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Isolation of an Internal Clock

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Examples of time discrimination suggest that many animals have an internal clock that measures times on the order of seconds. This article reports five experiments that use a new procedure to study this clock. The new procedure is similar to a discrete-trials fixed-interval procedure. There are two types of trials, randomly mixed: (a) On food trials, the first response (lever press) after a fixed time—usually 40 sec—is rewarded with food; the trial then ends. (b) On empty trials, no food is given; the trial lasts an average of 160 sec and ends independently of responding. The main measures of performance are *peak time*, the time into the trial of the maximum response rate, and *peak rate*, the maximum response rate. Some of the main results are the following: The procedure produced a time discrimination (all five experiments); peak time was changed without changing peak rate (Experiments 1, 2, and 5); peak rate was changed without changing peak time (Experiments 1, 3, and 5); with a linear time scale, the response-rate functions have a close-to-Gaussian shape (all five experiments); a blackout increased peak time by about the length of the blackout (Experiment 2); prefeeding increased peak time (Experiment 3); the omission of food at the end of one trial decreased peak time on the following trial (Experiment 4). Some of the main conclusions are the following: The clock can be stopped (Experiment 2); food partially resets the clock (Experiment 4); the clock times intervals of different lengths, using the same starting point and rate (Experiment 5); the scale of the clock is linear (all five experiments); the error in the clock is small relative to other error (all five experiments); the stimulus-response path can be divided into a timing system, measured by peak time, and a response system, measured by peak rate (Experiments 1, 2, 3, and 5); when the time of food is constant, it is reasonable to assume that a change in peak time implies a change in the clock (all five experiments).

The inhibition-of-delay results of Pavlov (1927) showed that some animals can discriminate times on the order of seconds and minutes. Not much is known about the internal clock involved. To learn about the clock, one needs to "isolate" the clock, i.e., 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. This article introduces a time-discrimination procedure that to some extent isolates the clock. The main features of what I call *the peak procedure* are shown in Figure 1. It is similar to a discrete-trials fixed-interval procedure. There are two types of trials, randomly mixed: (a) On food trials, the first response after a fixed time—in Figure 1, 40 sec—is rewarded with food; the trial then ends. (b) On empty trials, no food is given; the trial lasts at least 80 sec, plus a random amount more that averages 80 sec, and ends independently of responding. Intervals of random length, averaging 60 sec, separate trials.

Figure 1 also shows the typical result. After training with this procedure, response rate within a trial reaches a maximum at

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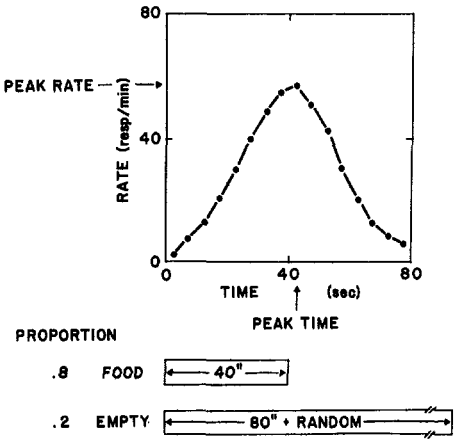

Figure 1. The basic elements of the peak procedure and some typical results. (The results shown are from the Sec 40 condition of Part 1 of Experiment 1.)

about the time that food is given. The main measures of performance 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.

The peak procedure is a slight modification of a procedure used by Catania (1970). Catania reported the results of one pigeon on the last day of two conditions; he found that changing the proportion of food trials to total trials from 90% to 10% lowered peak rate but had little effect on peak time.

Catania's result suggests, or at least raises the possibility, that peak time isolates part of the stimulus-response path. It seemed plausible that the part isolated included the clock; the underlying intuition was that response rate would peak when the setting of the rat's clock was closest to the times that the rat remembered receiving food. If peak time depends in part on the clock, it should usually change when the clock is changed; for example, a manipulation that increases the rate of the clock should decrease peak time (e.g., Maricq, Roberts, & Church, 1981). In addition, if (a) the intuition is correct and (b) the memories of food times are constant, then peak time should depend only on the clock; a manipulation that does not change the clock should not change peak time.

This work was based on these ideas. It extends Catania's work in several ways. First, it shows more conclusively that peak rate can be changed without changing peak time. Second, it shows that peak time can be changed without changing peak rate. Third, it measures the effect of a variety of manipulations on peak time, peak rate, and the shape of the response-rate function. Finally, it uses the results to draw conclusions about the structure of the stimulus-response path and the properties of the clock.

General Method

This section describes details that were common to all or most of the experiments. The Method sections of the individual experiments describe only details not described here.

Subjects

In all experiments the subjects were 10 male albino Norway rats (Charles River CD), about 160 days old when the experiment began. One group of 10 was used in Experiments 1 and 5; another, in Experiments 2 and 3; and a third in Experiment 4.

Apparatus

The rats worked in 10 similar lever boxes (23 × 20 × 19 cm). The roof and the side walls were transparent acrylic; the front and back walls were aluminum. The floor was 16 parallel stainless steel bars. A pellet dispenser (Gerbrands Model D-1 or Davis Scientific Instruments Model PD-104) delivered 45-mg Noyes food pellets through an opening in the front wall to a food cup. Because the sessions were long (4 hr), a 140-ml glass water bottle, at least half full, hung from the back wall of the chamber. The stopper was rubber, but a metal cover prevented the rats from chewing it. A retractable stainless steel lever (BRS/LVE Model 123-07 or Coulbourn Instruments Model E23-05) projected about 3 cm into the box through the front wall, 5 cm above the floor, on the left side of the food cup. Each lever box was housed in a large insulation-board chamber designed to minimize outside light and sound. Six boxes had a 6-W house light attached to the outside of the roof of the lever box; four boxes had a 7.5-W house light attached to the middle of the back wall of the chamber. A Grason-Stadler noise generator (Model 903A) delivered white noise of 8–10 dB above a background of 60–65 dB (C weighting, re 20 $\mu N/m^2$) through a speaker inside each chamber. There was a fan for ventilation and a small window—normally covered with black cloth—for observation. A PDP-12 computer controlled the equipment and recorded the data. It checked each box for a response 10 times per second.

Procedure

Maintenance. Whatever the treatment, there was one session a day, at about the same time each day

(within an hour). After the session, each rat was returned to its home cage, where it received about 15 g of Charles River Rat Formula mixed with water. (Experiment 3 is an exception.) Each cage had a water bottle.

Pretraining. On their first day, naive rats were trained to eat from the food cup and make the recorded response (lever press). Food was given once a minute for the first 30 min; each response produced food. The session ended when the rat had made 60 responses. On the second and third days, responses were rewarded on a random-interval 1-min schedule. Sessions lasted 3 hr.

Peak procedure. After pretraining came exposure to the peak procedure. Intertrial intervals were dark and silent. In Experiments 1 and 5, the lever was retracted between trials. Trials began with the start of a signal, either light or sound. On food trials, the first response after a fixed time—20 sec or 40 sec—produced food, and the trial then ended. On empty trials, no food was given; the trial lasted 80 sec plus a geometrically distributed duration with minimum 10 sec and mean 80 sec. The two types of trials were randomly mixed. Sessions lasted 4 hr. (The first 10 days of Experiment 1 are an exception.) The rats were run 7 days a week—other work showed that if days were skipped, there was a decrease in peak time on the day of resumption.

