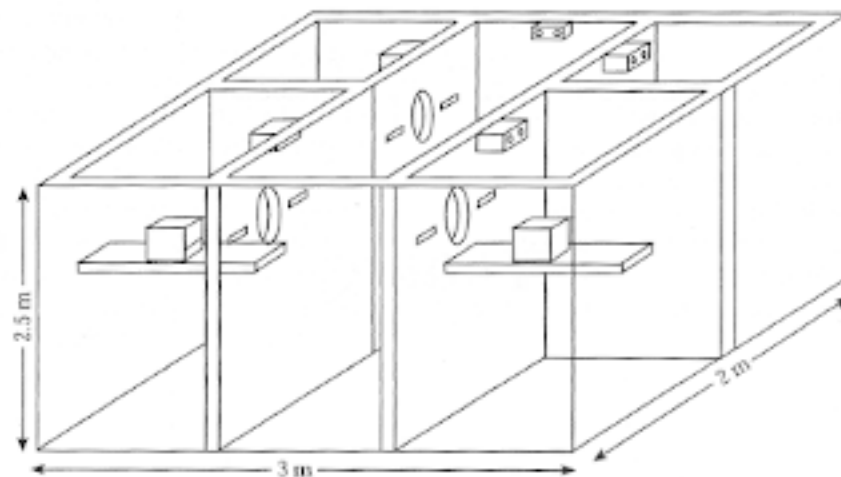


FIGURE 8.1. The experimental chamber used to study time-place learning in garden warblers. Birds could fly back and forth between a central living room and any one of four feeding rooms.

Within 10 days, all five birds trained learned to go to the rewarded room during the 3-hour period when food could be obtained in that room. These findings alone, however, do not prove that warblers associated food in a particular place with a particular time. Perhaps the birds initially sampled all four rooms until they found one that yielded food. They then stuck with this room until it failed to provide reward, at which time they sampled the other rooms until they found another one that contained food, and so on. Therefore, a critical test of time-place learning was carried out on two days on which all four rooms contained open feeders throughout the 12-hour period. As shown in Figure 8.2, birds made the majority of visits to each room during the time when that room had been rewarded during training. These data constitute an impressive demonstration of the effects of time-place training because the subjects could have obtained equal amounts of reward by going to the same room throughout the day or by visiting rooms randomly. Instead, the warblers regularly shifted from room to room at the time each room had been scheduled to yield food.

Circadian Time Cues

Changes in the environment provide salient circadian time cues both for people and animals. The change in illumination tells us when it is day and night, and the position of the sun in the sky acts as a clock during the day. In addition, internal or endogenous circadian cycles provide cues for time of day. For example, one's state of hunger may act as a rough indicator of time of day. It was suggested in Chapter 6 that the state of a circadian oscillator at the time of learning may act as a retrieval cue for memory of that learning. Endogenous oscillators refer to internal states of an organism that cycle through high and low states throughout the day. Examples are changes in rate of firing of neurons in the nervous system or changes in the concentrations of hormones in the blood stream.

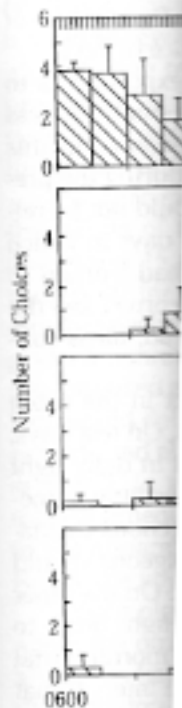


FIGURE 8.2. Frequent visits to Rooms 1, 2, 3, and 4 during the time when that room had been rewarded. The vertical line indicates the time of day.

Oscillators are involved in conscious, as well as unconscious, changes in internal states. Such changes are often referred to as circadian rhythms.

Endogenous oscillators are internal states of an organism that cycle through high and low states throughout the day. Although they are not necessarily conscious, they may have led to the evolution of food pecking. Although they are not necessarily conscious, they may have led to the evolution of food pecking. Although they are not necessarily conscious, they may have led to the evolution of food pecking. Although they are not necessarily conscious, they may have led to the evolution of food pecking.

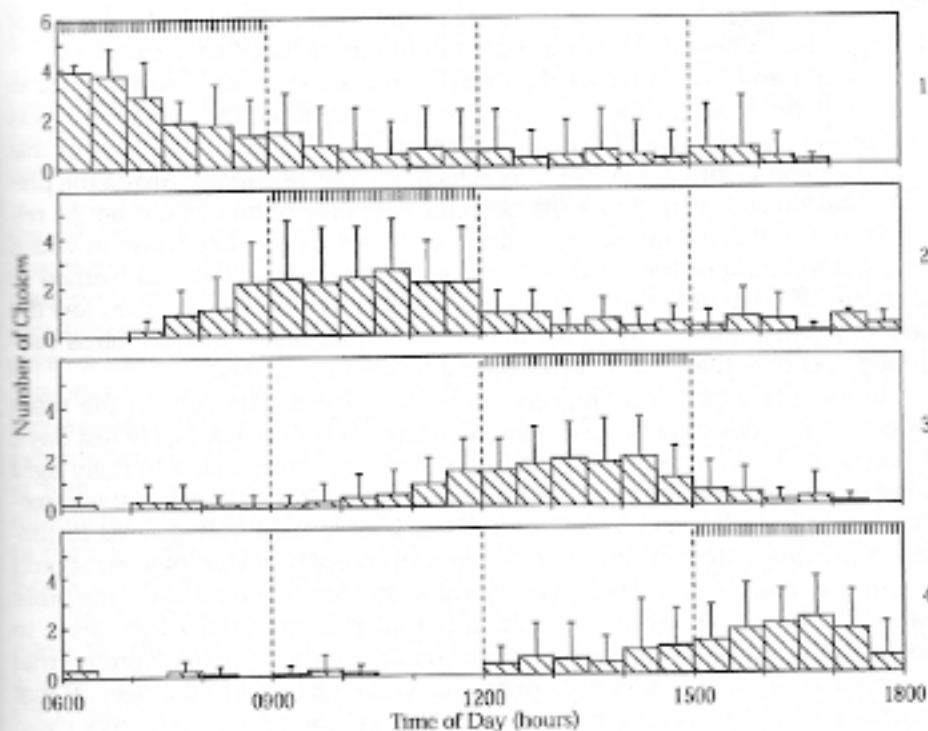


FIGURE 8.2. From top to bottom, the panels show the number of choices of feeding Rooms 1, 2, 3, and 4 over successive 3-hour periods from 0600 hours to 1800 hours. The vertical line above each bar is the standard deviation of five birds.

Oscillators affect behavior, such as changes in activity level, and state of consciousness, such as sleep and wakefulness. External circadian cues, particularly changes in illumination, act to *entrain* or maintain a regular oscillation of internal states. Such external modulators are called *zeitgebers* or "time givers."

Endogenous circadian cues would seem to be a prime candidate for explaining the time-place learning found in the Biebach et al. (1989) study. Birds may have learned to associate different internal states with the different locations of food. However, we cannot immediately rule out exogenous cues. Although the experiment was performed within an enclosed chamber, it is possible that warblers had access to environmental cues that might have controlled responding. A recent study by Saksida and Wilkie (1994) suggests such cues are not necessary. Saksida and Wilkie trained pigeons in an operant chamber that contained a pecking key on each of four walls. Birds were placed in this chamber for 17 minutes in the morning (about 0930 hours) and for 17 minutes in the afternoon (about 1600 hours). For the first minute of each session, no reward was delivered for key pecking. Thereafter, reward was delivered for key pecking, but Key 1 had to be pecked for reward in the morning, and Key 3 had to be pecked for reward in the afternoon. As warblers did in the Biebach et al. study, pigeons learned to peck Key 1 in the morning and Key 3 in the afternoon.

Of particular importance, these preferences appeared during the first minute of testing, when differential reward could not influence birds' choice of keys.

Saksida and Wilkie (1994) then carried out some control experiments to determine the basis for the pigeon's time-place learning. One possibility was that pigeons might have learned to alternate keys between sessions. In this case, a pigeon would remember only which key was rewarded during the previous session and then choose the alternate key; time of day would not be relevant. To test this hypothesis, pigeons were tested for blocks of days in which only the morning or the afternoon trial was given. If pigeons had learned to alternate, they should choose the correct key one day and the incorrect key the next day when tested only in the mornings or afternoons. Instead, birds continued to choose the correct key indicated by the time of day.

