PROPERTIES AND FUNCTION OF AN INTERNAL CLOCK

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The term time discrimination (shortened to timing) has no exact
meaning, but the common examples of it share two properties:
(a) The probability of some learned response changes with the
time since some event; and (b) the function relating response
probability and time changes with the time of the motivating
event (e.g., food or shock). As an example, Figure 1 (from
Roberts and Church, 1978) shows the result of training rats with
two signals that were followed by food at different times.
After a random intertrial interval, the 30-sec signal (light)
or the 60-sec signal (sound) began. After the appropriate time
--30 sec for light, 60 sec for sound--the next response (lever
press) was rewarded with food and the signal was turned off.
On the first day of exposure to this procedure, neither condi-
tion for a time discrimination was clearly met: (a) Response
ratio (response rate at the given time divided by overall re-
sponse rate) was almost constant with time, and (b) the 30-sec
and 60-sec functions were similar. On the last day, both condi-
tions were met: (a) Response ratio increased substantially with
time, and (b) the 30-sec and 60-sec functions were very dif-
ferent.

Russell Church, Mark Holder, Villu Maricq and I have done experi-
ments to determine how rats discriminate time (properties);
to our surprise, these experiments have also suggested why rats
discriminate time (function). This chapter summarizes our
work, emphasizing our conclusions about the internal clock that
is used. In addition, this chapter tries to place our work in
context--by describing the generality of animal timing, by
comparing our explanation with earlier explanations of animal
timing, and by pointing out connections between this work and
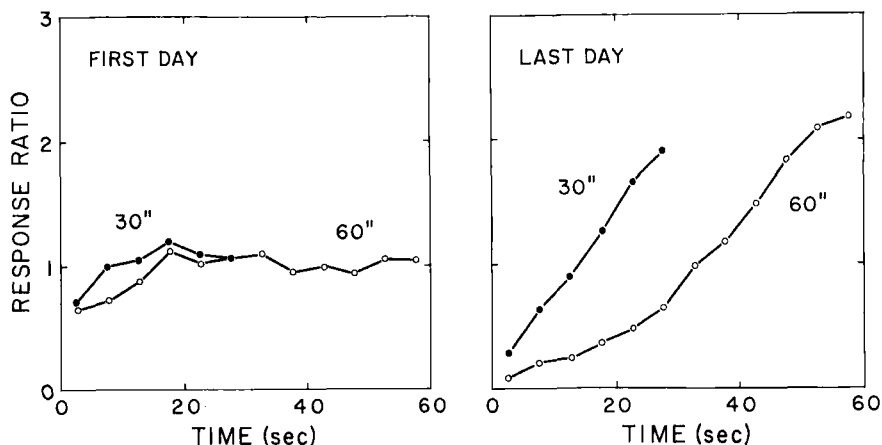work outside of animal timing.

Figure 1. The two features of a time discrimination, pre-
sent on the last day (right panel) but not on the first
day (left panel). Figure 10 of Roberts and Church,
1978. The left panel shows results from the first day
of fixed-interval training; the right panel shows the
results from the last day, 30 days later. "Time" is
time since the interval began. Response ratio is local
response rate divided by overall response rate; for
example, the response ratio for the interval Sec 5-10
is response rate during Sec 5-10 divided by the response
rate for the whole interval, Sec 0-30 or Sec 0-60.
Different curves are the results from different signals;
the label of each curve is the procedure of the signal,
FI 30 Sec or FI 60 sec. Each point is a mean over 12
rats. (Copyright 1978 by the American Psychological
Association.)

The Generality of Animal Timing

The inhibition-of-delay results of Pavlov (1926/1960) were the first examples of animal time discrimination. One of Pavlov's examples, originally published in 1980, used as the conditioned stimulus (CS) the sound of a whistle; it was followed after 3 min by the unconditioned stimulus (US), acid in the dog's mouth. During the first minute of the whistle there were 0 drops of saliva; during the second minute, about 5 drops; during the third minute, about 9 drops. This satisfies the first condition. In addition, Pavlov found that the pause before salivating was proportional to the length of the CS; this satisfies the second condition. The introduction by Skinner of fixed-interval schedules of reinforcement made it much easier to observe timing, especially in rats. Skinner was training rats in the first Skinner boxes. He began by rewarding every response, but changed to rewarding responses only once a minute (a fixed-interval schedule) in order to make his supply of pellets last longer (Skinner, 1956). After training with this procedure, a cumulative record of the number of responses showed the now-familiar fixed-interval scallops--response rate was low at the beginning of the interval and much higher near the end.

A figure in Skinner (1956) showed three cumulative records with fixed-interval scallops, one record from a rat, one from a pigeon, and one from a monkey. The three records were similar, and Skinner stated, "Pigeon, rat, monkey, which is which? It doesn't matter" (Skinner, 1956, p. 40). He was right--the ability to discriminate time is possessed by a wide range of vertebrates, and the accuracy of discrimination does not vary substantially. Not only dogs, pigeons, rats, and monkeys, but also mice (Sprott and Symons, 1974), opossums (Cone and Cone, 1970), rabbits (Rubin and Brown, 1969), racoons (King, Schaeffer and Pierson, 1974), bats (Schumake and Caudill, 1974), crows (Powell, 1973), and goldfish (Rozin, 1965) have discriminated time, usually with a fixed-interval schedule. On the other hand, bees apparently can not discriminate duration (Grossman, 1973), although they can discriminate other dimensions (e.g., color and smell: Klosterhalfen, Fischer and Bitterman, 1978) including time of day (Koltermann, 1974). Richelle and Lejeune (1980) reviewed results from 28 species scattered throughout the vertebrates; three of them (a bird, a fish, and a primate) did not clearly show timing.

The range of procedures that can produce timing is also wide. The duration that is discriminated can be: (a) the time from an experimenter-controlled event, such as food or shock (e.g., LaBarbera and Church, 1974); (b) the time from a response, as with differential-reinforcement-of-low-rate schedules

(Kramer and Rilling, 1970) and Sidman avoidance schedules
(e.g., Libby and Church, 1974); (c) the duration of an ex-
perimenter-controlled stimulus, such as a light (e.g., Libby
and Church, 1974); (d) the duration of a response, such as a
key peck (Ziriax and Silberberg, 1978) or lever press (Platt,
Kuch and Bitgood, 1973). The durations can be as short as tens
of milliseconds (Ziriax and Silberberg, 1978, with pigeons
or hundreds of milliseconds (Killeen, 1981, with pigeons;
Millenson, Kehoe and Gormezano, 1977, with rabbits) or as long
as tens of minutes (Pavlov, 1926/1960, pp. 41-2, with dogs)
or tens of hours (Dews, 1965, and Eckerman, Note 1, with
pigeons). With rats there seem to be two clocks available.
One seems to have a range roughly from 0 to 5 min (Richardson
and Loughead, 1974; Sherman, 1959), so that, for example,
accuracy is normal with FI 1 min and FI 3 min but much worse
with FI 10 min. Another seems to have a range roughly from
20 to 28 hrs (Boulos, Rosenwasser and Terman, 1980).

Some of the responses with which the discrimination can be
expressed are salivation, a lever press, a key peck, the cross-
ing of a shuttle box, a chain pull (Carlson, Wielkiewicz and
Modjeski, 1972), a choice response in a maze (Cowles and Finan,
1941), the closing of a nictating membrane (Millenson, Kehoe
and Gormezano, 1977), an attack (Azrin and Hutchinson, 1967),
general activity (Killeen, 1975), and scrabbling and gnawing
(Anderson and Shettleworth, 1977). Reinforcement can be food,
shock, water, blood (Shumake and Caudill, 1974), brain stimu-
lation (Cantor and Wilson, 1981), or drugs such as cocaine
(Balster and Schuster, 1973). The reinforcer can be response-
contingent or response-independent. For a longer review of
the timing literature, see Richelle and Lejeune (1980).

Explanations of Animal Timing

Any mechanistic explanation of timing must assume at least
two internal mechanisms or operations: (a) A clock (something
that changes with time in a regular way) that measures the
relevant duration. Because time changes performance in a
regular way, time must change something inside the animal in a
regular way. (b) A memory (something allowing storage and
retrieval) that stores and compares against storage the output
of the clock. Because the time of the reinforcer (on one
trial) changes performance (on later trials), the time of the
reinforcer must be measured and stored (on one trial) and
accessed (on later trials). In this chapter, I focus on the
clock and pay little attention to the memory. There has been
some controversy about what is and is not an explanation (e.g.,
Brown, 1965; Skinner, 1950). To simply say "a rat has an
internal clock" is neither an explanation of timing nor a
description of timing, but something in between the two for

which no word exists. It resembles a description because it
describes something hidden; it differs from an explanation
because it is not testable, it is more like an incomplete
sentence than anything else. The sentence is completed, and
becomes an explanation, when a theorist proposes a property
of the clock--e.g., "the rat has an internal clock that times
both light and sound."

Somewhere between ten and twenty explanations of animal timing
have been proposed. To give an idea of their range:

1. To explain his inhibition-of-delay results, Pavlov (1926/
    1960, p. 104) noted that "we get accustomed to stimuli of
    smell, sound or illumination"--their effective intensity
    changes (decreases) with time. Thus one intensity of the
    CS (at its end) is reinforced, but other intensities of
    the CS (e.g., at its beginning) are not. So the time
    discrimination is really an intensity discrimination.
    Logan (1979) proposed a more general version of this
    idea to explain fixed-interval performance. According to
    Logan, the brief event at the start of the interval--e.g.,
    a food pellet--produces a variety of memories that last
    different amounts of time. The short-lived memories do
    not reach the next reward and do not become associated
    with time since food because the ratio of long-lived
    memories (associated with reward) to short-lived memories
    (not associated with reward) increases with time since
    food.

2. Dews (1962) proposed that the fixed-interval scallop arises
    because the effectiveness of reward decreases with delay
    and responses early in the interval are rewarded with longer
    delays of reward than responses later in the interval.
    This assumes, of course, that responses early in the inter-
    val are somehow distinct from responses later in the inter-
    val.

3. Killeen (1975) used equations derived from control theory
    to fit the response-rate functions from a number of pro-
    cedures where food is given at fixed intervals. The empha-
    sis was more on the range of procedures used and the good-
    ness of fit than on the mechanism that would produce the
    equations.

4. Gibbon (1977) developed a detailed and quantitative theory
    to describe results from fixed-interval procedures, choice
    procedures, and a few others. The emphasis was mainly
    on how changes in the durations to be discriminated changed
    the accuracy of discrimination.

Some other recent theories are Staddon (1974), Ambler (1976), and Keller (1980).

All of these theories assume that something internal changes with time in a regular way. In Pavlov's theory, the clock (or its output) is the effective intensity of the CS, which decreases with time. In Logan's theory, the clock is the changing memory of food, increasingly composed of its long-lived components. In Dews' theory, the response changes with time, but not necessarily in a regular way; the required regularity is the progressive weakening of the effects of reward--not very different, in essence, from Logan's theory. The mechanistic derivation of Killeen's equations assumes that, with time, the animal passes through a progression of states. The probability of passing from one state to the next is constant with time, but of course the probability of being in one of the later states rises with time. Gibbon simply assumes that the animal has available an accurate estimate of the amount of time that has passed.

Our work differs from this earlier work in a number of ways. Perhaps the most important difference is that the theory is less detailed. The psychological process producing the clock is not named (in contrast to Pavlov, Logan and Dews); and assumptions about the shapes of distributions are not made (in contrast to Killeen and Gibbon). In general, the approach is to add to the assumption of a clock as little as possible, only enough to produce an experimental test. If it seems that we assume an internal clock and other theories do not, this is only because less has been added. A second important difference is that the data used to support the theory usually come from procedures designed for that purpose--procedures designed to choose between theoretical alternatives. Earlier theories have been based on procedures originated for other purposes (e.g., fixed-interval schedules). A third difference is that the clock metaphor is taken more seriously. A number of experiments (e.g., Roberts and Church, 1978) have been based on the differences between man-made clocks. For example, a stopwatch times up from zero while a kitchen timer times down from a preset value; we asked if the rat's clock timed up or down. Experimental comparisons of animal clocks and man-made clocks had not previously been made.

Properties of the Clock

This section describes the properties of the clock that our research has found.

Distinct

The clock is distinct from, or independent of, the other mental operations used in time discrimination. It is distinct in two ways: (a) the clock can be changed without changing other operations; and (b) other operations can be changed without changing the clock. This is the clock's most fundamental property; it has been taken for granted by almost every dis-cussion of "the clock" and by almost every detailed theory of timing. For example, Church and Deluty (1977) explained their results by assuming a clock, a criterion, and a response rule, each of which was distinct from the other two. Roberts and Church (1978) assumed that the clock could be changed without changing the translation of clock time to response rate. The theory of Gibbon (1977) has a number of parameters that are assumed to change without changing the clock. Although none of these writers had any evidence that the clock was distinct, it was a natural assumption to make. Distinctness is so common in our view of the world that it is hard to imagine a clock without it; it is in the nature of things that they are distinct from other things.