Data taken. No data were taken from the first 10 trials of a session. Afterward, responses were cumulatively recorded over trials as a function of time into the trials over the interval Sec 0–80. There were 16 bins, each 5 sec wide. In Experiments 2, 3, and 4, no data were taken on food trials, and, in addition to the cumulative measures, the data from individual empty trials were recorded on tape. Only the taped data from Experiment 4 were used.

Data Analysis

Definition of peak time and peak rate. Each rat for each condition on each day generated a response-rate function—the number of responses in each bin divided by the time spent in that bin. The peak time of a response-rate function was the "median" of the function over an interval centered around the peak time, the median being the time at which half of the responses were earlier and half later (assuming equal time spent in each bin and constant response rate within a bin). The centering was done differently in different experiments. In Experiment 1, the median was computed over the interval Sec 0–40 when food was primed at Sec 20, and over the interval Sec 0–80 when food was primed at Sec 40. In the rest of the experiments, the centering was done by iteration. First, the median over Sec 0–80 was found. Second, a new median was computed over the interval of which the first median was the center; for example, if the first median was 30 sec, the second median was computed over the interval Sec 0–60; if the first median was 50 sec, the second median was computed over the interval Sec 20–80. To state the rule in general, suppose that the first median is x sec. If $x <$ 40, the new interval was Sec 0–$2x$; if $x \geq 40$, the new interval was Sec $2(x - 40)$–80. The second median was "computed over" the new interval in the sense that response rates outside that interval were assumed to be zero. If the second median was within .05 sec of the first, the calculation stopped; if not, the second step was repeated. A third median was computed over the interval defined by the second, and so on. Peak rate was defined as the response rate at the peak time, computed by linear interpolation between the centers of the two nearest bins. For example, suppose that the peak time was 19.5 sec, and the bins centered at Sec 17.5 and Sec 22.5 had response (resp) rates of 20 and 30/min, respectively. Then the peak rate would be 24 ([.6 × 20] + [.4 × 30]) resp/min.

Averaging. Finding a summary value (usually a peak time, peak rate, difference of peak times, or difference of peak rates) for an experimental condition involved three steps. First, the measure was computed for each rat on each day. If, for instance, the condition lasted 5 days, this produced a 5 (Days) × 10 (Rats) table. Second, averaging over days produced one value for each rat. This was done in an unusual way: The Day × Rat table was analyzed with the row-plus-column method of McNeil and Tukey (1975), with a weighting constant of 9, and the value for each rat was the "fit" (Tukey, 1977, p. 335) for that rat. Finally, an average over rats produced a single summary value and a standard error based on between-rats variance. Between-rats variance was much larger than between-days variance (Roberts, 1979). The average used was the biweight (Mosteller & Tukey, 1977, p. 206), with a weighting constant of 9 and the measure of spread the median absolute deviation. Averages reported in the form $a + b$ are always biweight ± standard error based on between-rats variance. When response rates were analyzed, the second step (two-way analysis) was done with log rates (the transformation helped to equate the variance of different rats), and the fit for each rat was reconverted to "raw" rate before a biweight was taken. When differences between rates were analyzed, the rates were converted to log rates before the difference was taken, and the second step was done with the difference between the logs; then the fit for each rat was converted to a percentage before a biweight was taken. For a general justification of the biweight and the McNeil and Tukey method (which is based on the biweight), see Mosteller and Tukey (1977, pp. 203–219).

Unless otherwise stated, all p values are two-tailed.

Experiment 1

This experiment asked if peak time and peak rate were independent measures—if peak time could be changed without changing peak rate, and if peak rate could be changed without changing peak time. Trials were defined by light or sound, and the two signals were associated with different conditions. The experiment had two parts. In the first part, food was primed at Sec 20 (20 sec after the beginning of the trial) during one signal, at Sec 40 during the other. The peak times for the two signals would surely be different; would the peak rates be

different? In the second part, the probability of a food trial was .8 with one signal, .2 with the other. The peak rates for the two signals would surely be different; would the peak times be different?

Method

Procedure. After pretraining (see General Method), Part 1 began. On trials with one signal (light for half of the rats, sound for the rest) food was primed at Sec 20; on trials with the other signal, at Sec 40. The two signals were equally likely; for both, the mix of trials was 80% food, 20% empty. Part 1 lasted 15 days. The first 10 days had 6-hr sessions; the rest had 4-hr sessions. During Part 2, the mix of trials with the Sec 20 signal of Part 1 was 80% food, 20% empty; with the other signal, 20% food, 80% empty. Again, the two signals were equally likely; for both, food was primed at Sec 20. Part 2 lasted 10 days, with 4-hr sessions throughout. On the second day of Part 2, by mistake, both signals had 20% food trials, 80% empty trials.

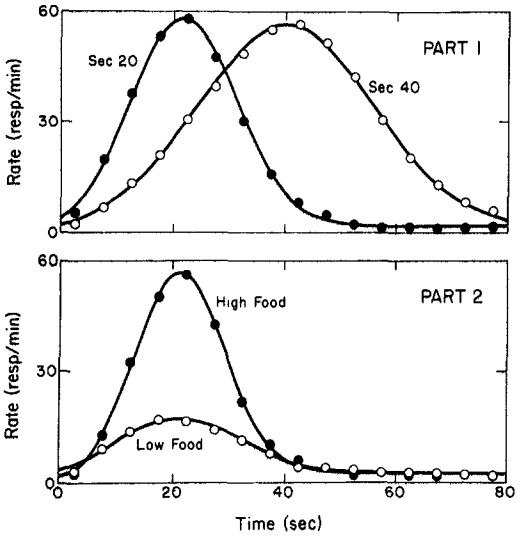

Figure 2. Mean response rate as a function of time into the trial during Part 1 (upper panel) and Part 2 (lower panel) of Experiment 1. (The data are from the last 5 days of each part. The fitted curves and the method of fitting are described in Results of Experiment 1.)

Results

The results described here are from the last 5 days of each part. Figure 2 shows the response-rate functions. All conditions showed a time discrimination (response rate changed with time into the trial), and the differences between signals had the effects one would expect (changing the time of food changed peak time, and changing the probability of food changed peak rate). Those are the "baseline" results. The major results are the clear independence of peak time and peak rate and the Gaussian shape of the response-rate functions.

Independence of peak time and peak rate. Table 1 gives the peak times and peak rates for each of the four conditions. It confirms the general impression produced by Figure 2. Changing the time of food from 20 sec to 40 sec (Part 1) increased peak time by 19.4 ± .7 sec but increased peak rate by only 1% ± 4%. Changing the probability of food from .8 to .2 (Part 2) decreased peak rate by 76% ± 6% but decreased peak time by only 1.2 ± 1.0 sec.