In another experiment, pigeons were *clock shifted*. The light in the room where the pigeons were housed normally came on at 0600 hours. On test days, it was shifted back 6 hours to 2400 hours. Although such a shift in daily light onset eventually entrains new endogenous rhythms, it should have little immediate effect on endogenous oscillators. If the state of these endogenous oscillators is providing time-of-day cues that control choice behavior, pigeons should continue to make correct choices on morning and afternoon tests. On the other hand, if pigeons were somehow timing the interval since daily light onset to determine which key was correct, errors should appear since the morning trial occurred at an interval after light onset that was equivalent to the interval that normally preceded the afternoon test in training. The results were very clear: pigeons continued to peck correct keys on both morning and afternoon tests. These findings suggest quite clearly that pigeons' place selection was controlled by the time of day as indicated by the state of endogenous circadian cues.

Interval Timing

Circadian timing is a mechanism by which an organism keeps track of the time of day. At specific temporal points within a 24-hour day, an animal may be affected by endogenous cues that establish a motivational state or retrieve a memory that prompts a particular behavioral act. In addition to this time-of-day timing, animals often need to keep track of short intervals of time that may elapse at any time of day. For example, foraging animals may pause in one location to search for prey for a fixed interval of time before moving to a new location. Each interval is timed to give the animal time to adequately search for potential food but also to keep it from becoming the target of a predator. Since the animal may forage at numerous times throughout the day, it must be able to time short intervals at any time. Some mechanism other than circadian cues is necessary to accomplish this interval timing.

To illustrate the phenomenon of interval timing, we examine some further experiments from Wilkie's laboratory that appear to be highly similar to the Saksida and Wilkie (1994) studies just discussed but that suggest a different timing process. In these experiments, all four of the keys mounted on different walls were used. Pigeons were placed in the apparatus for 60 minutes. During the first 15 minutes, pecking on Key 1 delivered reward; pecks on Key 2 produced reward during the next 15 minutes, and so on for Keys 3 and 4

(Wilkie & Wilkie 1994). It yielded reward for 15 minutes. During the next 15 minutes, pecking on Key 2 produced reward. This sequence was repeated, alternating between the next available key.

In other experiments, the effects of time-of-day cues were tested. Pigeons completed 15 trials, then the lights were turned off for 15 minutes. Any key peck during this period would deliver reward. Pigeons used the same key for the first 15 minutes of the period, but then switched to the next available key for the second 15 minutes. In the next 15 minutes, they switched to the next available key again. This sequence was repeated for the final 15 minutes of the period.

When pigeons were tested in the afternoon, the overall pattern of key pecking was similar to that in the morning. However, the overall pattern of key pecking was shifted relative to the time of day. This was true for the first 15 minutes of the period, but not for the second 15 minutes. This suggests that pigeons were able to time short intervals of time, but that they were also able to time these intervals relative to the time of day. This is consistent with the idea that pigeons use endogenous circadian cues to time their behavior relative to the time of day.

One of the most interesting findings of these studies was that the interval timing process was not affected by the time of day. This suggests that pigeons use a different mechanism to time short intervals of time than they use to time their behavior relative to the time of day. This is consistent with the idea that pigeons use endogenous circadian cues to time their behavior relative to the time of day.

(Wilkie & Willson, 1992). Pigeons learned to peck at each key during the time it yielded reward and then to switch to the next key near the end of 15 minutes. During test sessions, reward was omitted during the 5-minute periods preceding and following the points in time at which reward had been switched from one key to the next. Subjects continued to shift from one key to the next at approximately 15-minute intervals, showing time-place learning.

In other experiments, Wilkie, Saksida, Samson, and Lee (1994) examined the effects of introducing a timeout on time-place behavior. After pigeons completed 15 minutes of pecking on Key 1, the lights on all four keys were turned off for a 15-minute period during which no reward was delivered for any key pecks. The key lights then were turned back on, and the pigeons were given a nonrewarded 5-minute test during which they could peck any key. If pigeons used endogenous circadian cues to keep track of the time at which each key would deliver reward, they should have pecked Key 3 since two 15-minute periods had elapsed since the beginning of the session. Instead, pigeons pecked at Key 2. In another experiment, the same procedure was used, but the 15-minute timeout was spent in the pigeons' home cage. When they were returned to the apparatus, they pecked Key 1. In neither experiment did pigeons peck Key 3, the key that should have been indicated by endogenous cues.

When pigeons were trained to peck different keys in the morning and afternoon, the omission of opportunity to peck a key in either the morning or the afternoon had no effect on control of behavior by time-of-day cues. However, the omission of a 15-minute opportunity to peck a key when the rewarded key was shifted every 15 minutes led to very different behavior—either pecking the key that was appropriate at the beginning of the timeout or returning to the key that was correct at the beginning of the session. The difference between these phenomena is explained by the large difference in the lengths of the time periods during which keys deliver reward. When the location of reward stays fixed for periods of 3 hours, as in the Biebach et al. (1989) experiment, or during morning versus afternoon sessions, animals use endogenous circadian cues to determine time and the correct location of food. When the location of reward changes every 15 minutes, however, changes in endogenous circadian cues are not sufficient to allow such fine temporal discriminations. Yet, pigeons clearly were able to learn the different locations of correct keys that changed every 15 minutes. To do this, it appears that animals use a quite different timing system: *interval timing*. In interval timing, the subject keeps track of the amount of time that has elapsed since the beginning of an event, such as the beginning of a trial or a session. Thus, pigeons in the Wilkie and Willson (1992) and Wilkie et al. (1994) studies timed successive 15-minute intervals from the start of a session and switched keys at the appropriate times.

One theory of interval timing suggests that animals accomplish the timing of intervals by the use of an *internal clock* (Church, 1978). The theory suggests that the internal clock has many of the properties of a common stopwatch. Thus, it may be stopped at a particular value for a period of time and then restarted at that value, or it may be stopped and reset back to zero for timing a new interval. These properties may help us understand the effects found in the Wilkie et al. (1994) experiment. Pigeons given a 15-minute timeout in the apparatus after completing 15 minutes of pecking on Key 1 then pecked Key 2 when

the keys were relit. If the internal clock was stopped for the 15-minute period and began to run again when the keys were relit, the time on the internal clock would indicate that the subject was in the second 15-minute period and should peck Key 2. On the other hand, removing the pigeon from the apparatus may have signaled that the session was completed and that the internal clock should be reset to zero. When the subject was returned to the apparatus 15 minutes later, it would begin timing the first 15-minute interval again, and Key 1 should be the appropriate key to peck.

Considerable data and theory on interval timing in animals has accumulated over the past 20 years, and a number of timing phenomena can be understood by theories of the internal clock. In the remainder of this chapter, these issues are discussed in some detail.

PROCEDURES FOR THE STUDY OF TIMING IN ANIMALS

Methods for studying interval timing in animals usually consist of *discrimination procedures* or *production procedures*. *Discrimination procedures* require a subject to respond differentially to signals that vary in their length of presentation. In the case of *production procedures*, the subject actually tells the experimenter its estimate of a time interval through its behavior. As we shall see, the development of the *peak procedure* provided a particularly powerful production tool for determining behavioral estimates of time in animals.

Discrimination Procedures

In some early studies of time discrimination in rats, an animal was trained in an apparatus in which it could enter a left or right chamber after first being delayed for some period of time in a delay chamber. Cowles and Finan (1942) rewarded rats for choosing one door of a discrimination apparatus after a delay of 10 seconds and rewarded choice of another door after a delay of 30 seconds. Six out of nine rats were able to learn this problem to above a chance level of accuracy. In a similar experiment, Heron (1949) trained rats to discriminate between intervals of 5 and 45 seconds and then gradually reduced the length of the longer interval. The number of animals that could maintain this discrimination dropped progressively until only 1 of the 11 rats that learned the initial discrimination could discriminate between intervals of 5 and 10 seconds.

In a more modern version of this type of experiment, an operant chamber is used, and rats are presented with a signal—a houselight or a noise—that lasts for a “short” period of time or a “long” period of time (Meck, 1983; S. Roberts & Church, 1978). When the signal ends, two retractable levers emerge from the wall of the chamber. One lever is correct after the short signal, and the other lever is correct after the long signal. It should be realized that “short” and “long” are defined on a relative basis by the experimenter. Thus, 10 seconds is the long stimulus if 2 seconds is the short stimulus, but 10 seconds is the short stimulus if 50 seconds is the long stimulus.

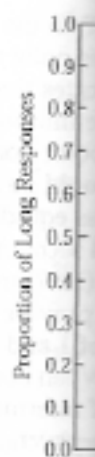


FIGURE 8.3. A plot of the proportion of long responses as a function of the duration of the signal. The midpoint is 8 seconds.