The simplest evidence that the clock is distinct comes from the application of logic that I will call the independent-measures method; it is similar in form and goals to Sternberg's (1969) additive-factor method. The method is essentially three assumptions and a prediction. The assumptions are:

> Distinct operations. There are (at least) two distinct operations, A and B, that control the observed response.

> Selective influence. Factor F changes A and not B, and Factor G changes B and not A ("factor" meaning "experi-mental factor," or "independent variable").

> Selective measurement. Measure M changes when A changes and does not change when A does not change; Measure N changes when B changes and does not change when B does not change.

The prediction: If the assumptions are true, Factor F should change Measure M but not Measure N, and Factor G should change Measure N but not Measure M. The predicted result is some-times called "double dissociation" (Teuber, 1955), but "independent measures" seems more descriptive. A result of independent measures suggests that all three assumptions are correct. Warrington and Weiskrantz (1973) used this logic to infer separate short- and long-term memories; Blackmore and Campbell (1969) used it to infer spatial-frequency analysis

by the visual system. In animal learning, one of its few uses
is by Maki (1979), who argued that discrimination learning and
delayed matching-to-sample involve different memories.

This logic applies to an experiment (unpublished) where rats
were trained to make two discriminations simultaneously--a
response discrimination and a time discrimination. The sub-
jects were six rats, who worked in standard lever boxes.
There were two measured responses: lever presses, of course,
and also pulls on a flexible metal bead chain that hung from
the ceiling of the chamber. The discriminative stimuli were
sound (white noise) and light (a houselight). Responses were
rewarded with a food pellet. There was one 3-hr session each
day.

After the rats learned to make both responses, a response
discrimination was trained: During one signal (light or
sound), only lever responses were rewarded; during the other
signal, only chain responses were rewarded. The lever signal
was light for half the rats, sound for the rest. The two
signals alternated with periods of darkness and silence when
neither response was rewarded. This procedure lasted 5 days.
Then a time discrimination was added to the response discrimi-
nation. After an intertrial interval of random length, one
of the two signals started. After 60 seconds, the next re-
sponse appropriate to the signal was rewarded. When the re-
sponse was rewarded, the signal went off. This procedure
lasted 10 days. The results described below are from the
last 5 days, when the time discrimination had stopped improv-
ing.

Figure 2 shows the time discrimination. The top panel shows
that response ratio was not affected by the modality of the
signal. In a context where time changed response ratio by
2.4, the largest absolute difference between light and sound
at any time was .11, and the median absolute difference (over
the 12 times) was .02. The middle panel shows the effect of
the meaning of the signal (whether lever or chain responses
were rewarded). Again, the two functions are very similar;
the median absolute difference is .03. The bottom panel shows
the effect of response (chain or lever) averaged over the two
signals. Again, the two functions are very close; the median
absolute difference is .02. The averages in the bottom panel
do not include Rat 6, which showed consistent differences
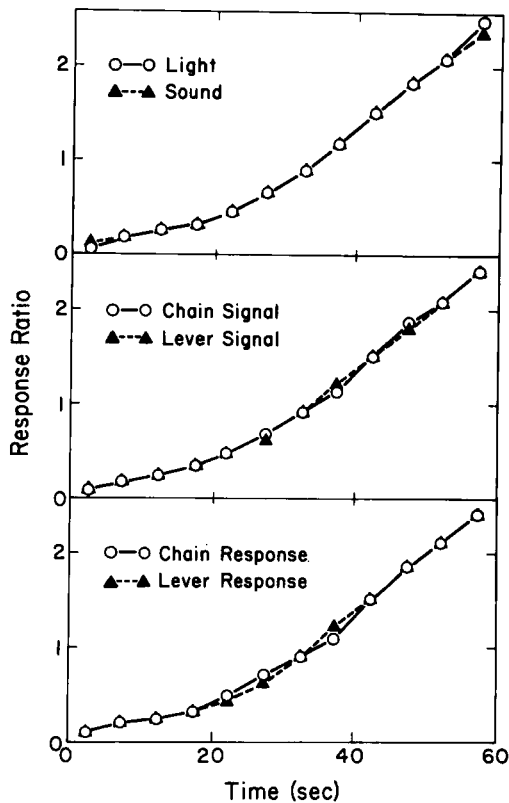between the two responses, as large as .57.

Figure 2. Time has a large effect on response ratio; modality (top panel), signal (middle panel), and response (lower panel) have very small effects. (The data are from the last 5 days of time-discrimination training. Response ratio is defined in the caption of Figure 1. In the top two panels, the two responses are not distinguished; e.g., a rate of 3 chain resp/min and 5 lever resp/min is considered 8 resp/min. In the bottom panel, the two signals are not distinguished. Each point in the upper two penels is a mean over six rats. Each point in the bottom panel is a mean over 5 rats; Rat 6 was omitted for reasons described in the text. For Rats 1, 2, and 6, the lever signal was light; for the rest, the lever signal was sound.)
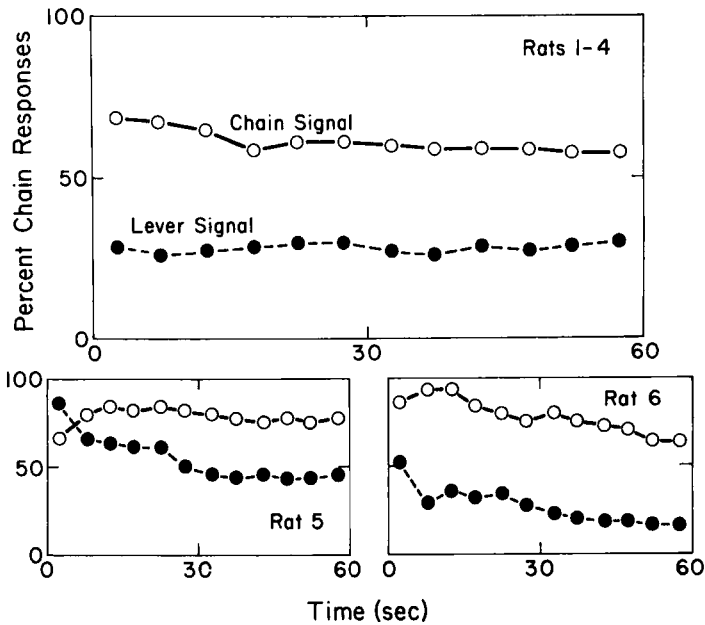
Figure 3.   Signal has a large effect on the percentage of
    chain responses; time has a small effect.   (The data
    are from the last 5 days of time-discrimination train-
    ing.   Percentage of chain responses refers to the
    percentage of chain responses relative to all re-
    sponses at a given time; for example if the chain
    rate was 3 resp/min and the lever rate was 7 resp/min
    during the interval sec 10-15, the percentage of
    chain responses would be 30%.)

Figure 3 shows the response discrimination.   It was nearly
constant throughout the interval for four rats, but clearly
varied for the other two.   Over the last 30 sec of the in-
terval, it was constant for both signals and all rats except
Rat 6.

Here, then, are two independent measures.   With a few ex-
ceptions, response ratio was changed by time and not by the
meaning of the signal, while the percentage of chain responses
was changed by the meaning of the signal and not by time.
This suggests that the clock (the operation changed by time)
was distinct from the operation changed by the meaning of the
signal.   Because response ratio was sensitive to changes in

the clock but did not change with modality or response, we
can also conclude that the clock was not changed by modality
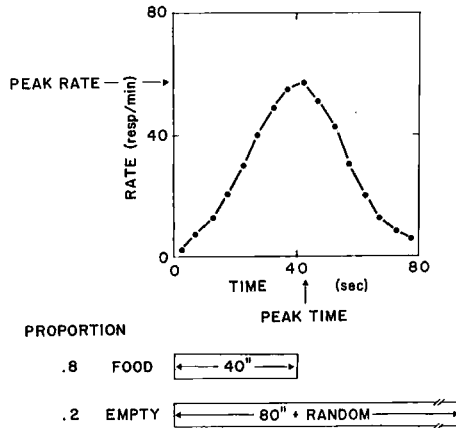or response.

Figure 4. The basic elements of the peak procedure
    and some typical results. (Figure 1 of Roberts,
    1981. Time is measured from the start of a
    signal, such as light. Copyright 1981 by the
    American Psychological Association.)

Because the clock is distinct, we can hope to "isolate" it;
that is, find a measure such that (a) a change in the measure
implies a change in the clock and/or (b) no change in the
measure implies no change in the clock. The results just
described suggest that response ratio has these properties
for some manipulations (the assumption of selective measure-
ment); however, I guess that with a wider range of manipu-
lations, some of them would change response ratio without
changing the clock. For example, it seemed likely that some
manipulations could change accuracy without changing the clock,
yet any change in accuracy would change response ratio. To
find a better measure, I used the peak procedure, a modifi-
cation of a procedure used by Catania (1970). The basic
elements of the peak procedure are shown in Figure 4. It is
similar to a discrete-trials fixed-interval procedure with
intermingled long extinction trials. There are two types of
trial, randomly mixed: (a) Food trials, on which the first
response after a fixed time--in Figure 4, 40 sec--is rewarded
with food; the trial then ends. (b) Empty trials, on which no
food is given. The trial lasts a relatively long time (say,

160 sec) and ends independently of responding. Figure 4
also shows some typical results. After training with this
procedure, response rate within a trial reaches a maximum at
about the time that food is given. The main measures of per-
formance are peak time, the time of the maximum response rate
measured from the start of the trial, and peak rate, the value
of the maximum. I hoped that peak time would isolate the
clock. Underlying this hope was the idea that the peak in
response rate happened when the rat expected food--when
elapsed time, as measured by its clock, matched the time when
food had been given on earlier trials. Changing the clock
would thus change peak time; for example, speeding up the
clock would decrease peak time. And with the time of food
constant, a change in peak time would imply a change in the
clock. The work to check these ideas had essentially two
parts. The first part asked if peak time isolated something;
i.e., if it was sensitive to changes in one operation that
controlled responses and not to changes in another operation
that controlled responses. The second part asked if the
operation isolated was the clock.

Peak time isolates something. Figure 5 shows evidence that
peak time isolated something (Experiment 1 of Roberts, 1981).
The subjects and apparatus of this experiment were much like
those in the experiment just described. The experiment of
Figure 5 had two phases. During both phases, there were two
signals (light and sound) with different treatments. In the
first phase, food trials with one signal had food primed at
Sec 20 (i.e., 20 sec after the start of the trial); food
trials with the other signal had food primed at Sec 40. For
both signals, food trials were 80% of all trials. In the
second phase, food trials with both signals had food primed
at Sec 20. The difference between the signals was that for
one signal (high food), food trials were 80% of all trials;
for other signal (low food), they were 20% of all trials.
The main result, shown in Figure 5, was that peak time and
peak rate were independent measures. The time of food changed
peak time but not peak rate, while the probability of food
changed peak rate but not peak time. Roberts and Holder
(Note 2) also found that changing the probability of food did
not change peak time. Based on the independent-measures
logic (the assumption of selective measurement), we can con-
clude the peak time isolated something.

Peak time isolates the clock. In general, the support for
this statement is that conclusions about the clock based on
peak time--assuming that peak time isolates the clock--agree
with conclusions about the clock based on other evidence
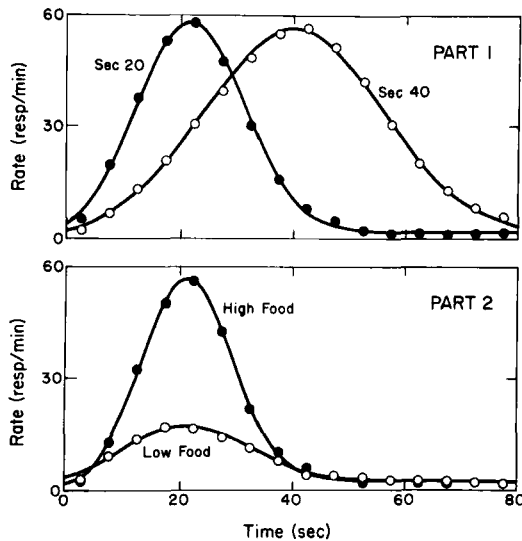(Maricq, Roberts and Church, 1981; Roberts, 1981, 1982;

Figure 5. Peak time and peak rate are independent.
(Figure 2 of Roberts, 1981. Each point is a mean
over 10 rats. The two curves in each panel are the
results from different signals. During Part 1,
food was given at different times with the two
signals. During Part 2, food was given with dif-
ferent probabilities during the two signals. For
more details, see the text. Copyright, 1981 by
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Roberts and Holder, Note 2). It is clear enough that peak
time is sensitive to the operation that changes with the
duration of the signal, which by definition is the clock.
Consider, for example, what would happen if trials with light
were preceded by a 20-sec interval of light. The 20-sec
interval of light, just before the trial, would decrease peak
time by about 20 sec, and this shows that peak time is sensi-
tive to the operation measuring the duration of the light.
However, it is possible that peak time is sensitive to other
operations as well, and this is why it is important that con-
clusions about the clock based on peak time agree with con-
clusions based on other evidence. The most important agree-
ment has been with conclusions from choice procedures, where
rats are trained to make one response after one duration and
another response after a second duration. For example,

Roberts (1981, Experiment 3) found that feeding the rats be-
fore the session increased peak time, suggesting that pre-
feeding slowed down the clock. Support for this conclusion
came from an experiment by Yagi (1962), who found a similar
result using rats trained to choose between the arms of a T-
maze based on their duration of confinement before the choice.
The procedure of Yagi and the peak procedure both required the
rat to use its clock, but they differed in other ways, such
as the input operations (how the rat responded). However,
both the peak procedure and choice procedures also require
use of a long-term memory for durations; to conclude that a
change in peak time was due to a change in the clock rather
than a change in this memory required other evidence (Roberts,
1981).