The results for individual days were similar. None of the effects varied systematically with day. During Part 1, the difference in peak rates ranged from −4% to +4%, none reliably nonzero, $ts(6) < 1.4$, $ps > .10$. During Part 2, the difference in peak times ranged from .7 to 2.1 sec, none reliably nonzero, $ts(6) < 2.3$, $ps > .05$.

Shape of the response-rate functions. The smooth curves of Figure 2 are the sum of two functions: (a) a function with the shape of a Gaussian (normal) distribution (with parameters for peak time, peak rate, and standard deviation) and (b) a ramp

Table 1
Peak Time and Peak Rate as a Function of Signal (Experiment 1)

Signal	Peak time (in sec)	Peak rate (responses/min)
Part 1		
Sec 40	41.1 ± 1.3	59.7 ± 4.9
Sec 20	22.0 ± .9	59.3 ± 5.5
Part 2		
High food	21.4 ± .4	58.0 ± 6.3
Low food	21.1 ± 1.2	14.6 ± 4.3

Note. Values are biweight ± standard error based on between-rats variance. Standard errors based on between-days variance were roughly a quarter of those given here (Roberts, 1979); e.g., for the peak time of Part 1, Sec 40, the standard error based on between-days variance was .4 sec.

function that is 0 resp/min at Sec 0, increases linearly until Sec 30, and is constant after that (with a parameter for final level). The ramp function is meant to represent responses not controlled by time, called *noise*. Many results (e.g., Catania & Reynolds, 1968; Roberts & Church, 1978; Figure 4 of this article) suggest that noise reaches its final level only after about 30 sec; that is the reason for the ramp. Curves were fit to the response-rate functions by using a hill-climbing procedure with a least squares criterion (Roberts, 1979). Table 2 describes the fitted curves and the closeness of the fits. Except for the low-food condition of Part 2, the fits are very close. The residuals from these fits are described in General Discussion. The data were also fit after being corrected for binning (Tukey, 1977, p. 654); the correction had no important effects.

Discussion

Peak time and peak rate were independent measures. One not very interesting explanation of the equality of peak rates in Part 1 is that it was due to a ceiling effect close to the output, e.g., the rats were not able to respond more quickly. But the shapes of the two response-rate functions argue against this in three ways. First, if it were true, one of the response-rate functions should have had a flatter top than the other. This was not the case. Second, the shapes of the two functions were very similar, similar in the sense that both were fit very well by curves of the same equation. A ceiling effect would distort the shape, and it is implausible that dissimilar shapes were distorted into similar shapes. Finally, the shapes were simple, i.e., similar to a familiar shape. It is implausible that complicated shapes were distorted into simple shapes. Similar arguments apply to the idea that the equality of peak times in Part 2 was due to a floor effect.

A rough equality of the peak times in Part 2 was to be expected; food was primed at the same time in both conditions. But the precision of the equality is somewhat surprising. Peak time must be determined by the distribution of times that food is given; and when food is given depends not only on when it is primed but also on the time between when it is primed and the rat's next response. A rat responding randomly at a rate of 60/min (the approximate peak rate in one condition of Part 2) will have a mean delay of 1 sec between when food is primed and when it is given; a rat responding randomly at a rate of 10/min (the approximate peak rate in the other condition) will have a mean delay of 6 sec. This might lead one to predict that the decrease in probability of food would have increased peak time by about 5 sec. In fact, the observed change was reliably less than a 5-sec increase. (A weakness of the prediction is that it is based on averages, but there is room for error—the observed change was reliably less than a 2-sec increase.) This tentatively suggests that the rat's way of summarizing the distribution of food times corresponds to some statistic other than the mean; for example, the minimum of the distribution of food times would be about the same in both conditions.

Figure 3 is a diagram of a theory that might explain the change in response rate with time, the change in response-rate function with time of food, and the independence of peak time and peak rate. It assumes three sequential operations (stages) between the stimulus being timed and the measured response. The stages are distinct in the sense that each can be changed without changing the others. The first stage is the clock; its output changes in a regular way with the duration of the stimulus. The second stage is a comparison of the output of the clock with the memory of the times when food was given. Its output is a measure of the similarity between the two. The third stage is everything between the output of the comparison stage and the response. According to the theory, the time of food changes either the first or the second stage; the probability of food changes the third stage. The brackets below the boxes in Figure 3 are meant to suggest that peak time is only sensitive to changes in the first two stages and that peak rate is only sensitive to changes in the third stage.

The most important feature of this theory is that it makes explicit an idea about what peak time measures. The operations proposed are common to almost all theories of discrimination learning (e.g., Sutherland

Table 2
Parameters of Fitted Curves

Condition	Days	Peak time (in sec)	Peak rate (responses/min)	*SD* (in sec)	Noise (responses/min)	Fit (%)
Experiment 1						
Sec 20	Part 1	21.6	56.7	9.5	1.9	99.8
Sec 40	Part 1	40.1	55.1	15.8	1.5	99.8
High food	Part 2	21.3	54.9	8.0	2.6	99.7
Low food	Part 2	20.6	15.1	11.6	2.5	98.3
Experiment 2						
Baseline	21–30	44.2	41.9	15.1	1.5	99.8
	31–40	43.9	42.3	13.0	2.2	99.9
	41–55	44.9	41.8	13.2	1.2	99.9
Break	21–30	57.9	44.2	15.3	0	99.1
	31–35	53.3	41.1	13.2	1.1	99.3
	36–40	52.3	42.3	12.6	1.1	99.4
Experiment 3						
Baseline	6–15	43.3	40.3	13.5	2.2	99.9
	16–25	43.4	33.3	13.8	2.0	99.8
Prefed	6–15	45.1	20.0	13.6	2.6	99.8
	16–25	43.8	20.9	15.1	1.2	99.7
Experiment 4						
Baseline	38–42	47.3	45.4	12.7	4.1	99.8
	43–52	49.4	46.9	12.5	1.5	97.8
Omission	43–52	39.5	28.7	23.2	2.7	97.0
Experiment 5						
Sec 20	all 15	21.2	66.9	8.3	1.9	99.8
Sec 40	all 15	41.7	57.2	14.7	2.3	99.5

Note. Fit = variance described by the fitted curve.

& Mackintosh, 1971). The explicit statement of the distinctness of these operations (each can be changed without changing the others) is perhaps new. The distinctness of the clock and the comparison from the rest of the stimulus-response path is based on the results of this experiment; the distinctness of the clock and the comparison from each

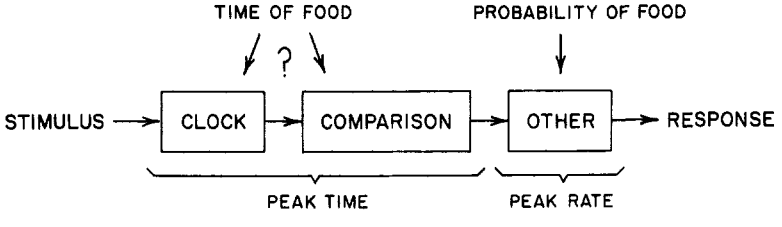

Figure 3. A stage theory to explain the independence of peak time and peak rate observed in Experiment 1. (The time of food changed the clock, the comparison, or both; the probability of food changed the third stage. Peak time was a measure of the clock and the comparison; peak rate was a measure of the third stage.)

other is based on the results of Experiments 2, 3, and 5 (see General Discussion for details).