As an example, two white noise durations of 2 and 8 seconds are required to reach a level of 0.5. After the short (short) lever is moved, a signal, food is delivered. In a discrimination task, about 10 sessions are required once a discrimination subject's response is between 2 and 8 seconds. At signal duration, the response to either the short or long lever is plotted. The curve can be plotted as a function of signal duration. The *peak procedure* is a function of signal duration, and subjects usually learn to discriminate which judgment is longer duration.

An important feature of the *peak procedure* is that the subject can discriminate the test duration (short) or the right or long training stimulus at which the

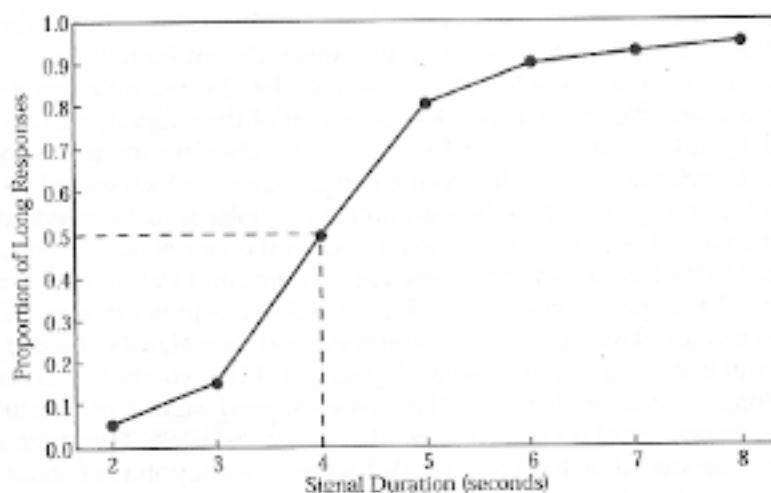


FIGURE 8.3. A psychophysical curve based on hypothetical data showing the proportion of choices of the "long" response following test stimuli varying from 2 to 8 seconds in duration. The broken lines show determination of the subjective midpoint.

As an example of such an experiment, suppose that rats are presented with two white noise signals that last for either 2 seconds or 8 seconds. The two durations of noise occur in a random order, and a response to the right or left lever is required after each noise signal. After the 2-second signal, the left (short) lever must be pressed for the rat to earn a food pellet. After the 8-second signal, food is delivered for a press on the right (long) lever. Rats acquire this discrimination readily and respond at 90 percent or greater accuracy after about 10 sessions of training. A typical psychophysical procedure followed once a discrimination between extreme durations has been formed is to test the subject's response to intermediate durations. While the original discrimination between 2 and 8 seconds is maintained, probe test trials are occasionally given at signal durations of 2, 3, 4, 5, 6, 7, and 8 seconds. No reward is given for response to either lever on these test trials, but the subject's choice of the short or long lever is recorded. After sufficient test trials have been carried out, a curve can be plotted that shows the proportion of responses to the long lever as a function of signal duration (see Figure 8.3). This curve is called a *psychophysical function*, and its shape is an *ogive*; it starts out with a flat portion, over which subjects usually choose the short lever, then rises rapidly, over durations in which judgments change from short to long responses, and flattens out at longer durations, in which subjects regularly choose the long lever.

An important property of the ogive shown in Figure 8.3 is that we can estimate the *subjective midpoint* of the curve. The subjective midpoint is that value on the test dimension at which the subject is equally likely to press the left (short) or the right (long) lever, thus indicating it is midway between the short and long training stimuli. We calculate the subjective midpoint as the test stimulus at which the subject shows indifference between the short and long keys.

A line is drawn parallel to the abscissa from the 50 percent point on the ordinate to the psychophysical curve. A vertical line is drawn from this point to the abscissa, and the point at which the curve hits the abscissa indicates the subjective midpoint. Notice that such an estimation of the subjective midpoint in Figure 8.3 yields a value of about 4 seconds. The subjective midpoint does not occur at the arithmetic mean between 2 and 8 seconds, which would be 5 seconds. In fact, rats judged that the duration of the noise signal was equidistant in time between 2 and 8 seconds when it had been on for about 4 seconds.

This finding has considerable generality. Church and Deluty (1977) trained rats in a lighted operant chamber and darkened the chamber to provide short and long signals. Rats were trained with short and long signals of 1 and 4 seconds, 2 and 8 seconds, 3 and 12 seconds, and 4 and 16 seconds. When accurate discrimination between these durations was achieved, signals of intermediate length were presented during nonrewarded probe test trials. The psychophysical curves produced by test trials yielded subjective midpoints of about 2 seconds between 1 and 4 seconds, 4 seconds between 2 and 8 seconds, 6 seconds between 3 and 12 seconds, and 8 seconds between 4 and 16 seconds. Notice that a pattern appears in these data that allows us to predict the subjective midpoint. The subjective midpoint has the same ratio to the short duration as the long duration has to the subjective midpoint. Thus the ratio of $4/2$ is the same as the ratio $8/4$. The subjective midpoint is the geometric mean of the short and long stimuli, as calculated by the square root of their product. Thus the square root of $2 \times 8 = 16$ is 4. Comparable data from pigeons similarly suggest that the subjective midpoint falls at the geometric mean of training durations (Gibbon, 1986; Platt & Davis, 1983; Stubbs, 1976).

Production Procedures

Fixed-Interval Responding

Some well-known conditioning experiments originally performed by Pavlov (1927) involved delay conditioning and temporal conditioning. In delay conditioning, the CS precedes the food by a constant interval of time; in temporal conditioning, no CS is presented, and the food US is delivered to the dog at regular time intervals. With both procedures, dogs typically inhibit salivating during the interval preceding the US but salivate copiously just before food delivery. This result is a form of inhibition of delay, as discussed in Chapter 5. One interpretation of this finding is that the dog learned to time the interval between the CS and US in delay conditioning or between food deliveries in temporal conditioning.

In operant conditioning, a similar example is found in the behavior generated by a fixed-interval (FI) schedule of reinforcement. In this schedule, a response yields reward only after a fixed interval of time has passed since the preceding reward. An animal well trained on an FI schedule shows the scalloped cumulative response curve found in Figure 8.4. Rate of response is very low during the initial part of the interval but accelerates during the latter part of the interval. This behavior maximizes the rate of reward collection but tends to minimize effort; an ability to time the FI should lead to little response at the beginning of the interval, when it is clearly too early to obtain food, and frequent response at the end of the interval so that the reward may be obtained as soon



FIGURE 8.4. The scallop is shown acceleration of

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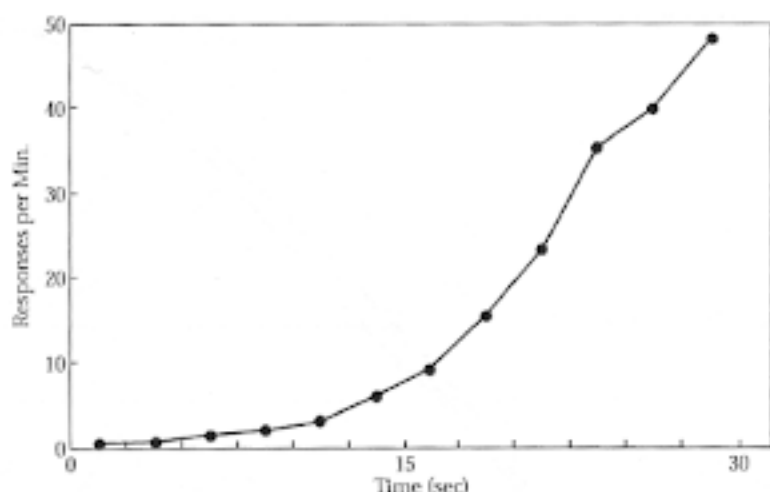


FIGURE 8.4. The increase in rate of responding over an FI 30-second period. The scallop is shown in the low rate of responding over the first 15 seconds and the rapid acceleration of responding over the last 15 seconds.

as it becomes available. The smooth curve shown in Figure 8.4 is produced by averaging data from a number of trials in which animals begin responding at different times around the midpoint of the FI. The importance of averaging data from trials with different start times is emphasized further in the theoretical section at the end of this chapter.

Similar behavior is seen when a form of temporal aversive conditioning is used. Free-operant avoidance conditioning involves schedules in which shock follows each response by a fixed interval of time, and shock can be delayed only by another response. If the response-shock interval is 20 seconds, rats learn to respond very little during the first 10 seconds after a response, but the probability of a response increases progressively as the last 10 seconds of the interval elapse (Gibbon, 1972; Libby & Church, 1974). In this way, both punishment and effort are minimized.