The experiments of Roberts (1981) also suggested two problems
with the assumption that peak time isolates the clock. First,
although changing the time of food changed peak time, it
apparently did not change the clock (Roberts, 1981, Experiment
5). This was not surprising, and it s-emed to be best dealt
with simply by limiting the statement: When the time of food
is constant, peak time isolates the clock. Second, two ex-
periments (Roberts, 1981, Experiments 3 and 4) suggested that
under some circumstances a change in the clock would produce
an opposite change in memory; the net effect would be no
change in peak time, even though the clock was changed. How-
ever, these circumstances seemed easy to avoid. Roberts (1981)
discusses these problems in detail.

As the following sections show, the operation isolated by peak
time has many clock-like properties--in particular, many stop-
watch-like properties. This is another sort of justification
for the statement that peak time isolates the clock.

Linear Scale

The sclae of the clock seems to be linear with physical time,
in the sense that equal differences in seconds produce equal
differences along the scale. This conclusion is based on the
symmetry of the response-rate functions from the peak pro-
cedure (Figure 5). Equal distances in seconds from the peak
of the response-rate function--comparing a move toward earlier
times with a move toward later times--produce roughly equal
changes in response rates; we assume that the behavioral
equality reflects an equality on the underlying scale. An-
other way to make the argument is to note that the response-
rate functions have a simple shape (symmetric) on a simple
scale (linear with physical time). While any single-peaked
function will be symmetric on some scale, and any function

will have some shape on a linear scale, the conjunction of the two simplicities is remarkable. If the rat's clock does not have a linear scale, it is hard to explain. The symmetry result has been found by others using a different procedure and shorter times (Church and Gibbon, 1982). The slight asymmetry in the function (it starts at zero resp/min, but flattens out above zero resp/min) can be explained in various ways that are compatible with a linear scale (Church and Gibbon, 1982; Roberts, 1981). A more serious problem is that Millenson, Kehoe, and Gormez (1977) found a timing function that was symmetrical on a log scale (where the distance between 10 sec and 20 sec equals the distince between 20 sec and 40 sec) rather than on a linear scale. They were studying the rabbit's nictating-membrane response using durations of a few hundred milliseconds; the best resolution of the difference in results is probably that a different clock was involved.

Earlier scaling with animals has usually taken the underlying scale to be the one on which overall discriminability is constant (e.g., Church and Deluty, 1977). If we apply this criterion to the data of Figure 5 (upper panel), we would conclude that the underlying scale is logarithmic, because the response-rate function with a peak near Sec 40 is about twice the width of the function with a peak near Sec 20. A logarithmic scaling of the time axis would give both functions the same shape and width, a criterion for scaling used by Shepard (1965). With exactly the same data, then, we can argue either for a linear scale or a logarithmic scale, and one of the arguments must be wrong. A simple reason for thinking that the equal-discriminability argument is wrong (or at least unattractive) is that it leads to the conclusion that a stopwatch does not have a linear scale. A stopwatch inevitably measures longer times with more error (on a linear scale) than shorter times; it will measure all times with equal error only on a scale transformed away from linearity toward logarithms. Other reasons for doubting the equal-discriminability argument are that work not involving symmetry supports a linear scale (Gibbon and Church, 1981), and that earlier data taken to support a logarithmic scale is compatible with a linear scale (Gibbon, 1981). It is probably wrong to use the equal-discriminability criterion to scale continua that have natural zeros, such as time and length.

Accurate

Another conclusion from the symmetry of the response-rate functions of Figure 5 is that the clock is relatively accurate--that the error in the measurement of duration is a small part

of the total error in performance ("error" meaning variance).
The argument behind this conclusion is given in full by Roberts
(1981); it is outlined below.

If all aspects of the discrimination were done without error,
there would be a sharp rise near the time of food and a sharp
decline thereafter. In fact, the response-rate functions have
considerable spread. What produces the spread? Other work
(Roberts, 1981; Roberts and Church, 1978) suggests that per-
formance in this task is based on a comparison of the current
time (measured from the start of the trial) to the memories of
the times when responses had been rewarded on earlier trials.
so the spread in the functions has at least three possible
sources: (a) error in measuring the current time (clock error);
(b) error in remembering the time of reward; and (c) error in
comparing the two. Whatever the size of the clock error, we
expect it to increase with longer times, perhaps doubling when
the measured duration is doubled. For example, if the clock
measures 20 sec with a standard deviation of 2 sec, we expect
it to measure 40 sec with a larger standard deviation, perhaps
4 sec. If the clock error is large relative to other error,
longer times should be measured with noticeable less accuracy
than shorter times; in particular, the discrimination after
the peak. In fact, the two sides of the function are about
equally steep, implying that the clock error is about the same
on both sides. Because the clock error is probably small at
short times (e.g., 5 sec will be measured with a small standard
deviation), it is probably small throughout.

This may be the most surprising conclusion from this work.
Earlier theoretical work on the accuracy of timing both
human and animal, had always assumed that the clock was the
main source of error (e.g., Church, Getty and Lerner, 1976;
Creelman, 1962; Getty, 1976; Kinchla, 1972). A similar
assumption--that the important error is in the sensory signal
--is made by most theoretical applications of signal-detection
theory. For timing, apparently, this assumption is false.

Can be Stopped

Like a stopwatch, the clock can be stopped and restarted at
the time it was stopped. Some of the evidence for this is
shown in Figure 6 (Roberts, 1981). Rats were trained with the
peak procedure with light as the signal. After they learned
the discrimination, I compared their performance on two types
of empty trials: (a) baseline trials, where the signal comes
on and goes off without interruption; and (b) blackout trials,
with a 10-sec blackout starting at Sec 10. Figure 6 shows
the results. The blackout simply shifted the response-rate
function rightward by roughly the length of the blackout.

Five-sec blackouts shifted the function about half as much as 10-sec blackouts. This is what would be expected if the clock stopped during the blackout, and it is hard to explain in other ways. More evidence that the clock can be stopped, based on different durations and two other procedures, comes from Roberts and Church (1978) and Church (1978).
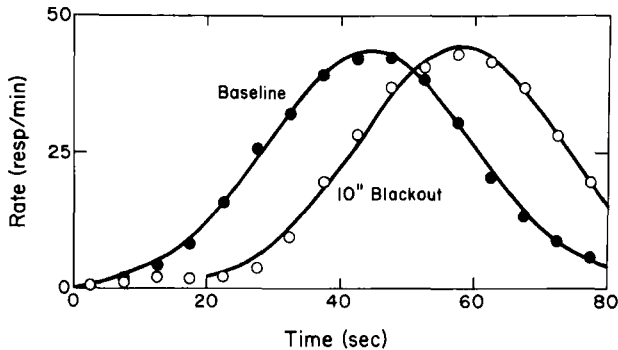

Figure 6. The effect of a blackout. (Figure 5 of Roberts, 1981. The signal timed was light; the blackout started 10 sec after the beginning of the trial and lasted 10 sec. Each point is the mean over 10 rats. Copyright 1981 by the American Psychological Association.)

Internal Pacemaker

Most man-made clocks are essentially counters. They may count, for example, the swings of a pendulum (a grandfather clock) or the reversals in the direction of house current (a wall clock). The source of the events counted is the clock's pacemaker. The pacemaker may be near the counter (a stopwatch) or far away (a wall clock). If the rat's clock is a counter, its pacemaker(s) might be inside the rat (e.g., a cell that fired at regular intervals), outside the rat (e.g., the stimulus energy), or both (if the clock counted events from more than one source).

The results of two manipulations suggest that the clock has an internal pacemaker. First, Roberts (1981), using the peak procedure, found that feeding the rats just before the experimental session increased peak time. Assuming that this reflected a change in the clock, it might have been due to (a) an increase in clock latency--the time between the start of the signal and the start of the clock--or (b) a decrease in clock rate. A change in latency would "shift" the response-

rate function (as in Figure 6) while a change in rate would
"stretch" it (as in the upper panel of Figure 5). In fact,
prefeeding stretched rather than shifted the response-rate
function, suggesting that it changed clock rate. Second,
Maricq, Roberts and Church (1981) found that methamphetamine
injections decreased peak time. This suggested that metha-
mphetamine changed the clock but by itself does not indicate
if the drug changed latency or rate. To distinguish these two
possibilities we used a choice procedure. After the signal
(a blackout), the rats had a choice of two levers. The correct
(rewarded) response depended on the duration of the blackout;
for example, if the blackout had been short (e.g., 1 sec),
responses on the right lever were rewarded, while if the
blackout had been long (e.g., 4 sec), responses on the left
lever were rewarded. After blackouts of intermediate duration
(between 1 and 4 sec), neither choice was rewarded; the
intermediate durations were used to estimate the duration that
the rat would classify as "long" and "short" equally often
(the indifference point). There were three groups: One
learned to discriminate 1 and 4 sec, another 2 and 8 sec, and
the third 3 and 12 sec. After the discrimination was learned,
we injected the drug. Based on our earlier work, we expected
the drug to decrease the indifference point. If methampheta-
mine changed only the latency of the clock, then the indif-
ference point should decrease equally for all three groups.
But if methamphetamine changed the rate of the clock, the
decrease should be largest in the 3-vs.-12-sec group. Figure
7 shows that this is what happened. The change in the in-
difference point was roughly proportional to the duration
being measured. We concluded that methamphetamine changed
the rate of the clock.

Because manipulations that produce only internal changes (pre-
feeding, methamphetamine) can change the rate of the clock,
the clock apparently has an internal pacemaker. Note, how-
ever, that the clock may also have an external pacemaker--
e.g., its rate may depend on features of the signal being
timed, such as its intensity or modality.

Times Up

Some man-made clocks, such as stopwatches, time "up" from
zero; others, such as kitchen timers, time "down" toward zero.
The essential difference is whether it is the starting point
(timing up) or the ending point (timing down) that is the same
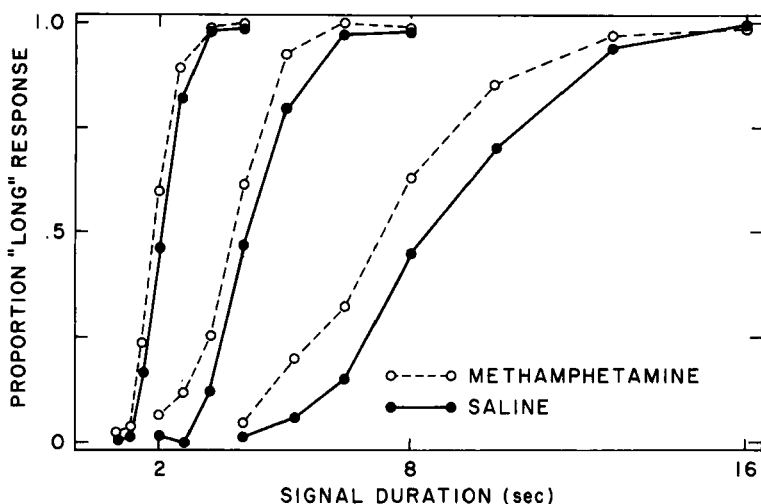for different durations.

Figure 7. The effect of methamphetamine (Figure 7 of
  Maricq, Roberts and Church, 1981. Each pair of curves
  is from a different group of rats. Unfilled circles
  show results from sessions with methamphetamine;
  filled circles show results from sessions with
  saline. Each point is the median over 8 or 10 rats.
  Copyright 1981 by the American Psychological Associ-
  ation.)

The rat's clock apparently times up. The simplest evidence
for this comes from choice experiments like the one just
described, where the rat is trained to press one lever after
a short duration and the other lever after a long duration.
These experiments have used retractable levers. The levers
are retracted during the intertrial interval and during the
presentation of the duration; after the duration, they are
extended, and the rat chooses-essentially classifying the
duration as "long" or "short." In this situation, no duration
at all--a 0-sec signal--is usually classified as "short"
(Church, 1980; Roberts and Holder, Note 2), and this suggests
that the clock times up. This conclusion assumes that if the
clock times down, it is not set to the appropriate duration
until the signal begins; however, other work, not making this
assumption, also suggests that the clock times up (Roberts and
Church, 1978, Experiment 3, using a fixed-interval procedure;
Roberts, 1981, Experiment 5, using the peak procedure).

Cross-modal

As Figure 1 (right panel) shows, rats can discriminate the
durations of both lights and sounds. The two modalities might
be timed by different clocks or by the same clock; apparently
they are timed by the same clock.