There are some problems. If the time of food were increased to some very large value, peak rate would undoubtedly decrease; the theory does not allow for this. Another problem is that time of food and probability of food are both parameters that exert their effects through long-term memory, so it is strange that they should affect entirely different operations. A more generalizable explanation of the equality of peak rates in Part 1 may be that peak rate is limited in two ways. One limit (X) is constant with time of food; the other limit (Y) decreases with time of food. Limit Y is less than Limit X only with food times greater than those used in this experiment. Changing the time of food did not change peak rate because Limit X (constant with time of food) was always less than Limit Y. This explanation predicts a discontinuity in the graph showing peak rate as a function of the time of food, at the time where Limit Y crosses Limit X.

Experiment 2

This experiment measured the effect of various stimulus changes (breaks) early in the trial. Trials were defined by light; intertrial intervals were dark. Food was primed at Sec 40. The breaks were, in order of use, a 10-sec blackout starting at Sec 10, a 5-sec blackout starting at Sec 15, a 5-sec blackout starting at Sec 10, and a 10-sec noise starting at Sec 15.

Roberts and Church (1978) used breaks with a fixed-interval procedure and a choice procedure, and they concluded that (a) breaks stopped the clock and (b) the clock added time measured after the break to time measured before the break. In part, this experiment was done to check these conclusions; it used a different timing procedure, different breaks, and, to some extent, different reasoning.

Method

Procedure. The rats were first pretrained (see General Method). For the next 20 days (Days 1–20), they were exposed to the basic form of the peak procedure. Intertrial intervals were dark; trials were defined by light. The mix of trials was 80% food, 20% empty. On food trials, food was primed at Sec 40. One important change from Experiment 1 was that the lever was always extended, rather than retracted between trials. This restricted the possible cues for the start of a trial, but it also meant the rats could respond during intertrial intervals. For many days, two rats showed consistently high response rates (over 10/min) during the first 5 sec of a trial. It seemed likely that the start of a trial was rewarding intertrial responding, and this led to a change in procedure. Before Day 15, intertrial intervals were geometrically distributed with minimum 15 sec and mean 60 sec—in other words, after every 15 sec of intertrial interval a trial would begin with probability .25. On Day 15 and later days, after every 15 sec of intertrial interval a trial would begin with probability .25 only if there had been no responses during the preceding 10 sec. This modification quickly brought response rates during the first 5 sec of a trial much closer to zero.

Over the next 35 days (Days 21–55), some trials (break trials) included breaks. Break trials were otherwise the same as ordinary empty trials (baseline trials). The procedure of Days 15–20 continued except that the mix of trials was now 80% food, 10% baseline, and 10% break. Break and baseline trials came in pairs. If the first non-food trial of the session was a break trial, the second non-food trial would be a baseline trial, and vice versa. If the third non-food trial of the session was a baseline trial, the fourth would be a break trial, and so on. In order, the four conditions were as follows: light turned off for 10 sec starting at Sec 10 (Days 21–30); light turned off for 5 sec starting at Sec 10 (Days 31–35); light turned off for 5 sec starting at Sec 15 (Days 36–40); and sound turned on for 10 sec starting at Sec 10 (Days 41–55). Responses were recorded in bins 5 sec wide beginning at the start of the trial; thus on break trials the third bin (Sec 10–15) and/or the fourth bin (Sec 15–20) were under the altered stimulus conditions.

Results

Figure 4 shows the response-rate functions from the first 2 days and last 2 days of discrimination training. The function from the first 2 days is roughly flat after the first 30 sec; the function from the last 2 days is the usual shape. A measure of discrimination is the ratio of the median of the response-rate function to its interquartile range. For flat functions (no discrimination) the ratio will be 1.0; more peaked functions (better discrimination) will have higher ratios. The ratio leveled off at about 2.6 after about 40 days of training.

Blackouts. Blackouts increased peak time and did not change peak rate. The increase in peak time was close to, and depended on, the length of the blackout. The 10-sec blackouts increased peak time by 13.3 ± .9 sec

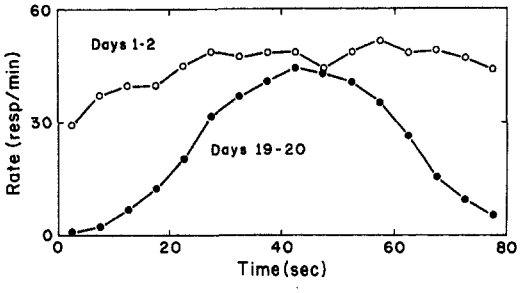

Figure 4. Mean response rate as a function of time into the trial on Days 1–2 and Days 19–20 of Experiment 2.

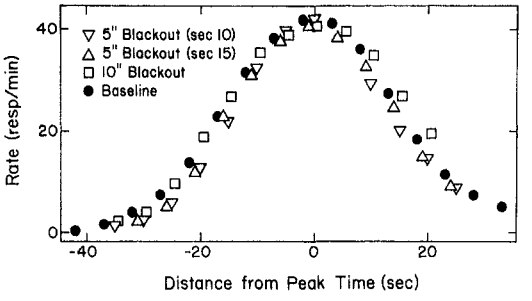

Figure 6. Mean response rate as a function of distance from peak time. (The baseline function is from Days 21–40. The functions have been shifted horizontally so that their peak times coincide. The blackout functions include performance only after the blackout.)

and decreased peak rate by 2% ± 2%. The 5-sec blackouts at Sec 10 and Sec 15 increased peak time by 7.2 ± .8 sec and 9.2 ± .7 sec, respectively; they decreased peak rate by 5% ± 4% and 4% ± 5%. The difference between the increases in peak time caused by the two 5-sec blackouts was not reliable ($W = 13$, $p > .20$). On the days with blackouts (Days 21–40), the peak time on baseline trials was 45.3 ± 1.4 sec, and the peak rate was 44 ± 5 resp/min.

Figure 5 shows the effects of a 10-sec blackout on the response-rate function. The change is remarkably simple: The function is shifted rightward. In Figure 6, the blackout and baseline functions are equated for peak time. The functions overlap almost completely, which shows that blackouts changed only peak time.

Figure 7 shows the day-by-day results. Peak time and peak rate in all conditions were essentially constant over days. The introduction of breaks had no clear effect on baseline performance; the difference between the baseline peak times on Day 20 and Day 21 is not reliable ($W = 25$, $p > .20$).

Sound. The effects of the 10-sec sound (Days 41–55) were quite different. Figure 8 shows the day-by-day results. Sound did little at first, but eventually it increased peak time and lowered peak rate. On the first day (Day 41), the increase in peak time was −1.0 ± 2.3 sec; on the last day (Day 55), it was 17.0 ± 3.0 sec. On the first day, the decrease in peak rate was 1% ± 11%; on the last day, it was 70% ± 7%. On the days with sound (Days 41–55), the peak time on baseline trials was 46.0 ± 1.2 sec; the peak rate was 41 ± 6 resp/min.