In a number of different interval timing situations involving production, the *proportionality result* has been found (Dews, 1970; Church, 1978; Gibbon, 1977). If animals are trained under different FI schedules for food reward, a family of scalloped curves can be plotted, with the period of low responding extending further into the interval the longer the FI. The proportionality principle tells us that curves obtained under different FIs can be transformed to duplicate one another by plotting response rate as a proportion of the terminal rate and time as a proportion of the length of the FI. An impressive example of proportionality is seen in Figure 8.5, taken from Dews (1970). Three curves are shown based on pigeons' behavior under FI schedules involving intervals between reinforcements of 30, 300, and 3,000 seconds. When a relative time scale is used, and when rate of response is based on proportion of terminal rate, the curves for the three FIs are virtually identical. Similar instances of proportionality are found in experiments in which aversive stimulation is delivered at regular intervals (LaBarbera & Church, 1974; Libby & Church, 1974).

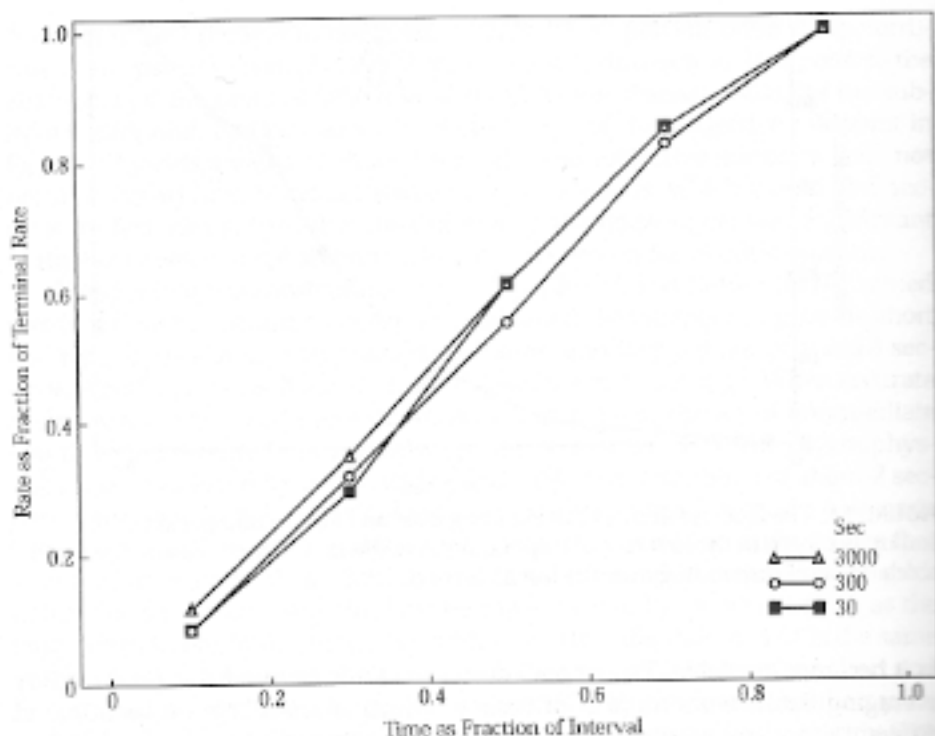


FIGURE 8.5. Rate of response throughout FIs of 30, 300, and 3,000 seconds. The abscissa plots time as a proportion of the total FI, and the ordinate plots rate of response as a proportion of the terminal rate of response under each FI.

An important theoretical implication that has been drawn from these repeated demonstrations of proportionality is that animal timing is based on a scalar process (Church & Gibbon, 1982; Gibbon, 1972; 1977; 1991; Gibbon & Church, 1981). Scalar timing suggests that animals use the fixed interval in effect during a particular phase of training as a base time or unit of measurement. A ratio is computed between the absolute time elapsing within an interval and the base time, and response decisions are determined by the ratio of times. Thus, after 20 seconds have elapsed in a 40-second FI, an animal responds at about the same rate as it would after 10 seconds have elapsed in a 20-second FI because the ratio between the base time and the time elapsed is 2:1 in both instances.

The Peak Procedure

Based on a procedure originally used by Catania (1970), Seth Roberts (1981) introduced an important new technique for studying timing in animals: the *peak procedure*. Rats were trained to time light and noise signals by rewarding responding according to different FI schedules in the presence of the two signals. During training of performance under FI schedules, occasional probe trials called *empty trials* were inserted among the FI trials. Either the light or the noise signal was presented, no reward was given, and the trial extended a



FIGURE 8.6. (bottom graph) Mean rate of response throughout FIs of 30, 300, and 3,000 seconds. (top graph) Rate of response throughout FIs of 30, 300, and 3,000 seconds.

considerable time. The animal responded throughout the trial and then died. Some of the upper graph shows the mean rate of response to FIs of 20 seconds. It signaled the reward. When indicating the

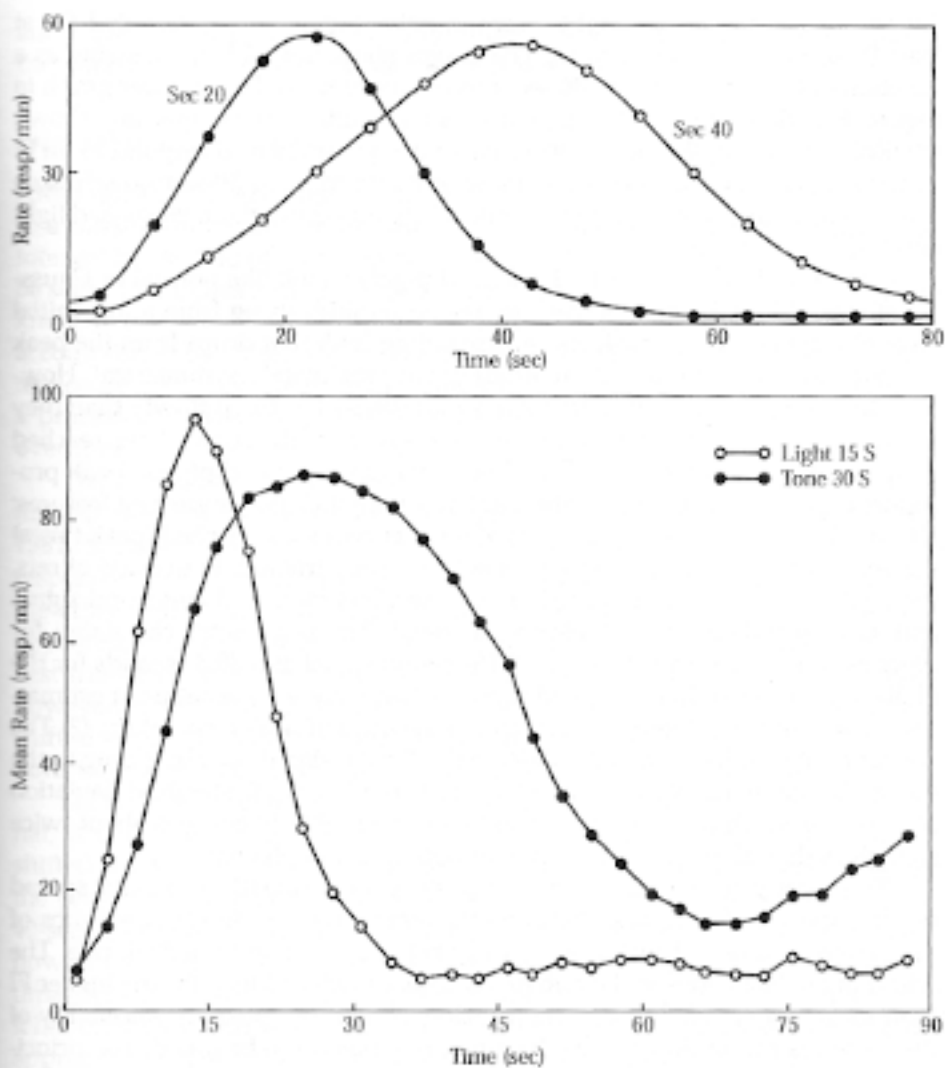


FIGURE 8.6. Data gathered with the peak procedure from rats (top graph) and pigeons (bottom graph). Rate of response is plotted as a function of time on empty trials for light and sound signals that correspond to FIs of different length.

considerable time beyond the length of the FI. Rate of response was observed throughout the empty trial. It peaked at a point very close to the value of the FI and then declined as the trial continued beyond this interval.