The best evidence for this comes from an experiment by Roberts
(1982). Rats were trained with the peak procedure using both
trials of light and trials of sound, so that they developed
time discriminations in both modalities. Then transfer trials
were added; these consisted of a short (10 or 20 sec) signal
of one modality followed by a long (e.g., 180 sec) signal of
the other modality. The first signal defines the preset inter-
val; the second signal, the measurement interval. The main
empirical question was the effect of preset intervals on peak
time during the measurement interval (measured from the start
of the measurement interval). If light and sound are timed
by the same clock, then preset intervals should decrease peak
time (because the clock will not be at zero when the measure-
ment interval begins). If light and sound are timed by dif-
ferent clocks, there is no reason to expect preset intervals
to change peak time.

Figure 8 shows that preset intervals decreased peak time dur-
ing the measurement interval. The size of the decrease roughly
corresponded to the length of the preset interval: The de-
crease was about 4 sec with the 10-sec preset interval and
about 14 sec with the 20-sec preset interval. The fact that
preset intervals decreased peak time suggests that the same
clock times light and sound; the fact that the transfer was
less than perfect (e.g., a 10-sec preset interval decreased
peak time by less than 10 sec) suggests that the clock can
distinguish light and sound. There is apparently a single
clock that receives separate inputs from different modalities.
The results of Figure 8 have been repeated in other experiments
(Roberts, 1982; Roberts and Holder, Note 5); the conclusion
that there is a cross-modal clock is also supported by results
not involving the peak procedure (Meck and Church, 1982;
Roberts, 1982).

In a way, the experiment of Figure 8 unites two earlier lines
of work. On the one hand, there had been about ten previous
findings, with five different dimensions, of cross-modal
transfer of training with animals (see Roberts, 1982, for
references). As an example of this work, Over and Mackintosh
(1969) trained rats to respond fast or slowly depending on the
intensity of a light. For some rats, a high intensity meant
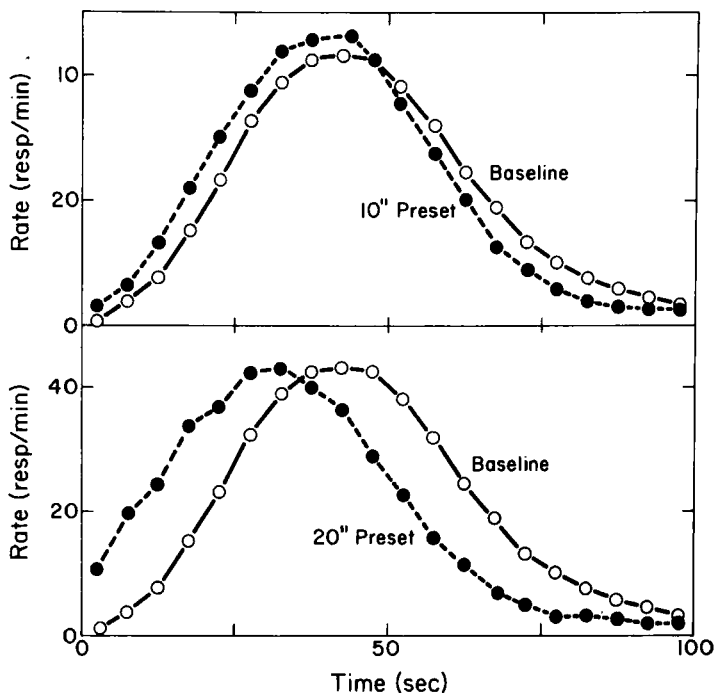"respond fast"; for others, it meant "respond slowly." When

Figure 8. Preset intervals of sound (or light) decrease
peak time during light (or sound). (Figure 9 of Roberts,
1982. If the preset interval was sound, the measure-
ment interval was light, and vice versa. The baseline
function comes from all trials without preset intervals.
Each point is a mean over six rats. Copyright 1982
by the American Psychological Association.)

exposed to sound, the rats to some extent treated stimuli in
the new modality as if they were stimuli in the old modality;
for example, rats trained to respond fast to a high-intensity
light responded faster to a high-intensity sound than rats
trained to respond slowly to a high-intensity light. This
kind of result shows that non-verbal animals can perform cross-
modal abstraction that directs learned behavior. (This is
"abstraction" because one quality of the stimulus--its modality
--is being ignored while another quality--its intensity--is
being attended to.) However, the abstraction might have been
due to associative learning. For example, tactile-to-visual
transfer of shape discriminations (e.g., Cowey and Weiskrantz,
1975, with monkeys) is probably the result of earlier experi-
ence with co-occuring visual shapes and tactile shapes. On
the other hand, in the physiological literature there had been
about five previous reports (see Roberts, 1982), based on

single-cell recording, of cross-modal cells sensitive to
location. For example, Morell (1972) found cells in the
visual cortex of cats that responded only to stimuli in a
particular horizontal direction, but to both lights and sounds.
This sort of result suggests that there is cross-modal ab-
straction not due to associative learning; however, the
abstraction does not necessarily direct learned behavior--it
might be used for orienting, for example. The timing work
described above is an example of cross-modal abstraction that
both directs learned behavior and cannot plausibly be due to
associative learning.

Path-independent

Figure 9 shows the response-rate functions of Figure 8 plotted
so that their peak times coincide; the three functions are now
very similar. The same result has been found in other situ-
ations (Roberts, 1981, Experiment 2; Roberts, 1982, Experiment
4). One way of describing this result is to say that response
rate was path-independent, in the sense that response-rate
functions shifted to be equal at one time were equal at all
later times. The term path-independent was, of course, origi-
nally used to describe mathematical learning theories that
assumed that learning curves horizontally shifted to be equal
on one trial would be equal on all later trials. The in-
dependence of path shown by response rate presumably reflects
the independence of path of the underlying clock: What the
clock will read after, say, 10 sec, depends only on the current
reading, and not on how the current reading was reached.

All man-made clocks (e.g., stopwatches, wall clocks) are path-
independent, and it may be hard to imagine other possibilities.
Another way to describe the property of path independence is
to say that the state of the clock is one-dimensional: it
can be fully described by a single number, in the sense that
by knowing only a single number (its current reading) we can
predict what it will read, say, 10 sec from now. But if we
consider clocks in general--anything that changes with time
in a regular way--we can see that not all clocks have this
property. Consider a man driving home from work. We plot
distance travelled from work versus physical time since leaving
work, and we see that distance travelled is a clock--it changes
with time in a regular way. But the clock has at least two
dimensions because future progress depends not only on current
position but also on the time of day; for example, there will
be less progress during rush hour. To predict where the man
will be 10 min from now requires knowing not only where he is
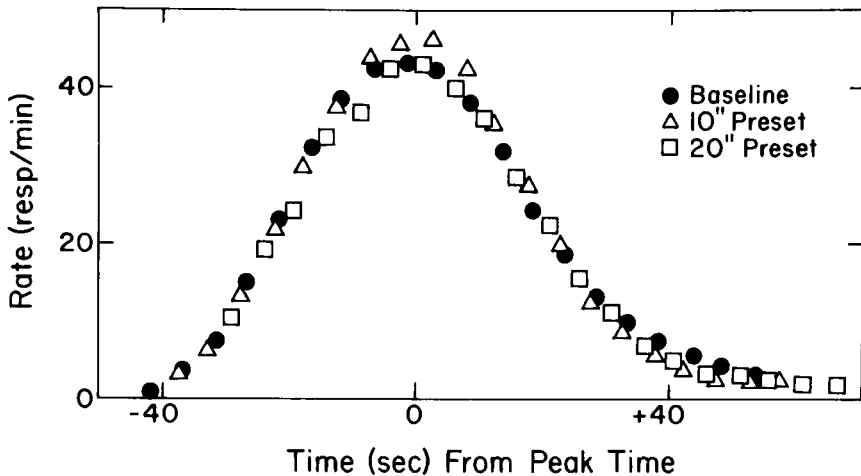now, but also the time of day. Functions from two trips

Figure 9. The path independence of response rate.
(Figure 10 of Roberts, 1982. This shows the
functions of Figure 8 of this paper shifted so that
their peak times coincide. Copyright 1982 by the
American Psychological Association.)

horizontally shifted to be equal at one time will not always
be equal at all later times. The rat could have a two-
dimensional, path-dependent clock if the output of the clock
that guides behavior, Clock A, was the result of combining
the output of two other clocks, Clocks B and C.

Times Different Intervals and Times Different Intervals Using the Same Rate

Some man-made clocks, such as eggtimers, can only time a
single interval, but most can time a range of intervals. Some
of the clocks that time a range of intervals use different
rates with different intervals. For example, there is a lab
clock whose rate is set according to the interval to be timed;
it times 30 sec at twice the rate that it times 60 sec. Most
computer clocks measure similar intervals using the same rate
but measure very different intervals (e.g., 1 sec and 1 hour)
using different rates. A stopwatch, however, measures all
intervals using the same rate.

The rat apparently times different intervals using the same
clock and the same rate. Some of the evidence for this comes

From an experiment by Roberts (1981) using the peak procedure.
As in the cross-modal experiment described above, there were
both trials with light and trials with sound. Unlike the
cross-modal experiment, the two signals differed in the time
of food: During one signal, the first response after Sec 20
was rewarded, during the other signal, the first response
after Sec 40. After the discrimination was learned, shift
trials were added: They began with the Sec-20 signal but
shifted to the Sec-40 signal at Sec 5, 10, or 15 (i.e., after
5, 10 or 15 sec of the Sec-20 signal). Shift trials were the
same length as empty trials, and they ended without food.

On shift trials, when will the rats expect food? There are
three cases to consider: (a) The Sec-20 and Sec-40 signals
are timed by different clocks; (b) the Sec-20 and Sec-40
signals are timed by the same clock at different rates; and
(c) the Sec-20 and Sec-40 signals are timed by the same clock
at the same rate. If the two signals are timed by different
clocks--case (a)--then the duration of the Sec-20 signal should
have no effect on when rats expect food during the Sec-40
signal; the peak in response rate should happen about 40 sec
after the shift regardless of the time of the shift. Measured
from the start of the Sec-20 signal, peak time should be about
45 sec (shift at Sec 5), 50 sec (Sec 10), or 55 sec (Sec 15).
If the two signals are timed by the same clock at different
rates--case (b)--the most plausible arrangement is that the
rate of the clock is proportional to the interval to be timed
(the shorter the interval, the faster the clock). Then the
clock essentially measures the proportion of the interval
completed, and later shifts will produce earlier peaks.
Suppose the shift is at Sec 5. At the time of the shift the
clock will essentially read "25% done," and 30 sec (75% of
40 sec) of the Sec-40 signal will be required to finish the
interval. Or suppose the shift is at Sec 15. At the time of
the shift the clock will essentially read "75% done," and 10
sec will be required to finish the interval. Measured from
the start of the Sec-20 signal, peak time should be about 35
sec (shift at Sec 5), 30 sec (Sec 10), or 25 sec (Sec 15).
Finally, it is possible that the two signals are timed by the
same clock at the same rate--case (c). In this case, the clock
essentially measures absolute time, and the time of the shift
will not change peak time. Suppose the shift is at Sec 5. At
the time of the shift the clock will essentially read "5 sec
done," and 35 sec of the Sec-40 signal will be required to
finish the interval. Measured from the start of the Sec-20
signal, peak time should be about 40 sec (shift at Sec 5),
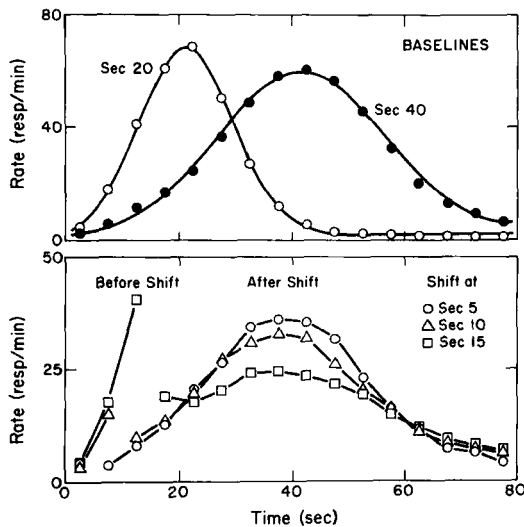40 sec (Sec 10), or 40 sec (Sec 15).

Figure 10. The effect of changing from a Sec-20 signal
to a Sec-40 signal early in the trial. (Figure 15 of
Roberts, 1981. The upper panel shows response rates
on trials with only one signal present throughout the
trial. Different curves show the results from dif-
ferent signals; the label for each curve is the time
that food was primed during the signal. The lower
panel shows response rates on trials that began with
the Sec-20 signal but shifted to the Sec-40 signal
at Sec 5, 10, or 15. Each point is a mean over 10
rats. Copyright 1981 by the American Psychological
Association.)

Figure 10 shows the results. The upper panel shows the dis-
crimination between the two signals, and the lower panel shows
the effect of shifts. Measured from the start of the Sec-20
signal, peak time was near 40 sec for all three shifts. This
suggests that the two intervals were measured by the same
clock, and that the clock timed both intervals at the same
rate. Roberts and Church (1978, Experiment 3) reached the
same conclusions using a fixed-interval procedure.

Times Selectively

As we move from sensory processes to cognitive processes, there
is a considerable increase in selectivity. We see more events
than we notice, and we notice more events than we think about.