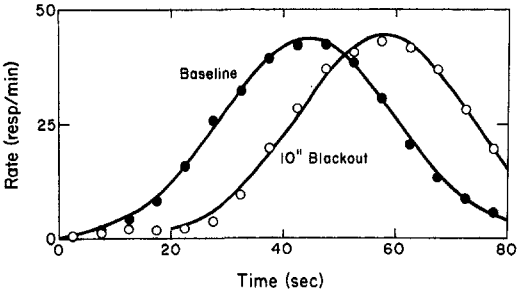

Figure 5. Mean response rate as a function of time into the trial on Days 21–30 of Experiment 2. (The fitted curves and the method of fitting are described in Results of Experiment 1.)

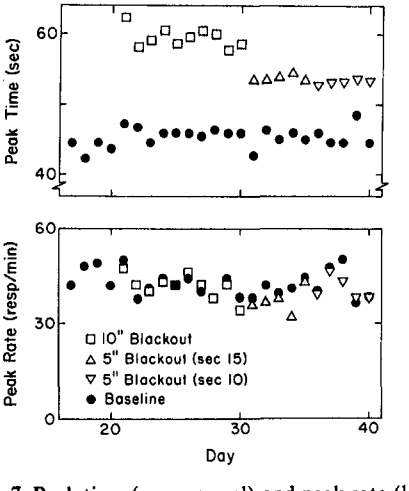

Figure 7. Peak time (upper panel) and peak rate (lower panel) as a function of day in Experiment 2.

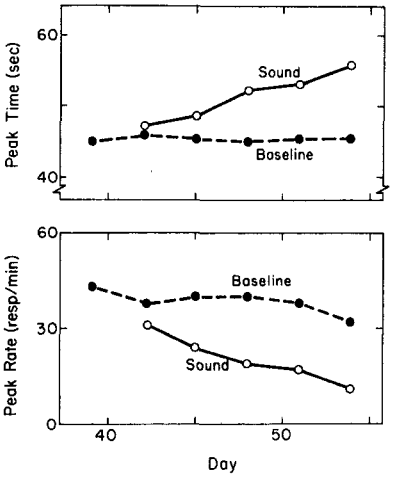

Figure 8. Peak time (upper panel) and peak rate (lower panel) as a function of day in Experiment 2. (Each point is a median over 3 days.)

Shape of the response-rate functions. Curves were fitted to the blackout and baseline functions with the procedure described in Results of Experiment 1. (The sound function was not fit because it was not stable across days.) The functions from the blackout conditions were fit using only responses after the blackout. The fits are described in Table 2, and two examples are shown in Figure 5. They are close, especially the fits from the baseline conditions, and the parameters are similar across fits (with the obvious exception of peak time). One discrepancy is the fit for the break condition on Days 21–30 (10-sec blackout), which has an unlikely value for noise (0 resp/min). One possibility is that the function was not stable across days and was distorted by averaging; however, a fit to just Days 26–30 is essentially the same.

Discussion

Blackouts. If a blackout stops the rat's clock, if the clock adds time after the blackout to time before the blackout, and if blackouts do not change the subsequent speed of the clock, then (a) a blackout will increase peak time by the length of the blackout, (b) the starting time of the blackout will not affect the size of the increase, and (c) a blackout will not change the spread of the response-rate function. The first prediction assumes that blackouts do not reset the clock and that the lag between starting the blackout and stopping the clock equals the lag between ending the blackout and restarting the clock.

The results are close to these predictions: (a) A 10-sec blackout increased peak time by about 13 sec, and a 5-sec blackout increased peak time by about 8 sec; (b) the effects of 5-sec blackouts starting at Sec 10 and Sec 15 did not differ reliably; and (c) the spread of the response-rate functions did not change (Figure 6). The one difference between results and predictions (the increase in peak time was 3 sec more than the length of the blackout) may be due to the fact that restarting the clock took longer than stopping it or that blackouts partially reset the clock. Intertrial intervals must reset the clock, and blackouts resemble intertrial intervals; therefore it seems likely that blackouts would reset the clock to some extent. The similarity between results and predictions suggests that blackouts stopped the clock and that the clock added time after the break to time before the break.

Another explanation of the increases in peak time is that blackouts *only* reset the clock. But this explanation is incompatible with the sizes of the increases. Suppose that the start of a blackout reset the clock and the rest of the blackout had no effect. Then the 5-sec blackout starting at Sec 10 should have had the same effect as the 10-sec blackout starting at Sec 10—but it did not. Or suppose that the end of a blackout reset the clock and the rest of the blackout had no effect. Then the 5-sec blackout ending at Sec 20 should have had the same effect as the 10-sec blackout ending at Sec 20—but it did not.

The conclusions that blackouts stopped the clock and that time after the blackout was added to time before the blackout agree with the conclusions of Roberts and Church (1978).

Sound. The reason that sound lowered peak rate is probably that sound was learned to be a signal for the absence of food. Trials with sound were always without food. This explanation is incomplete, though, because trials with blackouts were always without food yet blackouts did not lower peak rate.

One plausible reason is that blackouts were similar to intertrial intervals. Intertrial intervals were often followed by an interval of light with food, and sound was always followed by an interval of light without food.

At first, sound did not change peak time, but eventually it increased peak time by about 17 sec. Both the size of the increase and its change over days are different from the blackout results, which suggests that the mechanism is different. One explanation is that the clock is reset and started by stimuli that are signals for important events (e.g., food, shock), and only by such stimuli. As sound became a signal for the absence of food, it began to reset and start the clock. This explanation is entirely post hoc, but the assumption that the clock is started by signals for important events makes intuitive sense.

Experiment 3

This experiment was mainly an attempt to find more evidence that peak rate can be changed without changing peak time. On some days, rats were fed half of their daily ration of food just before the experimental session. If prefeeding simply changes motivation, it should decrease peak rate and not change peak time.

Method

Subjects and apparatus. The subjects were 10 rats. Nine had been used in Experiment 2; the tenth was a replacement for a rat with a particularly low response rate. The replacement had been trained in other experiments with the peak procedure, none involving prefeeding. The rats were about 150 days old when the experiment began. They had been on a regimen of restricted feeding (15 g of Charles River Rat Formula once a day) since they were about 50 days old. Their weights ranged from 310 g to 415 g (median of 325 g). For a description of the apparatus, see General Method.

Procedure. The mix of trials was 50% food, 50% empty. Otherwise, the procedure was the same as in Experiment 2, Days 15–20. The rats were given 5 days (Days 1–5) to adjust to the new mix of food and empty trials—now 50/50, previously 80/20—and then the main part of the experiment began. The next 20 days (Days 6–25) consisted of 10 baseline days and 10 prefed days, randomly arranged with the restriction that each pair of days (Days 6–7, Days 8–9, etc.) must contain one baseline day and one prefed day. On baseline days, the rats were run as usual and were fed their daily ration of 15 g just after the end of the session. On prefed days, the rats were fed half of their ration just before the session and half of their ration just after. The prefeeding was done like this: The food (Charles River Rat Formula) was mixed with 15 ml of water and let sit for 5 min; then it was given to the rats in their home cages. Forty minutes later the rats were taken from their home cages and put in the testing chambers. By then they had always finished the food. Between Day 15 and Day 16 was a day when, by mistake, two of the rats were prefed and the other eight were not; the results from this day are not included in the results described below.