Some typical data from the peak procedure are shown in Figure 8.6. The upper graph shows data from rats trained with two signals that corresponded to FIs of 20 and 40 seconds (S. Roberts, 1981). Whenever a houselight came on, it signaled a 20-second FI; the first lever press after 20 seconds would yield reward. When a white noise signal was sounded, it signaled a 40-second FI, indicating that reward could be obtained for the first response after 40 seconds.

On empty trials, the houselight or white noise signals were presented for at least 80 seconds without reward. The curves show rate of lever pressing as a function of time over the first 80 seconds of empty trials. In the lower graph in Figure 8.6, data taken from pigeons using similar procedures are shown (W. Roberts, Cheng & Cohen, 1989). Pigeons were trained to respond to an FI 15-second schedule signaled by a houselight and to an FI 30-second schedule signaled by a tone. The curves show rate of pecking throughout 90-second light and tone empty trials.

Note that the curves for both rats and pigeons look like normal or Gaussian curves. All of the curves have an ascending limb rising from a low initial level of response to the peak and a descending limb that drops from the peak to a low level of response. These limbs are approximately symmetrical. However, in the pigeon data, the curves descend somewhat more slowly than they ascend, and there is a tail of continued response after the curves have reached the bottom of the descending limb. These data from rat and pigeon peak procedure experiments are remarkably similar and contain two important features: (1) The times at which the peak rates of these curves were reached (peak times) are very close to the FIs under which subjects were trained. In the case of rats, the peak times were calculated to be 22.0 seconds for the FI 20-second signal and 41.1 seconds for the FI 40-second signal. The peak times calculated for pigeons were 15.2 seconds for the FI 15-second signal and 30.3 seconds for the FI 30-second signal. Both rats and pigeons then were very accurate at estimating the length of the interval to reward on the basis of peak responding. (2) The spread of the curves is considerably greater for the signal corresponding to the longer FI than to the shorter FI. In fact, a calculation of the standard deviation of these curves shows that the variability of the higher FI curve is about twice as high as that of the lower FI curve for both rats and pigeons.

This same principle can be seen visually by observing the horizontal spread of the curves or the distance between the ascending and descending limbs of each curve at a rate of response midway between zero and the peak rate. The width of the line between the two limbs is about twice as long for the higher FI than for the lower FI. The general principle is that the spread or variability of the curves is proportional to the length of the interval to be timed. The principle of proportionality then extends to the variability of peak time curves. This observation may be recognized as an instance of *Weber's law*. When making estimates of the size of points along a dimension that increases in magnitude (such as time), the variability of estimation increases proportionally to the magnitude of the point estimated (Cheng & W. Roberts, 1991; Gibbon, 1977).

PROPERTIES OF THE INTERNAL CLOCK

Various fundamental questions about timing in animals have been addressed experimentally, and the answers generally suggest that the internal clock used for interval timing has many of the properties of a common stopwatch (S. Roberts & Church, 1978). Some of the well-known properties of a stopwatch are that it usually times up from zero to some finite amount of time, it can be stopped and either reset to zero or restarted at the time it was stopped,

and it can time the interval of

Direction of

Although a stimulus interval by itself can be set at 50 ms, we know that the system could grow a process of over time to

The direction of the signal is not important. In fact, rats will respond to a tone when the other signal appeared, even if the test trials are shifted to the conditions indicated

Let us take the example of a 40-second signal, which is shifted from the time of the 40-second signal to now in effect a 5-second timer when it has only 5 seconds appropriate second signal

The use of the 40-second signal is gone by and in this case, peak response to the second signal is second signal

In Figure 8.6, the 20-second and 40-second signals were shifted to 5, 10, or 15 seconds

Direction of Timing

Although a stopwatch times up, many other timers time down. The countdown to a missile launch is down-timing. Turning over an hourglass and timing an interval by the loss of its contents is down-timing, and an oven clock that may be set at 50 minutes and then times down to zero is a down-timer. Although we know that the internal clock accurately times fixed intervals, this could be accomplished by either up- or down-timing. Some process in the nervous system could grow over time until a magnitude criterion is reached (up-timing), or a process of a fixed magnitude established by reinforcement could dwindle over time to zero (down-timing).

The direction of timing was examined in experiments that involved shifting rats midway through a trial from one FI schedule to another (S. Roberts, 1981; S. Roberts & Church, 1978). In S. Roberts' study, rats were trained to respond to two FIs, with one signal (light or noise) indicating FI 20 seconds and the other signal indicating FI 40 seconds. When clear patterns of FI scalloping appeared, empty trial tests were carried out, and peaks near the FIs were found. Test trials then were performed that always began with the 20-second signal; however, after 5, 10, or 15 seconds of the 20-second signal, an animal was shifted to the 40-second signal. Peak curves obtained under these shift conditions indicated when the animal expected to receive reinforcement.

Let us take the case in which 15 seconds have elapsed in the 20-second signal, at which time a rat is shifted to the 40-second signal. When the animal is shifted from the 20-second signal to the 40-second signal, it is presumed that the time accumulated during the 20-second signal is transferred to timing the 40-second signal. However, a new criterion dictated by the 40-second signal is now in effect. If a down timer was used, only 5 seconds should be left on the timer when the switch to 40 seconds occurs. It should seem to the animal that it has only 5 seconds left to reach the 40-second criterion, and it should respond appropriately. The peak of response then should appear 5 seconds after the 40-second signal started or 20 seconds from the start of the 20-second signal.

The use of an up timer leads to quite a different prediction. When switched to the 40-second signal, the internal clock should indicate that 15 seconds have gone by and that 25 seconds are left to reach the 40-second criterion. In this case, peak response should not appear until 25 seconds have gone by on the 40-second signal or until 40 seconds have elapsed since the beginning of the 20-second signal.

In Figure 8.7, response rate is plotted as a function of time both for the 20-second and 40-second signals. Note that response rate dropped when rats were shifted from the 20-second signal to the 40-second signal after 10 and 15 seconds, indicating that animals were adjusting their response rate downward for that amount of time into the 40-second signal. Of primary importance, peak response occurred at about 40 seconds regardless of whether the shift occurred at 5, 10, or 15 seconds. These findings suggest that rats timed up to 5, 10, or 15 seconds during the 20-second signal and then continued to time up when

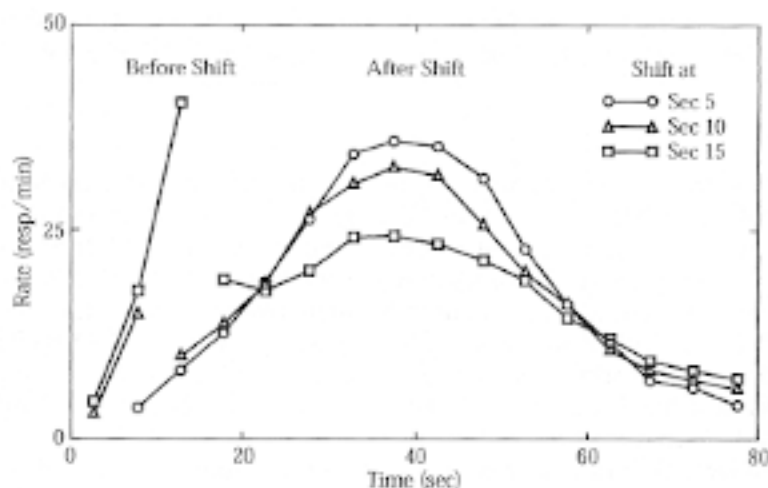


FIGURE 8.7. Mean rates of response over time on the 20-second signal before the shift and on the 40-second signal after the shift. Rats showed peak response at around 40 seconds after each shift, indicating that they were using an up timer.

shifted to the 40-second signal, having shifted the criterion time for reinforcement from 20 seconds to 40 seconds when the signals changed.

Note that the results of this experiment indicate that rats added time that passed in the presence of the second signal to time that had accumulated in the presence of the first signal. There are two important properties of the internal clock shown by this outcome. First, the continuity of timing indicates that the timer added the time from these two signals together. This was not the necessary outcome of the experiment; rats could have reset the internal clock back to zero when a signal in a new sensory modality was presented. Second, the fact that time continued to accumulate across a switch from noise to light or vice versa suggests that the internal clock is centrally located in the nervous system and is readily accessed by different sensory modalities. It also indicates that time is an abstract property that animals represent independently of other properties of a signal, such as whether the signal is a light or a noise (Meck & Church, 1982).