The clock might time all stimuli above some sensory threshold, or it might time only some of them. In fact, the clock seems to be selective; apparently, it only times stimuli that signal important events.

To learn what stimuli are timed, we took advantage of cross-modal transfer. After rats were trained to time stimuli from one modality (light or sound), we asked if they timed stimuli from the other modality. An example is an experiment by Roberts and Holder (Note 2) that used a choice procedure. During an initial training phase, rats were trained to press one lever ("short") after a 3-sec signal and the other lever ("long") after a 12-sec signal. We then added treatments and tests of the untrained modality. For concreteness, suppose the trained modality was light and the untrained modality was sound. Sound was treated in three ways: (a) First, it was presented alone, for random durations. (b) Second, it was paired with food. The sound lasted 20 sec and ended with a food pellet. (c) Finally, it was extinguished. The sound lasted 20 sec and ended without a food pellet. The effect of the treatments was measured with test trials. There were two kinds: (a) 0-sec tests. No stimulus was presented, and then the levers were extended into the box. (b) 12-sec tests. The sound was presented for 12 sec, and then the levers were extended into the box. The two tests differ in the duration of the sound. If the rats are timing the sound, they should respond differently on the two types of test; if they are not timing the sound, they will not respond differently.

Figure 11 shows the results. During the first treatment, when sound was presented alone, the rats treated the 0-sec and 12-sec sounds similarly. During the second treatment, when sound was paired with food, the 12-sec sound was treated as longer than the 0-sec sound. During the third treatment, when sound was extinguished, the 0-sec and 12-sec sounds were again treated similarly. During all three treatments, there was no change in the rats' response to light (not shown). These results suggest that the rats timed sound during the second treatment, but not during the first or third treatments. We have found similar results using a 3-sec test instead of a 0-sec test; we have also found similar results with the peak procedure (Roberts and Holder, Note 2). Generalizing from these results, we conclude that (a) rats time stimuli that signal important events and (b) they do not time stimuli that do not signal important events. (We do not know if they time novel stimuli.) Our experiments have only used food as the reinforcer, but we generalize to "important events" because
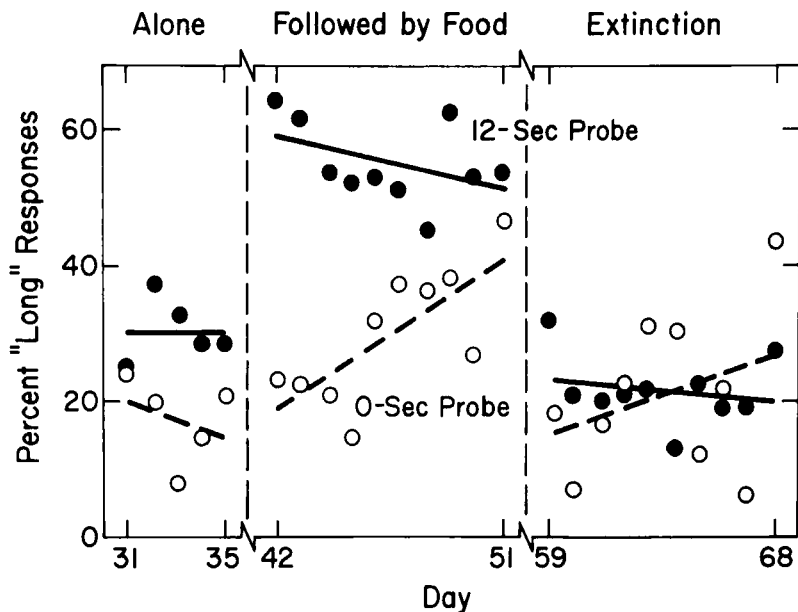
Alone   Followed by Food   Extinction

Figure 11. A stimulus paired with food is timed, but a
stimulus presented alone or extinguished is not timed.
(From Roberts and Holder, Note 2. Each point is a
mean over 8 rats.)

timing occurs when shock is the reinforcer (e.g., LaBarbera
and Church, 1974; Libby and Church, 1974); the term "important
events" is intentionally vague.

The Function of the Clock

Daniel (1976), writing about the design of experiments and the
need for contact with actual problems, commented: "Many
mathematical statisticians are under the illusion that they
and their graduate students are writing for a future which
they forsee without benefit of detailed knowledge of the pre-
sent. A tiny proportion of their work may be remembered 20
years from now" (p. 7). I have the same doubts about labora-
tory research that is inspired by other laboratory research.
When we began this work, the contact with a reality outside
the lab was not clear. We knew of no examples of timing in
natural situations; we did not even know where to look. We
could not cite a plausible, concrete way in which timing would
benefit an animal. I worried that the laboratory task was

entirely artificial, and that the clock was designed (evolved)
for a different purpose. As an example of what I feared, there
is the task of X-ray detection. Laboratory results show that
rats can detect X-rays, at some intensities, they do this with
their olfactory system (Garcia and Koelling, 1971). We can be
sure that animals in nature never detect X-rays, and that the
olfactory system was designed for another purpose. Since then,
however, three sets of facts have come along that show con-
clusively, I think, (a) that animals in natural situations
commonly measure time (duration), (b) that the clock was
designed for timing, and (c) that timing can be useful.

The first set of facts is the remarkable number of similarities
between the rat's clock and an ordinary stopwatch. The
similarities fall into two categories: (a) properties of a
stopwatch that distinguish it from other man-made clocks (e.g.,
that it can be stopped--not all clocks can be stopped); and
(b) properties of a stopwatch that it shares with other man-
made clocks (e.g., a linear scale--all man-made clocks that I
know of have a linear scale). Properties in the first category
(specific to stopwatches) shared by the rat's clock are: (a)
Can be stopped temporarily. Sundials, for example, cannot be
stopped. (b) Internal pacemaker. Electric clocks that require
wall current usually use its alternation in voltage to set
their rate; their pacemaker is at the power station. (c) Times
up. Kitchen timers, for example, time down. (d) Times inter-
vals of different lengths. An egg timer can only time a
single interval. (e) Times intervals of different lengths
using the same rate. Many computer clocks have adjustable
rates. (f) Selectively started. Sundials are always running.
Properties in the second category (general to most man-made
clocks) shared by the rat's clock are: (a) Distinct. Most man-
made clocks can be moved, started, stopped, etc., without
changing other objects. (b) Linear scale. (c) Cross-modal.
Few man-made clocks are restricted to timing stimuli in only
one modality. (d) Path-independent. Our notion of time is
one-dimensional. Two other similarities are less certain:
(a) Accurate. When a person uses a stopwatch to discriminate
duration (e.g., at a track meet), the variance in measurement
probably comes much more from such operations as starting the
clock and recording the result than from the stopwatch. (b)
Can be reset quickly--i.e., it can be moved back to zero much
more quickly than it moves away from zero. An egg timer can-
not be reset quickly unless the interval has finished. We
have not studied this property in the rat's clock; however, it
is suggested by the familiar observation that on an ordinary
fixed-interval schedule--where food delivery defines the be-
ginning of each interval--there is a sudden change from a
high response rate just before food is given to a very low

response rate just afterward. If we assume that response rate
reflects clock setting, then the change in rate reflects the
resetting of the clock. Roberts and Church (1978) describe
other evidence for this property.

It is unlikely that ten or more similarities are due to chance.
The only explanation seems to be that the similar properties
are the result of evolution to perform a similar function
(Roberts and Church, 1978). For the stopwatch, of course,
it was technological evolution; for the rat's clock, biologi-
cal evolution. We know that stopwatches were designed to
measure times on the order of seconds; therefore the rat's
clock was designed to measure times on order of seconds. This
is not the first time that a resemblance between biology and
technology has been used to suggest that the biology is
adaptive (although it may be the first case involving be-
havior). For example, Williams (1966) took the analogies
"between bird wings and airship wings, between bridge
suspensions and skeletal suspensions, between the vasculari-
zation of a leaf and the water supply of a city" (p. 10) as
convincing evidence that the biological structure served the
same purpose as the man-made structure.

The second set of facts is the evidence suggesting that the
clock times selectively; in particular, that it times stimuli
that signal important events and does not time stimuli that
do not signal important events. This property suggests that
animals commonly measure durations in natural situations
because they must commonly encounter signals for important
events, especially food.

Selective timing is also a guide to what the clock was de-
signed to do. A stopwatch-like clock could be used by an
animal in at least five ways: (a) to measure the time between
a stimulus and an important event; (b) to measure the time
between a response and an important event; (c) to measure
the overall density of an important event (Gibbon and Balsam,
1981); (d) to measure the density of an important event dur-
ing a stimulus (Gibbon and Balsam, 1981); and (e) to predict
when an important event will happen. Erasers make pencils
better for writing, but not for punching holes; the presence
of an eraser therefore suggests that a pencil has been de-
signed for writing, and not for punching holes. In a similar
way, the selective-timing property makes the clock better
for predicting when important events will happen (Use e) but
not better for the other uses (a-d); thus it suggests that
the clock was designed for predicting when important events
will happen.

Consider the following sequence of events: (a) At 1:00 p.m.,
a light goes on. (b) At 1:05 p.m., a sound goes on. (c)
At 1:10 p.m., food is given and the clock reading is stored.
At 1:10, the clock could read either "0 min," "5 min," or
"10 min." If we wish to predict the time of food, which
duration would be best to store? There are four cases to
consider: (a) If light is a signal for food and sound is not,
then the clock should read "10 min"--that is the actual
duration between the start of the signal for food and the food.
(b) If sound is a signal for food and light is not, by the
same reasoning the clock should read "5 min." (c) If neither
light nor sound is a signal, then the clock should read "0
min." If the clock timed non-signals, it would lose time
resetting to zero when an actual signal started. (d) If both
light and sound are signals, then the clock should read either
"5 min" or "10 min"; it is hard to say which reading would be
more helpful. The selective-timing results suggest that the
rat's clock will in fact produce the desired readings. Other
possible clocks would not. For example, a clock that timed
all stimuli, and reset completely when a new stimulus started,
would read "5 min" in all cases. This match--between the per-
formance of the clock and the needs of the task--suggests
that the clock was designed for the task.

The conclusion that the clock was designed to predict the time
of important events fits well with what we know about the
function of associative learning. New phenomena of the last
20 years, especially the blocking effect and the selective
nature of taste-aversion learning, make a strong case, I think,
that the function of associative learning is to predict the
future, especially the future likelihood of important events
such as food. Associative learning in rough outline seems to
be a mechanism for predicting the future, and subtleties such
as blocking and the ease with which tastes but not sounds be-
come associated with illness make it better for predicting
the future. Dickinson (1980) makes a similar argument. How-
ever, associative learning, by itself, only allows the animal
to predict what important events will happen. By timing the
signals that associative learning has detected, the animal will
be able to predict when important events will happen.

The third set of facts comes from the study of foraging by
zoologists. When foraging in a patchy environment (where food
is not uniformly distributed), an animal must decide when to
leave one patch and find another. A recent theory about how
animals make this decision (independently proposed by many;
see Krebs, 1978, for a review) emphasizes the use of a
criterion giving-up time, the length of time an animal should
wait without finding food before leaving the patch. The

mechanism is not made explicit, but the underlying idea is that the animal starts its clock at zero when it enters the patch, and resets the clock to zero whenever it finds food. When the clock time is greater than the giving-up time, the animal leaves the patch. The giving-up time is set and changed based on the measurement of interfood intervals. When food becomes sparse (longer interfood intervals), the giving-up time is increased; when food becomes plentiful (shorter interfood intervals), the giving-up time is decreased. This will help the animal maximize its rate of food intake.

This theory shows a specific way in which timing can be useful, and the generality of the problem (finding food in a patchy environment) more or less corresponds with the generality of timing (throughout the vertebrates, at least). More important, however, it has led to the collection of observations that show timing in a natural setting. In a large garden, Davies (1977) watched spotted flycatchers (a small bird) waiting on a perch for flies. Now and then, the birds would leave one perch and go to another. Davies measured the probability of departing as a function of time without a capture attempt (since arriving at the perch or since the last capture attempt). Figure 12 shows the results. The rate of departure increased with the time since the last capture attempt, as foraging theory would predict. Note that the times in Figure 12 are within the range we have been discussing, and that the accuracy of the time discrimination (the line is straight, rather than concave up or down) is not very different from the accuracy of the time discrimination seen in the data of this chapter (e.g., Figure 1). The accuracy is also similar to some laboratory data with pigeons (e.g., Dews, 1970, Figure 2-2). This makes it more plausible that the same timing system is being used in the lab and in nature.