Results

Figure 9 shows the day-by-day results. Prefeeding clearly lowered peak rate, but it also increased peak time, at least at first. Over the first half of the main part of the experiment (Days 6–15), peak time was 2.7 ± 1.1 sec higher ($p < .05$) on prefed days than on baseline days; peak rate was 48% ± 4% lower. Figure 10 shows the response-rate functions. Over the second half (Days 16–25), peak time was only .6 ± .6 sec higher on prefed days; peak rate was 45% ± 6% lower. The difference between baseline and prefed peak times was reliably more during the first half than the second half ($W = 37$, one-tailed $p < .05$).

If the baseline peak times were steady when prefeeding began, then prefeeding apparently decreased peak time on baseline days. The difference between the last baseline day before prefeeding (44.7 sec) and the first baseline day after (42.6 sec) is reliable ($W = 39$, $p < .05$). Over the first half, the

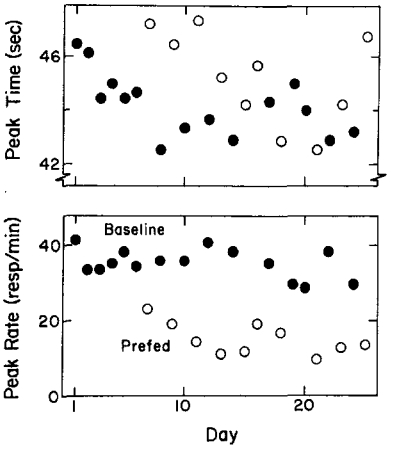

Figure 9. Peak time (upper panel) and peak rate (lower panel) as a function of day in Experiment 3.

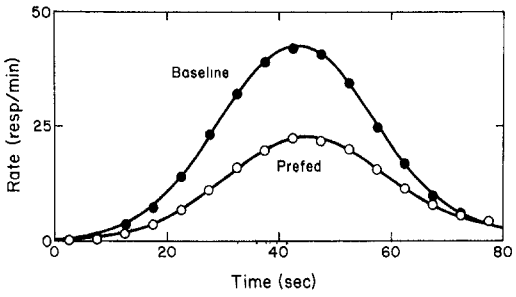

Figure 10. Mean response rate as a function of time into the trial during the first half of Experiment 3. (The fitted curves and the method of fitting are described in the Results section of Experiment 1.)

baseline peak time was 43.3 ± .7 sec; over the second half, 43.8 ± .5 sec. Over the first half, the baseline peak rate was 39 ± 6 resp/min; over the second half, 45 ± 6 resp/min.

Curves fit to the response-rate functions are described in Table 2, and two examples are shown in Figure 10. The curves fit very well.

Apart from its effects on peak rate, prefeeding might have either "shifted" or "stretched" the response-rate function. An example of a shift—an additive change—is the difference between the baseline and blackout functions of Experiment 2 (Figure 5); shifted functions overlap when plotted in terms of distance from peak time (Figure 6). An example of a stretch—a multiplicative change—is the difference between the Sec 20 and Sec 40 functions of Part 1 of Experiment 1 (upper panel of Figure 2); stretched functions would overlap when plotted in terms of percentage of peak time. In both of these examples, peak rates were already equated. Figure 11 shows the baseline and prefed response-rate functions from the first half of the experiment equated for peak rate and plotted in terms of both distance from peak time (upper scale) and percentage of peak time (lower scale). The two functions overlap more closely when plotted in terms of percentage of peak time than when plotted in terms of distance from peak time. Although the difference between the two ways of plotting is visually small, it is large relative to the error in prediction. A curve fit to the baseline function (shown in Figure 10) describes all but .1% of its variance. When this curve is used to predict the prefed function, it describes all but .5% of the variance when the two functions are equated for percentage of peak time; it describes all but 1.4% of the variance when they are equated for distance from peak time. During the first half of the experiment, prefeeding increased the peak times of 9 of the 10 rats; the fit is better when equating for percentage for 8 of the 9 ($p < .05$).

Discussion

Prefeeding increased peak time, although only during the first half of the experiment. Because the increase was small and unexpected, it might be dismissed as an artifact of the change in peak rate. (For instance, it might be argued that because peak rate was lower, food was received later, and the increase in the time of food caused the increase in peak time.) But a number of findings make this unlikely: (a) Prefeeding also changed peak time on baseline trials, when peak rate was normal. (b) In the second half of the experiment, the change in peak rate was roughly the same, but the change in peak time diminished. (c) In Part 2 of Experiment 1, a larger decrease in peak rate did not increase peak time.

The best explanation of the various changes in peak time seems to be that prefeeding decreased the rate of the clock and that this effect persisted throughout both halves of the experiment. On the first pre-

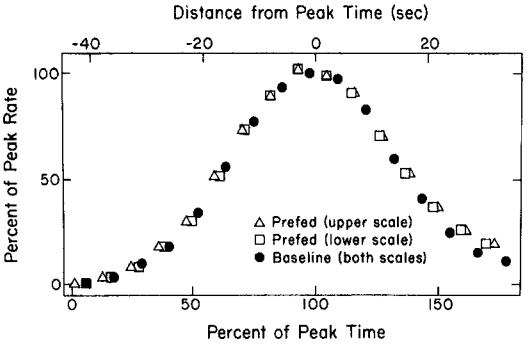

Figure 11. Percentage of peak rate as a function of seconds from peak time (lower scale) and percentage of peak time (upper scale). (The baseline function is correct on both scales. The prefed function is plotted twice, once with the upper scale, once with the lower.)

feeding day, from the rat's point of view food came earlier than usual. On the following days, therefore, the rats expected food earlier, and peak time decreased. Because the discrimination of prefed days from baseline days was imperfect, peak time decreased on baseline days as well as prefed days. As the discrimination between prefed days and baseline days improved, peak time decreased more on prefed days, and the change in the expected time of food on prefed days eventually canceled the change in the clock. Many experiments have shown that rats can discriminate levels of hunger (e.g., Capaldi & Davidson, 1979). One virtue of this explanation is that it accounts for the disappearing change in peak time without using a physiological notion of tolerance (e.g., buildup at receptors). It is hard to believe that the rats would become "tolerant" in any way to the effects of prefeeding because they had had similar feedings for most of their lives.

An increase in the latency of the clock—the time between the start of the signal and the start of the clock—would have also increased peak time. The conclusion that prefeeding changed clock *rate* predicts, assuming no change in variability, that the response-rate functions will overlap when stretched; Figure 11 shows that they did. If prefeeding changed clock latency, the functions should have overlapped when shifted.

Yagi (1962), using a T-maze, trained rats to choose one alley ("short") after a 10-sec confinement and the other alley ("long") after a 50-sec confinement. He found that a decrease in hours of deprivation increased the probability of a "short" response. Rapp (Note 1) found a similar result; she used rats discriminating 3- and 7-sec tones. An increase in the probability of a "short" response corresponds to an increase in peak time; the direction of the change produced by reduced hunger is the same in those two studies as in this one. Although there are two studies that found no effect of food deprivation on timing (Weiss & Moore, 1956, with rats; Killeen, 1975, Experiment 4b, with pigeons), the results of Yagi and Rapp support the conclusion that prefeeding changes the clock.