Timing through a Gap

Suppose you were asked to use a stopwatch to measure how much time a friend of yours took to run a mile. However, during the run, your friend stopped for several seconds to have a drink of water. You are faced with a decision: Should you keep the watch running during the water break and count this time as part of the run, or should you stop the stopwatch during the drink and restart it when your friend begins to run again, thus counting only the time your friend is actually running? Fortunately, most modern stopwatches give you the option between these two possibilities. It is possible either to keep the

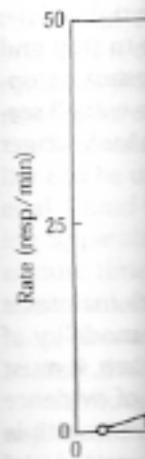


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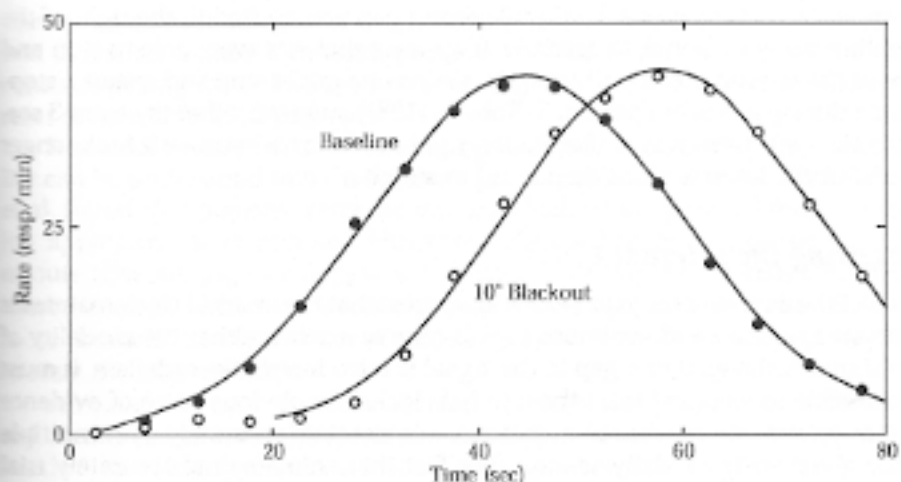


FIGURE 8.8. The mean response rate of bar pressing in rats over time on empty trials. The baseline curve comes from trials in which the houselight signal was presented without interruption. The 10-second blackout curve shows the effect of a 10-second timeout introduced 10 or 15 seconds after the houselight came on.

watch running or to stop the watch for a timeout and then to restart it at the point where it was stopped.

A question very similar to this one has been asked of the rat's internal clock. Once an animal begins to time a signal, what happens if a timeout is introduced in the middle of the signal? S. Roberts (1981) carried out an experiment in which the onset of a houselight initiated a trial, with food primed to be delivered at the first response made after 40 seconds (an FI 40-second schedule). On empty test trials, the houselight stayed on for at least 80 seconds, and no reward was delivered. On selected empty trials, gaps were introduced by blacking out the experimental chamber for 10 seconds after the light had been on for 10 or 15 seconds. The question of interest is how a rat responds to this gap or timeout in the light signal to be timed. One possibility is that it will continue to run the internal clock during the gap; in this case, its rate of responding should peak at 40 seconds after the signal began, and there should be no difference between response curves on empty trials with and without gaps. Another possibility is that a rat will stop the internal clock during the gap and restart it when the light comes back on; if it does this, the response curve for empty trials with a timeout should be shifted to the right of one for empty trials without a timeout. Still a third possibility is that the rat might reset the internal clock back to zero when the gap is introduced and start timing the signal all over again when the light is relit. If it reset the internal clock, the peak response rate should be shifted far beyond 40 seconds since the initial houselight time of 10 or 15 seconds and the timeout time of 10 seconds would be added to the regular signal time of 40 seconds before the peak would be reached.

The result of the experiment was quite clear, as can be seen in Figure 8.8. The curve for baseline or empty trials without a gap peaked at slightly over

40 seconds, and the curve for the 10-second gap was shifted to the right of the baseline curve by about 13 seconds. It appears that rats were able to stop and restart the internal clock during a gap, just as one might stop and restart a stopwatch during a timeout period. S. Roberts (1981) suggested that the extra 3 seconds the gap curve was shifted to the right might arise because it took longer to restart the internal clock than it did to stop it.

Resetting the Internal Clock

Both of the experiments just described suggest that the internal clock maintains time accumulated and continues to add time to it when either the modality of the signal is changed or a gap in the signal is introduced. Nevertheless, it must be possible to stop and reset the internal clock. The obvious piece of evidence that supports this conclusion is that animals can time accurately over multiple trials given within a daily session. The fact that animals time accurately trial after trial suggests that the clock is reset at the end of each trial. Presumably, salient signals for the end of a trial provide a resetting instruction. The most obvious signals are the delivery of reward and the introduction of the intertrial interval. If one of these signals is omitted, it should adversely affect timing on the next trial.

In fact, a phenomenon known as the *omission effect* suggests just such an outcome. If animals are trained to respond to an FI schedule over a series of trials, omission of reinforcement at the end of one trial leads to acceleration of responding on the next trial (Staddon & Innis, 1969). The omission effect may be explained as a failure to completely reset the internal clock between trials (S. Roberts, 1981; Staddon, 1974). If food delivery and the intertrial interval act as signals for resetting the internal clock, omission of food means the signal is incomplete, and the clock may be only partially reset. Since some time is then already on the clock at the beginning of the next trial, the FI seems to have timed out to the animal at a point that is short of the interval for food delivery on the experimenter's clock. The effect of this mismatch between internal and external clocks should be a shift of the response rate function to the left and an increased rate of responding early in the interval.

In an experiment carried out by S. Roberts (1981), the peak procedure was used to examine the omission effect. Reward was omitted on trials in which rats had to time an FI 40-second signal, and the effect of reward omission was observed during an empty test trial that followed the trial on which reward was omitted. It was found that rats responded sooner and reached a peak time earlier on empty trials following the omission of reward than on baseline empty control trials in which the reward was given on the preceding trial. Removing the reward at the end of an FI then appears to prevent the internal clock from completely resetting. It appears that reward, along with the intertrial interval, acts as a strong signal that normally resets the internal clock to zero and allows accurate timing trial after trial.

The modality switch experiment, the gap experiment, and the omission effect taken together suggest that the internal clock is quite flexible and has many of the properties of a common stopwatch. We have seen that it times up,

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that it can continuously time events signaled to different sensory modalities, and that it can hold a time setting over a timeout or gap in a signal and then continue timing after the signal resumes. Furthermore, it can be stopped and reset to zero by end-of-trial cues.

It should be noticed that the findings of Wilkie et al. (1994) discussed earlier can be understood in terms of these properties of the internal clock. Wilkie et al. found that pigeons reset the internal clock when removed from the testing apparatus for 15 minutes. However, when left in the apparatus for a 15-minute timeout, pigeons appeared to stop and restart the internal clock from where it left off. Although a timeout may only temporarily stop the clock, the more dramatic change in cues provided by a return to the home cage appears to reset the internal clock.

Although we have casually ascribed a number of properties to the internal clock, more formal theoretical development of the internal clock is needed to understand how it can accomplish the timing feats thus far described. In the following section, theoretical models of the internal clock are presented.

THEORIES OF INTERVAL TIMING

We usually keep track of time by noting changes in some physical indicator. The numbers on a digital clock or the positions of the hands on an analog clock tell us the time of day or measure elapsed time. Without these modern instruments, the position of the sun in the sky or the position its shadow casts upon a sundial may be used to measure time. In our discussion of time-place learning experiments, it was held that changes in the states of internal circadian oscillators are used to determine time of day. Theories about the ability of animals to time intervals precisely are based on an internal clock. These appear to some dynamic or changing process within the organism that may form a basis for time detection. A popular conceptualization is that the internal clock is driven by a neural *pacemaker* that regularly emits pulses. Two well-known theories of animal timing are based on this premise: the *behavioral theory of timing* and the *scalar timing theory*.