Figure 12 shows one property of laboratory time discriminations--behavior changed with time in a regular way. The other property is that the function relating behavior to time depends on the time of the motivating event. With foraging, this corresponds to the finding that the rate of departure depends on the density of food. In the situation of Davies, the average wait before leaving was 30 sec. The density of food did not change; however, the mean time between captures was 18 sec, so an average wait of 30 sec before leaving was reasonable, and a computer simulation suggested that the average wait was roughly optimal (maximizing the rate of finding food). Other work with birds, in more artificial situations, has shown directly that the average waiting time before departure depends on the average density of food (Cowie, 1977; Krebs and Cowie, 1976; Krebs, Ryan and Charnov, 1974).
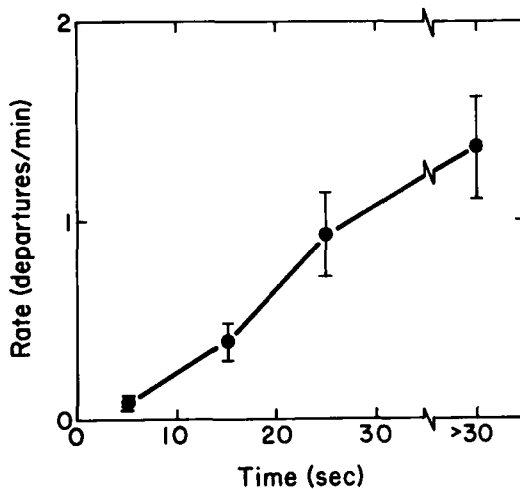
Figure 12. Departure rate changes with time. (Computed
    from data of Figure 21 of Davies, 1977. Before the
    first capture, time was measured from the bird's
    arrival at the perch; after the first capture, time
    was measured from the most recent capture. The
    vertical bars are standard errors based on the
    variance of a binomial probability.)

All three sets of facts suggest that timing is useful--that
an animal that can measure durations has an advantage over one
that cannot. The first set of facts, the convergent evolution
of the stopwatch and the rat's clock, would hardly have been
possible without the same selective force acting on both, and
that force must have been the usefulness of timing. The second
set of facts, the evidence for selective timing, suggests that
timing helps animals predict the future. Prediction of the
future increases control of the future, which is obviously
useful. The third set of facts, the foraging results, shows
a concrete way in which prediction of the future by timing is
useful: It allows the animal to forage more efficiently.

Questions about the "function" of a tool may refer (a) to the
goal of the designers of the tool (its intended function);
(b) to how the tool is used (its actual function); or (c)
especially in the life sciences, to the usefulness of the tool,
its adaptive value. In summary, our work and the work of
others suggest answers to all three questions about the
function of the clock. (a) The rat's clock is designed for
timing--in particular, for predicting the time of important

events. This is suggested both by the similarity between the
rat's clock and a stopwatch and by the fit between the pro-
perties of the clock and the properties needed to use timing
to predict the future. (b) Animals in natural situations use
the clock for measuring durations. This is suggested both by
the conclusion that the clock times all signals for important
events and by the observation of timing in a natural situation.
(c) By helping the animal predict the future, timing helps the
animal control the future. When foraging, for example, timing
can help the animal increase its rate of food intake.

Timing is usually treated in textbooks of animal learning as
no more than a by-product of fixed-interval schedules of rein-
forcement. However, the facts described above suggest that
timing plays a role in the life of the animal similar to the
role of associative learning, which is the main subject of
these textbooks. Both associative learning and timing are used
by the animal to predict the future. Associative learning pre-
dicts what; timing, in conjunction with associative learning,
predicts when.

Relation to Work in Other Areas

Human Timing

Work on duration measurement by humans has covered a much
larger range of durations than our work--from times on the
order of milliseconds (e.g., Massaro and Idson, 1976; Thomas
and Weaver, 1975) to times on the order of many minutes (e.g.,
Block, George and Reed, 1980; Ornstein, 1969). My comments
below are restricted to work involving times of 1-20 sec; the
measurement of longer and shorter times is too likely to in-
volve clocks different from the one we have studied. In
animals, the clock used for measuring durations less than a
second may be different than the clock used with longer times;
the evidence is that, as mentioned earlier, Millenson, Kehoe
and Gormezano (1977), using durations of a few hundred milli-
seconds, found symmetry on a log scale of time, whereas our
work, using durations of seconds, has found symmetry on a
linear scale. In humans, work described below suggests that
the clock used for measuring durations less than 20 sec is
different than the clock used with longer times.

For the measurement of durations on the order of seconds, is
a human's clock the same as a rat's? We can compare the two
clocks on the following properties:

Internal pacemaker. The rate of the rat's clock is determined
internally, at least partially. The same seems to be true of
the human's clock. There are three lines of evidence: (a)

Drug effects. Adam, Rosner, Hosick and Clark (1971) found that
breathing anesthetic gases, such as cyclopropane, caused sub-
jects to produce time intervals about 20% longer than usual.
(With the method of production, subjects are told the name of
a time interval--say, "10 sec"--and asked to mark it off.)
The increase was roughly a constant proportion of the interval
to be produced; this is easy to explain if the drugs changed
the rate of the clock, and hard to explain otherwise.
Frankenhaeuser (1959) found similar evidence that nitrous
oxide slowed down the clock by about 20%; she used the method
of estimation (e.g., the subject is asked to name the interval
between two clicks). Agreement between the results of esti-
mation and production--e.g., a drug that causes 10% overesti-
mation also causes 10% underproduction--suggests that the drug
changes the clock; this is because the clock is probably the
only operation that the two tasks have in common. Goldstone,
Boardman and Lhamon (1958) and Goldstone and Kirkham (1968)
found that dextroamphetamine decreased by about 15% the physi-
cal duration that subjects judged equal to 1 sec. This is
similar to what we found with methamphetamine (Maricq et al.,
1981), and presumably the mechanism is the same--the rate of
the clock was increased. Many other experiments have found
that a drug changes time estimation or production, but none of
the twenty or so I have looked at had enough evidence to
suggest that the rate of the clock had been changed. (b)
Stress effects. Subjects said that more time had passed dur-
ing an interval when they expected a shock at the end of the
interval than when they did not expect a shock (Hare, 1968);
the overestimation was about 3 times larger with a 20-sec
interval than a 5-sec interval. Frankenhaeuser (1959) and
Langer, Wapner and Werner (1961) found similar results also
using the method of estimation; Falk and Bindra (1954) found
similar results using the method of production. (c) Tempera-
ture effects. Many experiments have found that increasing body
temperature causes overestimation and underproduction of dur-
ations, and lowering body temperature has the opposite effects.
The changes in body temperature have been produced by fever
(Hoagland, 1933), diathermy (Francois, 1927; Hoagland, 1933),
time of day (Francois, 1927, Pfaff, 1968), hot and cold air
(Fox, Bradbury, Hampton and Legg, 1967), and cold water
(Baddeley, 1966; Bell, 1975). Results of production and
estimation are similar (Pfaff, 1968), suggesting that the
clock is changed. Temperature effects are the evidence usually
used to suggest an internal pacemaker; actually, this line of
evidence is weaker than the first two because all of the
results could be explained by changes in any feature of the
clock, not just its rate. Better evidence would show that the
temperature effect increases linearly with the duration used.

Cross-modal. The rat has a clock that measures durations of
both light and sound. Likewise, there is something cross-
modal about the human timing system. The clearest evidence
is the work of Warm, Stutz and Vassolo (1975), who found that
training for accuracy in timing transferred from light to
sound and from sound to light. In addition, Behar and Bevan
(1961) found large cross-modal anchor effects in the judgment
of duration; for example, a 10-sec light changed the reported
durations of subsequent 1- to 5-sec sounds. Roberts (1982)
summarizes other experimental evidence. Another sort of
evidence, less convincing but more vivid, comes from language.
Duration is a word attached to no particular modality, and
adjectives of duration (brief, long) can be applied to stimuli
from any modality.

The human evidence, unlike the rat evidence, does not allow
us to say where the timing system for light and the timing
system for sound converge. It might be at the clock, or it
might be later. As an example, consider the cross-modal use
of adjectives of duration. Let us assume that two physical
events will be labeled with the same word if they produce to
some extent the same mental event. Then adjectives of duration
could be cross-modal for two reasons: (a) Learned associations.
We may use brief with both lights and sounds because brief
lights and sounds often occur together. Via learning, brief
sounds recall brief lights and vice-versa. Co-occurrence
is probably why sharp has both a visual and a tactual mean-
ing (a knife can both look and feel sharp). (b) Unlearned
wiring. Unlearned wiring is probably why we used red to
describe both left- and right-eye stimuli. Because similar
results (cross-modal effects in timing) in similar animals
(rats and people) are probably due to the same mechanism, it
is reasonable to conclude that adjectives of duration are
cross-modal due to unlearned wiring--light and sound are timed
by the same clock. Here is a case where a result in animal
learning (the rat's clock is cross-modal) seems to shed light
on a feature of human thought (our cross-modal concept of
duration). Usually, clearcut applications of animal learning
to human life are in less cognitive areas, such as food
preferences or fear.

Linear scale. The rat's clock has a scale that is linear with
physical time. The same seems to be true of the human's
clock. Eisler (1976) reviewed about a hundred scaling studies,
and concluded that clock time was a power function of physical
time with an exponent of about .9. Allan (1979), making
somewhat different assumptions, concluded that an exponent of
1.0 was most consistent with the literature. The difference
between .9 and 1.0 is not important for our purposes because

the rat data are not that precise. The symmetry of the re-
sponse-rate functions (e.g., Figure 3) suggests that the scale
of the rat's clock is much closer to linear (corresponding to
an exponent of 1) than to logarithmic (corresponding to an
exponent of 0-see Tukey, 1977, pp. 86-91); it does not allow
one to say if the exponent is closer to .9 or 1.0.

Range. The range of the rat's clock seems to be larger than
the range of the human's clock. In most of our work, we have
used procedures involving times on the order of 1-10 sec and
times on the order of 20-60 sec. The conclusions with both
ranges of times have been the same for four properties: (a)
can be stopped (Roberts and Church, 1978; Roberts, 1981);
(b) internal pacemaker (Maricq, Roberts and Church, 1981;
Roberts, 1981); (c) cross-modal (Roberts, 1982); and (d) times
selectively (Roberts and Holder, Note 3). This suggests that
rats use the same clock for measuring times in both ranges.
In contrast, there is evidence that humans use different
clocks with the two ranges. Richards (1973), studying the
patient H. M., found that his reproduction of durations was
normal (power function with exponent of 1.0) for times less
than 20 sec. and clearly abnormal (power function with ex-
ponent of .4) for times more than 20 sec. This suggests that
different clocks are used for the measurement of times less
than and greater than 20 sec. Because H. M.'s most obvious
deficit is the inability to form long-term memories, these
results also suggest that, in normals, the measurement of times
greater than 20 sec uses this ability; for example, we may
judge the duration of an interval by how much we remember from
it (e.g., Ornstein, 1969). This is probably different than
using a specialized clock. More evidence that humans measure
durations above and below 20 sec with different clocks comes
from Frankenhauser (1959). Her subjects read digits at what
the subject considered to be a 1-sec pace. The number of
digits read was determined by the experimenter. After reading
the required number of digits, the subject estimated how much
time had passed. The ratio of the estimated time to the actual
(physical) time varied with the actual time; the ratio started
at about .85 at 4 sec, declined to about .65 near 20 sec, and
was constant from 20 sec to 50 sec, the edge of the range.
The change in slope at 20 sec is evidence for a change in
mechanism.

As far as I know, there is no conclusive evidence that shows
if the human's clock has other properties of the rat's clock
that I have discussed above (e.g., distinctness). In general,
work on human timing has been much different than our work,
with much less emphasis on the underlying clock.

In summary, the human and rat clocks seem to be similar in three ways (internal pacemaker, cross-modal, linear scale) and different in one way (range). It is too early to say if the underlying mechanism is the same. It is clear, though, that data in one field bear on questions asked in the other field.

Associative Learning

One view of our work is that it provides a new example of associative learning: The situations that do and do not start the clock are similar to the situations that do and do not produce traditional examples of classical conditioning. A dog does not salivate during a sound after the sound has been presented alone; it salivates during the sound after the sound is followed by food; and it no longer salivates during the sound after the sound is extinguished. A rat's clock does not time a sound after the sound has been presented alone; it does time the sound after the sound is followed by food; and it no longer times the sound after the sound is extinguished (Roberts and Holder, Note 2). Whenever a new preparation is found to follow the rules of associative learning, the question arises: Are the new results (e.g., with the clock) due to the same mechanism as the older results (e.g., with salivation) on which the rules are based? earlier examples? Taste-aversion learning was different in three or four ways (e.g., learning with delays of hours between CS and US) from earlier examples of classical conditioning, and the differences led some people (e.g., Garcia, Hankins and Rusiniak, 1974) to conclude that the underlying mechanisms were different. Our results differ in at least one way from earlier examples of classical conditioning: The operations of associative learning (e.g., pairing, extinction) are apparently changing an earlier part of the stimulus-response path. Earlier examples of classical conditioning have all involved changes in the linkage of stimuli to responses, and could be explained by changes in associative memory. However, in this case what is changed is the clock; the clock is "earlier" than associative memory in the sense that the output of the clock goes to associative memory--the output of the clock can be a CS. We have only begun to assess the analogy between timing and earlier examples of associative learning, and it is too early to choose between two possibilities: (a) The operations of associative learning act on two different mechanisms, one before the clock, one after. This parallels the position that taste-aversion learning and earlier examples of classical conditioning are due to different mechanisms, i.e., that taste aversion is a new form of learning. (b) The operations of associative learning act on a single mechanism, and this mechanism is more complicated

than we thought--it must send output to operations from which
it receives input. This parallels the position that taste
aversion learning and earlier examples of classical condi-
tioning are due to the same mechanism, but this mechanism is
more complicated than we thought--e.g., a CS may sometimes
be stored for hours.