Because the changes produced by prefeeding were mainly internal and because prefeeding apparently changed the rate of the clock, the rate-determining part of the clock, its pacemaker, appears to be internal. Maricq, Roberts, and Church (1981) reached the same conclusion based on the effects of methamphetamine.

Figure 11 shows that after peak times and peak rates are equated, prefed performance was very similar to baseline performance. This suggests that prefeeding left something important unchanged—whatever it is that determines the shape of the response-rate function. It is reasonable to assume that the shape of the response-rate function is determined within the timing system and that later operations determine only the height of the function. Therefore something within the timing system was unchanged by prefeeding. Arguments described above lead to the conclusion that prefeeding did change the clock. That leaves the comparison; apparently, the comparison was unchanged by prefeeding. The same arguments apply to the finding of Experiment 2 that while blackouts changed peak time, they did not change the shape of the response-rate functions (Figure 6); this suggests that blackouts did not change the comparison.

Experiment 4

When animals respond on a fixed-interval schedule for food, the omission of food at the end of one interval increases overall response rate during the next interval. This is sometimes called *the omission effect* (Staddon & Innis, 1969). Food delivery is usually replaced by a short blackout (3 to 5 sec), although one study used a change of key color (Zeiler, 1972). Response rate after omission is usually about double the rate after food. The effect has been found in a number of laboratories (e.g., Scull, Davies, & Ansel, 1970; Staddon & Innis, 1966; Zeiler, 1972). Subjects have been rats (e.g., Staddon & Innis, 1969), pigeons (e.g., Kello, 1972), and, with a fixed-ratio procedure, monkeys (Davenport, Flaherty, & Dyrud, 1966; Davenport & Thompson, 1965). The reinforcer omitted can be water as well as food (Jensen & Fallon, 1973; Zimmerman, 1971). The effect occurs with fixed intervals ranging

from 30 sec (Scull et al., 1970) to at least 8 min (Zeiler, 1972). It occurs in the first session in which food is omitted and lasts many sessions, e.g., at least fourteen 160-min sessions (Staddon & Innis, 1969) and twenty-six 20-min sessions (Scull et al., 1970).

The usual result with a fixed-interval schedule is that response rate increases with time into the interval—with time on the horizontal axis and response rate on the vertical axis, a rising line. An increase in overall rate, such as the omission effect, can happen in three ways: (a) a vertical (upward) shift of the response-rate function, (b) a horizontal (leftward) shift of the response-rate function, or (c) a flattening of the response-rate function—what might be called a loss of stimulus control—without a decrease in the maximum rate. These alternatives are much easier to distinguish with the peak procedure than a fixed-interval schedule. The first would decrease peak time, the second would increase peak rate, and the third would not change either measure. With a fixed-interval schedule, a leftward shift and an upward shift could be identical.

An explanation of the omission effect that predicts a leftward shift is that the omission of food leaves the animal's clock not fully reset at the beginning of the next interval; something similar to this is proposed by Staddon (1974). An upward shift is predicted by the theory that the omission of food produces "frustration," an internal state that "energizes" behavior (Ansel, 1962). A theory that predicts flattening might emphasize that food was never omitted while the time discrimination was learned and that a change from the conditions of learning should produce some loss of stimulus control.

In this experiment, food was omitted on some of the food trials, and these trials were followed by an empty trial. In order to resemble other experiments that have found an omission effect, this experiment had fixed 5-sec intertrial intervals.

Method

Subjects and apparatus. The subjects were 10 naive rats, selected (see below) from an initial group of 16. For a description of the apparatus, see General Method.

Procedure. The rats were pretrained (see General Method), and the 10 rats with the highest response rates on the last day of pretraining were the ones used in the rest of the experiment. Their basic discrimination training (Days 1–42) was the same as the training of Experiment 2, Days 15–20, with three exceptions. First, the mix of trials was 75% food, 25% empty. Second, over the 10 days (Days 33–42) before the main part of the experiment, intertrial intervals were 5 sec long, and intertrial responding had no effect. A final difference, by mistake, was that on Days 1–17 the rats sometimes received food more than 80 sec after the start of the trial. During this period intertrial intervals were 5 sec long. This produced a response-rate function without a peak: Response rate increased during the first 40 sec of the trial and was roughly constant after that. When the procedural error was fixed, and the intertrial interval restored to its usual value (an average of 60 sec), the usual peak emerged.

During the main part of the experiment (Days 43–52), the mix of trials selected randomly continued to be 75% food, 25% empty. On a random half of the food trials, food was omitted. The choice of an empty trial was really the choice of a block of three trials, because empty trials were always preceded by two food trials. Baseline (empty) trials were preceded by two ordinary food trials; omission trials were preceded by an ordinary food trial and a food trial with food omitted. Food trials with food omitted were exactly the same as ordinary food trials except that the feeder did not operate (and no food was delivered) following the rat's final response. By restricting the sequence of trials, I hoped to reduce the distortions produced by averaging response-rate functions with different peak times. Baseline and omission trials came in pairs, as in Experiment 2. (The two food trials that preceded each empty trial are not included in the proportion of food trials selected randomly. Therefore food trials were not 75% but 83% of *all* trials.) Other details of treatment were the same as during the last days of discrimination training. An important feature of data collection was that the response-rate function of each empty trial was recorded separately (on magnetic tape); these functions were recorded in addition to the usual function cumulated over the whole session.

Results

An ordinary fixed-interval schedule shows only the left half of the response-rate function shown by the peak procedure, and therefore overall rate from a fixed-interval schedule seems most comparable with overall rate from a peak procedure computed over only the time before food is primed. For this experiment, then, an omission effect would be an increase in overall rate during the first 40 sec of a trial. With this definition, there was a large and persistent omission effect. Overall rates (Sec 0–40) were computed for all 10 days combined. (Unless otherwise stated, all results described here are from

the 10 days with food omission.) The median rate on baseline trials was 8.2 resp/min; the range was .4–13.0. The median ratio of rate on omission trials to rate on baseline trials was 2.4; the range was 1.4–11.9. The effect appeared on all 10 days: For instance, on the first day the median ratio was 3.2 (9 of 10 rats showed the effect); on the last day the median ratio was 3.1 (all 10 rats showed the effect).

Figure 12 shows the response-rate functions. It is clear that the omission effect was due to a leftward shift of the response-rate function. Food omission decreased peak time by 10.9 ± 2.5 sec; the baseline peak time was 50.2 ± 1.0 sec. Food omission lowered overall response rate (Sec 0–80) by only 2% ± 10%.