Behavioral Theory of Timing

According to the behavioral theory of timing advanced by Killeen and Fetterman (1988; 1993), a pacemaker emits pulses at successive points in time according to a Poisson distribution with a fixed mean probability. The cumulation of several pulses then drives behavioral states of the organism, which give rise to different classes of overt behavior. These classes of behavior are referred to as *adjunctive behaviors*—common forms of behavior performed by an animal that do not result in reinforcement. For example, a pigeon might be driven by the cumulation of pulses first to enter a state in which it pecks a wall, then to advance to a state in which it bobs its head, and finally to advance to a state in which it flaps its wings. If key pecking is reinforced with food during any of these states, that state comes to control or act as a discriminative stimulus for

key pecking. Suppose the pigeon is reinforced for key pecking while wing flapping. It learns to peck the key whenever the wing flapping class of response is made. On subsequent tests, the beginning of a timing signal initiates the pacemaker, and its successive pulses drive the subject through different behavioral states until it reaches wing flapping and the peck response is made. Because it takes the subject approximately the same amount of time to cycle through different behavioral states each trial, the subject's own behavioral state can act as an interval timing device.

Scalar Timing Theory

Scalar timing theory is also based on the activity of a pacemaker but suggests that timing is controlled by more central, computational processes. Because this theory is somewhat more developed and related to a number of empirical studies, it is presented and discussed in some detail. An information processing model of scalar timing is presented in Figure 8.9. Three different stages of the behavioral act of timing involve successively a clock process, a memory process, and a decision process. The clock process consists of a pacemaker that emits pulses at a constant average rate and an accumulator in which those pulses accumulate. Of critical importance, the flow of pulses from the pacemaker to the accumulator is controlled by an intermediate switch. Only when the switch is closed are pulses transmitted to the accumulator, and pulses cease to enter the accumulator when the switch is opened. Through learning, an external signal to be timed comes to control the switch, thereby closing the switch when it comes on and opening it when it goes off. The total pulses in the accumulator at the end of presentation of a signal are then correlated with the length of the signal and can be used to time the signal.

Information from the accumulator in the form of total pulses is then transmitted to working memory. Information in working memory may be transmitted to reference memory. The pulse total present in working memory when a response is rewarded is stored in reference memory. Finally, at the decision level, the current pulse count in working memory is transmitted to a comparator, as is a sampled value from the distribution of pulse totals in reference memory. The comparator process compares the working memory and reference memory totals. If the values match or are close to a match, a yes decision to respond is made; a rat begins to press a lever, or a pigeon starts to peck a key. If the values do not approach a match, a no decision is made, and responding is withheld.

The comparator process is carried out by calculating a ratio between the absolute value of the difference between the pulse total sampled from reference memory (RM) and the pulse total in working memory (WM) divided by the RM total. The decision ratio (DR) then is calculated as $DR = |RM - WM| / RM$. Note two things about this formula. First, by taking the absolute value of $RM - WM$, it makes no difference whether $RM > WM$ or $WM > RM$; only the absolute difference between them is used. Second, the numerator of the ratio, and hence the ratio, equals zero when $RM = WM$. Therefore, a decision that RM matches WM should occur as the DR approaches zero. The



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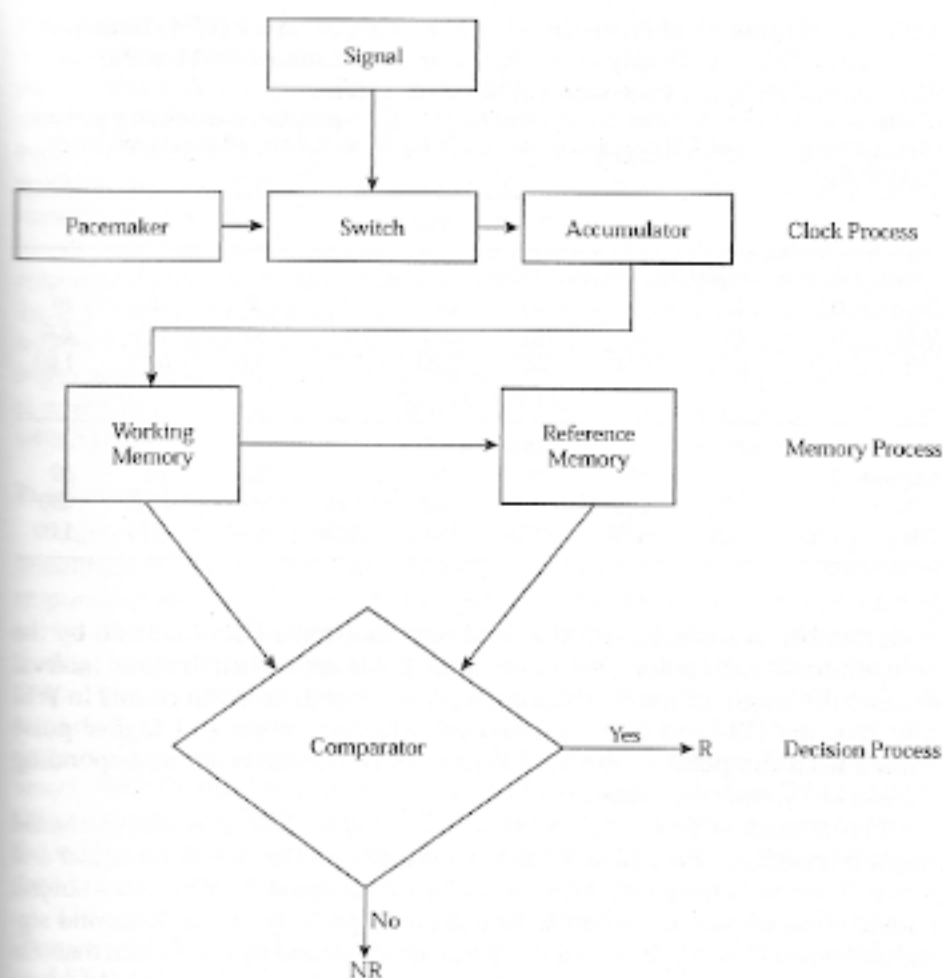


FIGURE 8.9. An information processing model for timing behavior that contains three processes: a clock process, a memory process, and a decision process.

model handles this decision by assuming that there is a threshold, b , above which no response occurs and below which the subject responds. Thus, when DR drops to b or less, the subject should begin to emit the operant response that indicates it is at or near the reinforced time interval.

The scalar timing model is now shown using a numerical example to help you better understand how it works. Two examples of timing on empty trials are shown in Table 8.1—one for timing after a subject has been trained with a signal that yields reward on an FI 20-second schedule and the other for timing a signal that indicates reward on an FI 40-second schedule. Let us assume that the pacemaker emits pulses at the rate of 5 per second. The successive seconds that accumulate on an empty trial are shown in the first row. The second row shows the pulse count that is transferred to working memory after

of the pacemaker (λ) changes between trials. The second source of memory variation is caused by variation in storage of working memory times in reference memory. A multiplicative constant, k^* , yields an exact transmission of the number of pulses in working memory to reference memory if $k^* = 1.0$. However, the value stored in reference memory may underestimate the value in working memory if $k^* < 1.0$ or may overestimate the value stored in working memory if $k^* > 1.0$.

A third source of variation in scalar timing theory is variation in the response threshold, b . Although a single constant threshold was assumed in Table 8.1, the theory actually assumes that momentary fluctuations in b cause a subject to begin responding early and to stop responding late if b is high or to begin responding late and stop responding early if b is low. The average times at which response begins and ends reflect the means of a distribution of b , from which trial to trial thresholds are sampled.

Break-Run-Break Response and Gaussian Curves

Although the numbers shown in Table 8.1 predict symmetry and proportionality, it is not clear how they could generate the Gaussian distributions of responding seen in Figure 8.6. Instead of gradually rising and descending curves, this numerical example suggests that an animal should fail to respond during the initial part of an empty trial, suddenly begin responding when DR drops below threshold, and continue responding until the threshold is exceeded, at which point response would stop altogether. In fact, exactly this pattern of response has been observed in both rats and pigeons (Cheng & Westwood, 1993; Cheng, Westwood & Crystal, 1993; Church, Meck & Gibbon, 1994; Gibbon & Church, 1990). Typically, a break-run-break pattern is seen in which the subject breaks into a high constant rate of response for an extended run and then breaks off response and returns to little or no response.

This pattern of response is shown in Figure 8.10, taken from Cheng and Westwood (1993). Cheng and Westwood trained pigeons to time a 12.5-second FI and then tested them on empty trials of several lengths. Performance was examined on individual trials; numbers of key pecks were counted in successive time bins of 1.25 seconds. Breaks from no response to response were identified when a bin with no responses was followed by responses in each of two successive bins. The zero point on the abscissa of the curve on the left side of Figure 8.10 represents the last bin before the break. Relative response frequency is plotted backward and forward from this point by averaging the number of responses in time bins before and after the break. The data were obtained over many trials given to three subjects. Similarly, the curve on the right side of Figure 8.10 is anchored at a zero point that represents the first of two bins in which no responses were made after a run of bins containing responses. The drop in the curve represents the break from the run phase to a no-response phase. Of particular importance, note that birds continued to respond at a high constant rate for a number of bins after the initial break and before the final break. These data look very much like what one would expect to see if the DR dropped below or rose above a threshold and changed the comparator's decision from no response to response or from response to no response.