Another view of our work emphasizes a more subtle similarity
to traditional associative learning. By a sort of triangu-
lation, conclusions about the function of the clock help us
decide the function of associative learning. Knowing only
one means to an end, it is hard to decide what is means and
what is end. A compass points in a certain direction; is it
attracted to the nearby tree, the distant mountain, or some-
thing else? To find out, we need another placement. In a
similar way, the function of a tool can be described with vary-
ing amounts of abstraction, and we need to study other tools to
choose the right amount. Are pencils for (a) making graphite
marks on paper or (b) making dark marks on paper? There are
no other tools that do (a); and there are pens, which do (b).
This suggests that (b) is a better answer than (a). The
existence of the more abstract goal of writing, which we might
deduce from video terminals, does not change the fact that
we have learned something about pencils by considering pens.
Is associative learning for (a) detecting cause and effect
(e.g., Dickinson, 1980, p. 9) or (b) predicting the future?
Because there is apparently no other mechanism designed to do
(a), and because the clock is apparently designed to do (b),
(b) is the better answer. The existence of the more abstract
goals of survival and reproduction, which we might deduce from
a hundred other adaptations, does not change this. This argu-
ment assumes that the mechanism responsible for associative
learning is somehow distinct from the clock, just as pencils
are distinct from pens. Support for this assumption comes
from the fact that bees show associative learning but not
timing.

Animal Cognition

Like other work in the field of animal cognition, this work
tries to study only part of what happens between stimulus
and response; but it does this in an unusual way. Three
methodological features of this work may be useful in other
situations.

First, this work provides evidence for the assumption that the
clock is distinct--i.e., that the clock can be changed without
changing other operations, and that other operations can be
changed without changing the clock. Assumptions of

distinctness are very common, but the supporting evidence is
usually weak or non-existent. For example, Rescorla (1978)
distinguishes between associative bonds and the representations
being bonded; in his words, between "knowledge about the re-
lation" of two events and "the value of the event repre-
sentations" (p. 39). The distinction is appealing, but, as
far as I know, there is no evidence for it. Rescorla (1978)
uses the notion of distinct event representations to inter-
pret four diverse experiments.

Second, this work makes explicit the notion of "isolating" a
mental process and shows one way of doing it. Isolating a
mental process, call it P, means finding a measure of be-
havior such that (a) a change in the measure implies a change
in P; and/or (b) no change in the measure implies no change
in P. P might be a clock, short-term memory, the association
between two events, an event representation, stimulus en-
coding, the retrieval stage, etc. To learn about P it is
essential to isolate P. Suppose you do an experiment that
varies Factor F (e.g., shock density, contingency, pre-
exposure). The results will reveal nothing about P unless you
can decide if changing F changed P; to decide, you need to have
isolated P. Of course, experimenters often use results to
draw conclusions about a mental process; they implicitly assume
that they have isolated the process. For example, Grant (1981)
takes a variety of results involving percent correct in delayed
-symbolic-matching-to-sample experiments to suggest that
pigeons remember the test stimulus rather than the sample
stimulus during the delay interval. Implicit in Grant's con-
clusion about the contents of memory is the assumption that
percent correct isolates the contents of memory. One experi-
ment, for example, measured the effect of repeating the sample,
and compared the effects of "physical" repetition (exacly the
same sample is presented twice) with "instructional" repeti-
tion (two different samples are shown, but both have the same
correct match, e.g., the green key, so that both mean "peck
green.") Repetition increased percent correct (two samples
were better than one), and this was taken to suggest that re-
petition changed the contents of memory; this assumes, of
course, that a change in percent correct implies a change
in the contents of memory. The two types of repetition pro-
duced the same increase, and Grant concluded from this that
the contents of memory were the same in the two cases; this
assumes, of course, that no change in percent correct implies
no change in the contents of memory. Without the assumption
that percent correct isolates the contents of memory, nothing
could have been concluded about the contents of memory; how-
ever, Grant gives no evidence for this assumption.

Third, this work uses a procedure (the peak procedure) chosen
to explain the result of interest (timing); most procedures
now used to study animal cognition seem chosen to demonstrate
the result of interest (e.g., associative learning, short-term
memory). To see this distinction, compare an ordinary fixed-
interval schedule with the peak procedure. The fixed-interval
schedule is better than the peak procedure for demonstrating
timing; it is easier to implement and to describe. On the
other hand, it is worse than the peak procedure for explain-
ing timing; with a fixed-interval schedule, most changes in
behavior could be equally well explained by a change in the
clock or a change somewhere else (for an example, see Roberts,
1981, Experiment 4). The Olton and Samuelson (1976) eight-
arm radial-maze procedure is another example of a procedure
that is good for demonstration but, probably, poor for ex-
planation. When the experimenter chooses the first few arms
that the rat will visit (Beatty and Shavalia, 1980), it is
apparently easy to demonstrate the existence of a high-
capacity, long-lasting spatial memory. However, it is pro-
bably hard to use the procedure to learn much more about this
memory. The usual measure of performance is percent correct.
Because of ceiling effects (accuracy is usually high), it is
unlikely that no change in percent correct implies no change
in spatial memory. Because the task requires more than
spatial memory (e.g., motivation, sensory input), it is un-
likely that a change in percent correct implies a change in
spatial memory. The interests of psychologists studying
animal behavior seem to have shifted over the last ten years
from the behavior in general to the mental components (e.g.,
short-term memory, associations) that produce the behavior
(e.g., Hulse, Fowler and Honig, 1978); it was probably in-
evitable that the procedures used would lag behind.

McFarland (1981) defines animal cognition as the study of
"mental processes that are presumed to be occurring within the
animal, but which cannot be directly observed" (p. 71). I
think that most people would agree with this definition (e.g.,
Skinner, 1950; Honig, 1978; but see Bolles, 1979, p. 192);
however, I do not. The phrase "directly observed" seems to
imply that there is a qualitative difference between the way
we observe, say, behavior (directly) and the way we observe
mental processes (not directly). We may say this, but it is
contradicted by our actions. I measure response rate
("directly") by counting the number of times a switch is
closed, and use my counts to make statements about what the
animal has done. Implicit in these statements is the as-
sumption that my counts isolate response rate--that a change
in count implies a change in rate and/or no change in count
implies no change in rate. It is a very plausible assumption,

but it is testable (measure rate in some other way, e.g., by
watching) and therefore could be wrong. I measure the clock
("not directly") by measuring peak time with the peak pro-
cedure. When I use peak time to make statements about the
clock, I am assuming that peak time isolates the clock--that
a change in peak time implies a change in the clock and/or no
change in peak time implies no change in the clock. It is
less plausible than the counts-to-rate assumption, but it is
testable (measure the clock in some other way, e.g., with a
choice procedure) and therefore could be right. Implicit in
eighty years of conclusions about the mental processes of
animals are eighty years of assuming that mental processes can
indeed be isolated. A more accurate definition of animal
cognition would refer to "mental processes . . . which cannot
be easily observed."

Footnote

References Notes

1. Eckerman, D. A. Performance fixed-interval reinforcer schedules of about a day. Paper presented at the meeting of the Psychonomic Society, November, 1977.

2. Roberts, S., & Holder, M. What starts an internal clock? Manuscript submitted for publication, 1982.

References

1   Adams, N., Rosner, B. S. Hosick, E. C. & Clark, D. L.
    Effect of anesthetic drugs on time production and
    alpha rhythm. Perception & Psychophysics, 1971,
    10, 133-136.

2   Allan, L. G. The perception of time. Perception & Psycho-
    physics, 1979, 26, 340-354.

3   Ambler, S.   A comparison of two models for performance
    under fixed interval schedules of reinforcement. Journal
    of Mathematical Psychology, 1976, 14, 53-71.

4   Anderson, M. C. & Shettleworth, S. J. Behavioral
    adaptation to fixed-interval and fixed-time food de-
    livery in golden hamsters. Journal of the Experimental
    Analysis of Behavior, 1977, 25, 33-49.

5   Azrin, N. H. Conditioning of the aggressive behavior of
    pigeons by a fixed-interval schedule of reinforcement.
    Journal of the Experimental Analysis of Behavior, 1967,
    10, 395-402.

6   Baddeley, A. D. Time-estimation at reduced body-tempera-
    ture. American Journal of Psychology, 1966, 79, 475-
    479.

7   Balster, R. L. & Schuster, C. R. Fixed-interval schedule
    of cocaine reinforcement: Effect of dose and infusion
    duration. Journal of the Experimental Analysis of Be-
    havior, 1973, 20, 119-129.

8   Beatty, W. W. & Shavalia, D. A. Spatial memory in rats:
    Time course of working memory and effect of anesthetics.
    Behavioral and Neural Biology, 1980, 28, 454-462.

9   Behar, I. & Bevan, W. The perceived duration of auditory
    and visual intervals: Cross-modal comparison and inter-
    action. American Journal of Psychology, 1961, 74, 17-26.

10 Bell, C. R. Effects of lowered temperature on time
    estimation. Quarterly Journal of Experimental Psychology,
    1975, 27, 531-538.

11 Blakemore, C. & Campbell, F. W. On the existence of
    neurones in the human visual system selectively sensitive
    to the orientation and size of retinal images. Journal
    of Physiology, 1969, 203, 237-260.

12 Block, R. A., George, E. J. & Reed, M. A.   A watched
    pot sometimes boils: A study of duration experience.
    Acta Psychologia, 1980, 46, 81-94.

13 Bolles, R. C. Learning theory (2nd Ed.). New York: Holt,
    Rinehart, and Winston, 1979.

14 Boulos, Z., Rosenwasser, A. M. & Terman, M.   Feeding
    schedules and the circadian organization of behavior
    in the rat. Behavioral Brain Research, 1980, 1, 39-65.

15 Brown, J. S. Generalization and discrimination.   In
    D. I. Mostofsky (Ed.), Stimulus generalization.
    Stanford, Calif.: Stanford University Press, 1965.

16 Cantor, M. B. & Wilson, J. F.   Temporal uncertainty as
    an associative metric: Operant simulations of Pavlovian
    conditioning. Journal of Experimental Psychology:
    General, 1981, 110, 232-268.

17 Carlson, J. G., Wielkiewicz, R. M. & Modjeski, R. B.   The
    Psychological Record, 1972, 22, 531-542.

18 Catania, A. C.   Reinforcement schedules and psychophysical
    judgments: A study of some temporal properties of be-
    havior. In W. N. Schoenfeld (Ed.), The theory of rein-
    forcement schedules. New York: Appleton-Century-Crofts,
    1970.

19 Church, R. M.   The internal clock. In S. H. Hulse,
    H. Fowler & W. K. Honig (Eds.), Cognitive processes in
    animal behavior. Hillsdale, N. J.: Lawrence Erlbaum
    Associates, 1978.

20 Church, R. M.   Short-term memory for time intervals.
    Learning and Motivation, 1980, 11, 208-219.

21 Church, R. M. & Deluty, M. Z.   Bisection of temporal
    intervals. Journal of Experimental Psychology: Animal
    Behavior Processes, 1977, 3, 216-228.

22 Church, R. M., Getty, D. J. & Lerner, N. D.   Duration
    discrimination by rats. Journal of Experimental Psycho-
    logy: Animal Behavior Processes, 1976, 2, 303-312.

23 Church, R. M. & Gibbon, J.   Temporal generalization.
    Journal of Experimental Psychology: Animal Behavior
    Processes, 1982, 8, 165-186.

24 Cone, A. L. & Cone, D. M. Operant conditioning of
    Virginia opossum. Psychological Reports, 1970, 26, 83-86.

25 Cowey, A. & Weiskrantz, L. Demonstration of cross-modal
    matching in rehesus monkeys, Macaca mulatta. Neuropsycho-
    logia, 1975, 13, 117-120.

26 Cowie, R. J. Optimal foraging in great tits (Paras major).
    Nature, 1977, 268, 137-139.

27 Cowles, J. T. & Finan, J. L. An improved method for
    establishing temporal discrimination in white rats. The
    Journal of Psychology, 1941, 11, 335-342.

28 Creelman, C. D. Human discrimination of auditory duration.
    Journal of the Acoustical Society of American, 1962, 34,
    582-593.

29 Daniel, C. Applications of statistics to industrial
    experimentation. New York: Wiley, 1976.

30 Davies, N. B. Prey selection and the search strategy of
    the spotted flycatcher (Muscicapa striata): A field study
    on optimal foraging. Animal Behaviour, 1977, 25, 1016-
    1033.

31 Dews, P. B. The effect of multiple S[delta] periods on
    responding on a fixed-interval schedule. Journal of the
    Experimental Analysis of Behavior, 1962, 5, 369-374.

32 Dews, P. B. The effect of multiple S[delta] periods on
    responding on a fixed-interval schedule: III. Effect of
    changes in pattern of interruptions, parameters and
    stimuli. Journal of the Experimental Analysis of Be-
    havior, 1965, 8, 427-435.