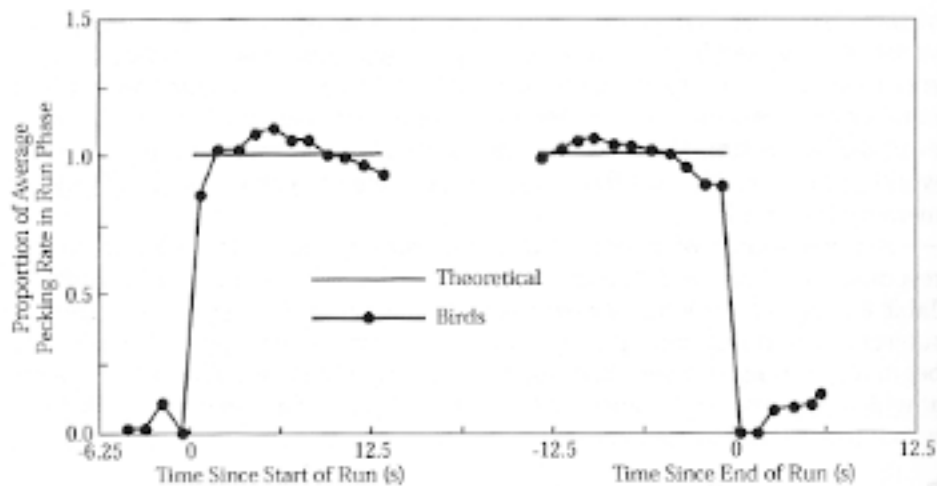


FIGURE 8.10. Break-run-break curves found in pigeons by averaging data from individual trials forward and backward from a zero time bin in which no response either preceded a run or ended a run.

Given that animals produce break-run-break patterns of response on individual trials, how are the smooth Gaussian curves seen in Figure 8.6 produced? Two factors explain this apparent inconsistency. First, variability in criterion times retrieved from reference memory and variation in response threshold occur between trials. As a consequence of variability in these trial parameters, break-run-break sequences do not show breaks at the same points in time on every trial. This point is shown in Figure 8.11. Considering just variability in the response threshold (b), the different rectangular break-run-break curves would be produced. If the threshold sampled on a given trial is low, the result is a narrow break-run-break function, as seen in Example b in Figure 8.11, because the accumulated pulses in WM have to be close to the total sampled from RM before the DR dips below threshold and triggers a response. By the same token, the animal stops responding at a high rate quickly because a relatively small increase in the WM total beyond the RM value takes the DR above threshold. On another trial, however, the threshold sampled is high, and a wide break-run-break curve, like that in Example c, occurs.

The second factor to consider is that the curves seen in Figure 8.6 represent averaged data from a number of trials and subjects. If a number of break-run-break curves varying in width are averaged together, the result is the smooth Gaussian curve shown at the top of Figure 8.11. Thus, average curves obtained on empty trials with the peak procedure are not inconsistent with the assumption that response to a signal is an all-or-none behavior, with the start of response triggered by the DR dropping below threshold and the end of response signaled by the DR rising above the threshold.

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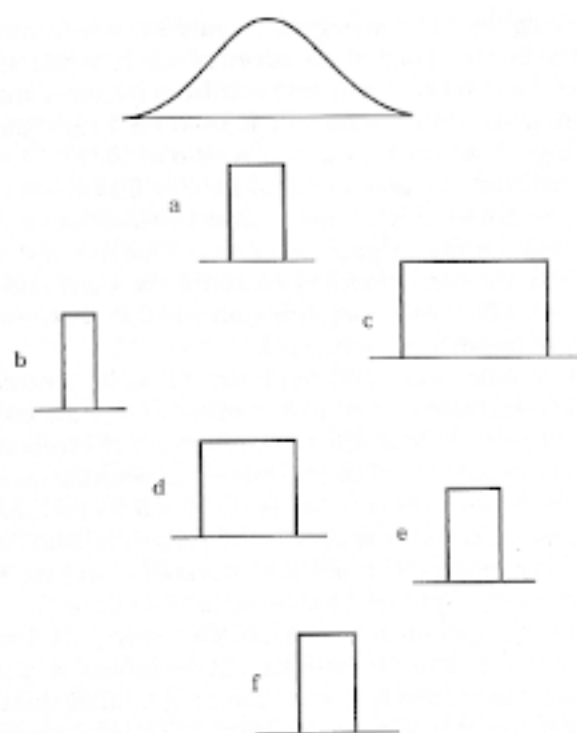


FIGURE 8.11. Variability in break-run-break functions is shown by the rectangular curves varying in width. These functions would arise on different trials if the threshold for response, b , in the scalar timing model varies from trial to trial. The smooth Gaussian curve at the top arises from averaging the separate break-run-break curves.

Point of Bisection

Recall the time discrimination experiment presented earlier in this chapter. Rats and pigeons are able to learn to make different responses to short and long time intervals. When then tested with times intermediate between the extreme values, animals produce a psychophysical curve with the subjective midpoint or the point of bisection of the curve lying at the geometric mean between short and long times.

One way in which this finding can be explained within the framework of the scalar timing theory is to assume that two distributions of reinforced or criterion times are stored in reference memory as pulse totals, one for the short signal and the other for the long signal. Whenever a test duration is presented, its similarity to both short and long criterion values is computed as a ratio between the shorter total and the longer total; choice of the manipulandum indicating short or long duration then is based on which ratio indicates closer similarity of its total to the test duration (Gibbon, 1981; 1986; Allan & Gibbon, 1991).

Assume again that pulses are emitted from the pacemaker at a rate of 5 per second and that an animal must discriminate between signals lasting 2 and

8 seconds. Following the 2-second signal, 10 pulses reside in working memory, and, following the 8-second signal, 40 pulses reside in working memory. Further, assume that the criterion totals sampled from reference memory also are 10 from the short-signal distribution and 40 from the long-signal distribution. When the short signal has been presented, a ratio of $10/10 = 1.00$ is computed for the short-signal criterion, and a ratio of $10/40 = 0.25$ arises for comparison with the long-signal criterion. The ratio nearest 1.00 indicates greater similarity to the criterion, and the short-signal response will be made. If the long signal has been presented, the corresponding ratios for the short and long criterion values are reversed, 1.00 for the long duration and 0.25 for the short duration, and the long-signal response is performed.

These ratios become closer and more similar as intermediate values are tested, making discriminations of relative similarity more difficult and yielding the ogive seen in Figure 8.3. When the geometric mean of 4 seconds is presented, 20 pulses should accumulate and be transmitted to working memory; the ratio of similarity to the short-signal criterion is $10/20 = 0.50$, and the ratio of similarity to the long-signal criterion is $20/40 = 0.50$. The 4-second duration should seem equally similar to the short and long durations, and the subject should make the short and long responses equally often. Thus, the assumption that subjects make similarity judgments based on ratios between pulse totals in working and reference memory accounts for the fact that the subjective midpoint usually falls at the geometric mean between short and long training durations.

Scalar timing theory provides an elegant and powerful model of the timing process that incorporates a number of empirical features of timing. By assuming that interval timing is accomplished by ratio comparisons between working and reference memory pulse totals, it accounts for the high degree of accuracy in animal timing and for phenomena such as proportionality, Weber's law, and bisection at the geometric mean.

SUMMARY

Like space, time is a fundamental dimension of animal and human experience, and it is therefore no surprise that animals are highly sensitive to time and able to judge it with considerable accuracy. Furthermore, it appears that animals judge time in two different ways. They are able to make gross discriminations between time of day, and they are able to make much finer judgments of short intervals of time. Experiments carried out with birds suggest that they can associate time of day with different spatial locations where food may be obtained. Time-place associations may be based on circadian cues, or daily cycles in an animal's endogenous state. When birds have learned stable time-place associations between widely separated times of day, control procedures that involve omission of test sessions or clock shifting show that birds depend on endogenous cues to determine the location of food.

Various experiments have shown that animals can also precisely time intervals in the range of seconds. Discrimination procedures are used to study fine discriminations between short and long signals that differ in length by only a few

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