33 Dews, P. B. The theory of fixed-interval responding. In
    W. N. Schoenfeld, The theory of reinforcement schedules.
    New York: Appleton-Century-Crofts, 1970.

34 Dickinson, A. Contemporary animal learning theory.
    Cambridge, England: Cambridge, 1980.

35 Eisler, H. Experiments on subjective duration 1868-1975:
    A collection of power function exponents. Psychological
    Bulletin, 1976, 83, 1154-1171.

36 Falk, J. L. & Bindra, B. Judgment of time as a function
    of serial position and stress. Journal of Experimental
    Psychology, 1954, 47, 279-282.

37 Fox, R. H., Bradbury, P. A., Hampton, I. F. G. & Legg,
    C. F. Time judgment and body temperature. Journal of
    Experimental Psychology, 1967, 75, 88-96.

38 Francois, M. Contribution a l'etude du sens du temps:
    La temperature interne comme facteur de variation de
    l'appreciation subjective des durees. Annee psychologie,
    1927, 28, 186-204.

39 Frankenhaeuser, M. Estimation of times: An experimental
    study. Stockholm: Almqvist & Wiksell, 1959.

40 Garcia, J., Hankins, W. G. & Rusiniak, K. W. Behavioral
    regulation of the milieu interne in man and rat. Science,
    1974, 185, 824-831.

41 Garcia, J. & Koelling, R. A. The use of ionizing rays as
    a mammalian olfactory stimulus. In L. M. Beidler (Ed.),
    Handbook of sensory physiology (Vol. 4). Berlin: Springer-
    Verlag, 1971.

42 Getty, D. J. Counting processes in human timing. Per-
    ception & Psychophysics, 1976, 20, 191-197.

43 Gibbon, J. Scalar expectancy theory and Weber's law in
    animal timing. Psychological Review, 1977, 84, 279-325.

44 Gibbon, J. On the form and location of the psychometric
    bisection function for time. Journal of Mathematical
    Psychology, 1981, 24, 58-87.

45 Gibbon, J. & Balsam, P. Spreading association in time.
    In C. M. Locurto, H. S. Terrace & J. Gibbon (Eds.),
    Autoshaping and conditioning theory. New York: Academic
    Press, 1981.

46 Gibbon, J. & Church, R. M. Time left: Linear versus
    logarithmic subjective time. Journal of Experimental
    Psychology: Animal Behavior Processes, 1981, 7, 87-108.

47 Goldstone, S., Broadman, W. K. & Lhamon, W. T. Effect
    of quinal baritone, dextrose-amphetamine, and placebo on
    apparent time. British Journal of Psychology, 1958, 49,
    324-328.

48 Goldstone, S. & Kirkham, J. E. The effects of secobarbital
    and dextroamphetamine upon time judgment: Intersensory
    factory. Psychopharmacologia, 1968, 13, 65-73.

49 Grant, D. S. Short-term memory in the pigeon. In N. E.
    Spear & R. R. Miller (Eds.), Information processing in
    animals: Memory mechanisms. Hillsdale, N. J.: Lawrence
    Erlbaum Associates, 1981.

50 Grossman, K. E. Continuous, fixed-ratio, and fixed-
    interval reinforcement in honey bees. Journal of the
    Experimental Analysis of Behavior, 1973, 20, 105-109.

51 Hare, R. D. The estimation of short temporal intervals
    terminated by shock. Journal of Clinical Psychology, 1963,
    19, 378-380.

52 Hoagland, H. The physiological control of judgments of
    duration: Evidence for a chemical clock. Journal of
    General Psychology, 1933, 9, 267-287.

53 Honig, W. K. On the conceptual nature of cognitive terms:
    An initial essay. In S. H. Hulse, H. Fowler & W. K. Honig
    (Eds.), Cognitive processes in animal behavior. Hillsdale,
    N. J.: Lawrence Erlbaum Associates, 1978.

54 Hulse, S. H., Fowler, H. & Honig, W. K. (Eds.). Cognitive
    processes in animal behavior. Hillsdale, N. J.:
    Lawrence Erlbaum Associates, 1976.

55 Keller, K. J. Inhibitory effects of reinforcement and
    a model of fixed-interval performance. Animal Learning
    & Behavior, 1980, 8, 102-109.

56 Killeen, P. On the temporal control of behavior. Psycho-
    logical Review, 1975, 82, 89-115.

57 Killeen, P. R. Learning as causal inference. In M. L.
    Commons & J. A. Nevin (Eds.), Quantitative analyses of
    behavior: Discriminative properties of reinforcement
    schedules. Cambridge, Mass.: Ballinger, 1981.

58 Kinchla, J. Duration discrimination of acoustically de-
    fined intervals in the 1- to 8-sec range. Perception &
    Psychophysics, 1972, 12, 318-320.

59 King, G. D., Schaeffer, R. W. & Pierson, S. C. Rein-
    forcement schedule preference of a racoon (Procyon
    lotor). Bulletin of the Psychonomic Society, 1974, 4,
    97-99.

60 Klosterhalfen, S., Fischer, W. & Bitterman, M. E. Modi-
    fication of attention in honey bees. Science, 1978, 201,
    1241-1243.

61 Koltermann, R. Periodicity in the activity and learning
    performance of the honeybee. In L. B. Browne (Ed.),
    Experimental analysis of insect behavior. Berlin:
    Springer-Verlag, 1974.

62 Kramer, T. J. & Rilling, M. Differential reinforcement of
    low rates: A selective critique. Psychological Bulletin,
    1970, 74, 224-254.

63 Krebs, J. R. Optimal foraging: Decision rules for pre-
    dators. In J. R. Krebs & N. B. Davies (Eds.), Behavioral
    ecology: An evolutionary approach. Oxford: Blackwell
    Scientific Publications, 1978.

64 Krebs, J. R. & Cowie, R. J. Foraging strategies in birds.
    Ardea, 1976, 64, 98-116.

65 Krebs, J. R., Ryan, J. C. & Charnov, E. L. Hunting by
    expectation or optimal foraging: A study of patch use by
    chickadees. Animal Behavior, 1974, 22, 953-964.

66 LaBarbera, J. D. & Church, R. M. Magnitude of fear as a
    function of expected time to an aversive event. Animal
    Learning & Behavior, 1974, 2, 199-202.

67 Langer, J., Wapner, S. & Werner, H. The effect of danger
    upon the experience of time. American Journal of
    Psychology, 1961, 74, 94-97.

68 Libby, M. E. & Church, R. M. Timing of avoidance re-
    sponses by rats. Journal of the Experimental Analysis of
    Behavior, 1974, 22, 513-517.

69 Libby, M. E. & Church, R. M. Fear gradients as a function
    of the temporal interval between signal and aversive
    event in the rat. Journal of Comparative and Physiological
    Psychology, 1975, 88, 911-916.

70 Logan, F. A. Hybrid theory of operant conditioning.
    Psychological Review, 1979, 86, 507-541.

71 McFarland, D. The Oxford companion to animal behavior.
    Oxford: Oxford University Press, 1981.

72 Maki, W. S. Discrimination learning without short-term
    memory: Dissociation of memory processes in pigeons.
    Science, 1979. 204, 83-85.

73 Maricq, A. V., Roberts, S. & Church, R. M. Methamphetamine
    and time estimation. Journal of Experimental Psychology:
    Animal Behavior Processes, 1981, 7, 18-30.

74 Massaro, D. W. & Idson, W. L. Temporal course of per-
    ceived auditory duration. Perception & Psychophysics,
    1976, 20, 331-352.

75 Meck, W. H. & Church, R. M. Abstraction of temporal
    attributes. Journal of Experimental Psychology: Animal
    Behavior Processes, 1982, 8, 226-243.

76 Millenson, J. R., Kehoe, E. J. & Gormezano, I. Classical
    conditioning of the rabbit's nictating membrane response
    under fixed and mixed CS-US intervals. Learning and
    Motivation, 1977, 8, 351-366.

77 Morrell, F. Visual system's view of acoustic space.
    Nature, 1972, 238, 44-46.

78 Olton, D. S., & Samuelson, R. J. Remembrance of places
    passes: Spatial memory in rats. Journal of Experimental
    Psychology: Animal Behavior Processes, 1976, 2, 97-116.

79 Ornstein, R. E. On the experience of time. Baltimore:
    Penguin, 1969.

80 Over, R. & Mackintosh, N. Cross-modal transfer of
    intensity discrimination by rats. Nature, 1969, 224,
    918-919.

81 Pavlov, I. P. Conditioned reflexes (G. B. Anrep, Ed. and
    trans.). New York: Dover, 1960. (Originally published,
    1926.)

82 Pfaff, D. Effects of temperature and time of day on time
    judgments. Journal of Experimental Psychology, 1968, 76,
    419-422.

83 Platt, J. R., Kuch, D. O. & Bitgood, S. C. Rats' lever-
    press duration as psychophysical judgments of time.
    Journal of the Experimental Analysis of Behavior, 1973,
    19, 239-250.

84 Powell, R. W. Time-based responding in pigeons and crows.
    Auk, 1973, 90, 803-808.

85 Rescorla, R. Some implications of a cognitive perspective
    on Pavlovian conditioning. In S. H. Hulse, H. Fowler
    & W. K. Konig (Eds.), Cognitive processes in animal be-
    havior. Hillsdale, N. J.: Lawrence Erlbaum Associates,
    1978.

86 Richards, W. Time reproductions by H. M. Acta Psycho-
    logica, 1973, 37, 279-282.

87 Richardson, W. K. & Loughead, T. E. Behavior under large
    values of the differential-reinforcement-of-low-rate
    schedule. Journal of the Experimental Analysis of Be-
    havior, 1974, 22, 121-129.

88 Richelle, M. & Lejeune, H. Time in animal behaviour.
    Oxford: Pergamon Press, 1980.

89 Roberts, S. Isolation of an internal clock. Journal of
    Experimental Psychology: Animal Behavior Processes,
    1981, 7, 242-268.

90 Roberts, S. Cross-modal use of an internal clock. Journal
    of Experimental Psychology: Animal Behavior Processes,
    1982, 8, 2-22.

91 Roberts, S. & Church, R. M. Control of an internal clock.
    Journal of Experimental Psychology: Animal Behavior
    Processes, 1978, 4, 318-337.

92 Rozin, P. Temperature independence of an arbitrary
    temporal discrimination in the goldfish. Science, 1965,
    149, 561-563.

93 Rubin, M. B. & Brown, H. J. The rabbit as subject in be-
    havioral research. Journal of the Experimental Analysis
    of Behavior, 1969, 12, 663-667.

94 Shepard, R. N. Approximation to uniform gradients of
    generalization by monotone transformations of scale.
    In D. I. Mostofsky (Ed.), Stimulus generalization.
    Stanford, Calif.: Stanford University Press, 1965.

95 Sherman, J. G. The temporal distribution of responses
    on fixed-interval schedules. Unpublished Ph.D.
    dissertation, Columbia University, 1959.

96 Shumake, S. A. & Caudill, C. J. Operant conditioning
    of licking in vampire bats, Desmodus rotundus. Behavioral
    Research Methods and Instrumentation, 1974, 6, 467-470.

97   Skinner, B. F. Are theories of learning necessary?
     Psychological Review, 1950, 57, 193-216.

98   Skinner, B. F. A case history in scientific method.
     American Psychologists, 1956, 2, 221-233. Reprinted
     in M. H. Siegel & H. P. Zeigler (Eds.), Psychological
     research: The inside story. New York: Harper & Row,
     1976.

99   Sprott, R. L. & Symons, J. P. Oqerant performance in in-
     bred mice. Bulletin of the Psychonomic Society, 1974,
     4, 46-48.

100 Staddon, J. E. R. Temporal control, attention, and
     memory. Psychological Review, 1974, 81, 375-391.

101 Sternberg, S. The discovery of processing stages:
     Extensions of Donders' method. Acta Psychologica, 1969,
     30, 276-313.

102 Teuber, H. L. Physiological psychology. Annual Review
     of Psychology, 1955, 6, 267-296.

103 Thomas, E. A. C. & Weaver, W. B. Cognitive processing
     and time perception. Perception & Psychophysics, 1975,
     17, 363-367.

104 Tukey, J. W. Exploratory data analysis. Reading, Mass.:
     Addison-Wesley, 1977.

105 Warm, J. S., Stutz, R. M. & Vassolo, P. Intermodal
     transfer in temporal discrimination. Perception &
     Psychophysics, 1975, 18, 281-286.

106 Warrington, E. K. & Weiskrantz, L. An analysis of short-
     term and long-term memory deficits in man. In J. A.
     Deutsch (Ed.), The physiological basis of memory. New
     York: Academic Press, 1973.

107 Williams, G. C. Adaptation and natural selection: A
     critique of some current evolutionary thought. Princeton,
     N. J.: Princeton, 1966.

108 Yagi, B. The effect of motivating conditions on "the
     estimation of time" in rats. Japanese Journal of
     Psychology, 1962, 33, 8-24.

109 Ziriax, J. M. & Silberberg, A. Discrimination and
     emission of different key-peck durations in the pigeon.
     Journal of Experimental Psychology: Animal Behavior
     Processes, 1978, 4, 1-21.