Figure 13 shows the day-by-day results. The baseline peak time during food omission (50.2 sec) was unusually high; in the other experiments, it was about 44 sec. In part, the discrepancy is due to the fact that food omission increased the baseline peak time. Food omission started on Day 43. On Days 33–37, peak time was 48.7 ± 1.1 sec; on Days 38–42, 47.5 ± .7 sec. But on Days 43–48, it was 49.5 ± 1.3 sec; on Days 48–52, 50.8 ± 1.0 sec. The difference between Days 43–48 and Days 38–42 is reliable ($W = 37$, one-tailed $p < .05$). As Figure 13 shows, peak time on omission trials may have increased over days: Over the first 5 days, it was 36.8 ± 2.6 sec; over the next 5 days, 41.7 ± 2.6 sec. The difference is close to reliable ($W = 27$, one-tailed $p < .10$). The difference in peak time between baseline and omission trials was greater during the first 5 days (12.1 sec) than the next 5 days (9.2 sec), but this change was not reliable ($W = 25$, one-tailed $p > .10$).

The high baseline peak time was also apparently due to the 5-sec intertrial interval, which began on Day 33. On the preceding 5 days, the peak time was 44.6 ± 1.1 sec. For Days 30–36, the daily peak times were (starting with Day 30) 45.1, 43.8, 46.7, 50.7, 50.9, and 50.0 sec (values from an analysis of Days 25–42). There is a clear break between Day 32 (46.7 sec) and Day 33 (50.7 sec), and their difference is reliable ($W = 45$, $p < .05$).

Figures 12 and 13 show that food omission

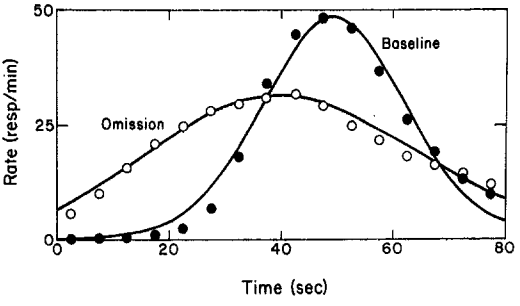

Figure 12. Mean response rate as a function of time into the trial on Days 43–52 of Experiment 4. (The fitted curves and the method of fitting are described in Results of Experiment 1.)

apparently lowered peak rate, the opposite of what one might expect on the basis of the omission effect alone. However, the change is to a large extent an artifact of averaging over trials. Figure 14 shows the distribution of peak times and peak rates on individual trials. (The data for 2 days, the first and the fifth, were not available.) In order to locate the peak, the mode was used instead of a median. Because of the small number of responses on many trials, a median could easily fall in a bin in which response rate was zero—probably not a good estimate of the peak rate on that trial. (A median would probably give a better estimate of peak time, but the emphasis of this analysis was on peak rate.) Peak time (upper panel) was much more variable on omission trials than base-

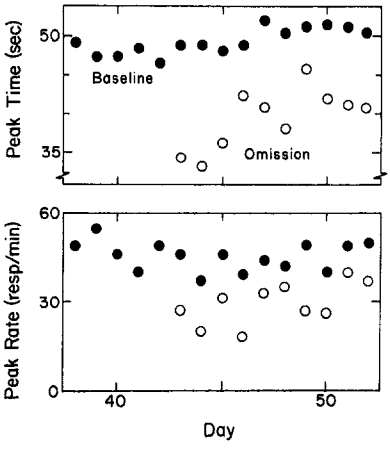

Figure 13. Peak time (upper panel) and peak rate (lower panel) as a function of day in Experiment 4.

line trials; thus averaging over trials (as in Figures 12 and 13) would make it seem as if food omission lowered peak rate.

The two distributions of peak rates (lower panel of Figure 14) differ in an interesting way. Peak rates were slightly lower on omission trials; the median of the baseline distribution is 77 resp/min, and the median of the omission distribution is 70 resp/min, a 9% decrease. However, the two distributions differ only because there is a sort of bump at low peak rates (0, 12, 24, and perhaps 36 resp/min, corresponding to 0, 1, 2, or 3 responses in a bin) in the distribution from omission trials. All 10 rats were more likely to have peak rates of 0–24 resp/min on omission trials than baseline trials. When one ignores the low peak rates (0–36 resp/min), the two distributions are similar. The medians of the baseline and omission distributions are then 87 and 89 resp/min, respectively; their interquartile ranges are 47 and 49 resp/min.

The curves fit to the response-rate functions are described in Table 2. The fits are worse than usual. This is understandable for the omission function, for which averaging was a severe problem, but there is no clear reason for the lack of fit with the baseline function. If the 5-sec intertrial interval was the cause, the fit should have been poor before the main part of the experiment. The indications are mixed. For Days 38–42, the fit is good (99.8% of the variance), but its parameters are strange (noise of 4.1 resp/min and a standard deviation of 12.7 sec).

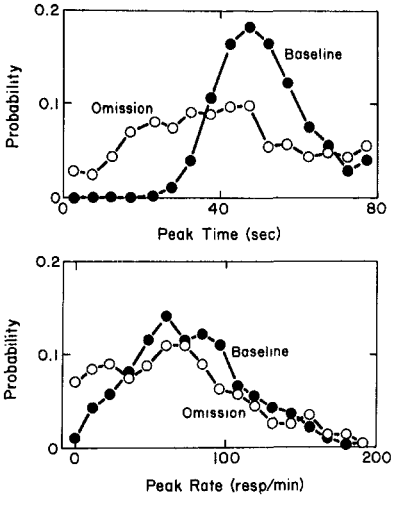

Figure 14. Frequency distributions of peak time (upper panel) and peak rate (lower panel) measured on single trials on Days 44–52 of Experiment 4. (The bins in which responses were recorded were 5 sec wide, so response rates are multiples of 12 resp/min; for example, 24 resp/min corresponds to 2 resp/bin. When the peak rate occurred in more than one bin, a fraction—one divided by the number of bins—was added to the counts of the bins where it occurred; for example, if the peak rate occurred in bins 1, 3, 4, and 16, ¼ would be added to the counts for bins 1, 3, 4, and 16.)

Discussion

The omission effect observed here was similar in size and persistence to what others have found. It was clearly due to a change in peak time. The most plausible explanation of the change in peak time is that food to some extent resets the clock; when food was omitted, the clock was reset less than usual.

This explanation is supported by the changes in peak time over days. Consider what happens the first time that food is omitted. Suppose that Trials 5 and 6 are both food trials and that food is omitted on Trial 5 but given on Trial 6. On Trial 6, if the clock is not fully reset when the trial begins, it will appear to the rat as if food is later than usual. This should increase peak time. Unless the rat perfectly distinguishes baseline and omission trials, peak time should increase on both; and, indeed, food omission reliably increased baseline peak time. Peak time on omission trials increased over days, and the change was almost reliable. If the rat could to any extent distinguish baseline and omission trials, it should increase peak time on omission trials more than on baseline trials. There was an unreliable change in that direction.

The conclusion that food resets the clock is supported by other experiments: (a) Zimmerman (1971), using water as reward, found that the presentation of water in the middle of a fixed interval decreased response rate for the rest of the interval, 100 sec. (Because the decrease lasted so long, it was not simply due to drinking time.) (b) When the animal does not show a time discrimination because of a drug (Innis & Staddon, 1969) or the pattern of reward (Harzem,

Lowe, & Priddle-Higson, 1978; McMillan, 1971), the omission of food does not increase response rate. When a clock is not controlling performance, changes in the clock should not change performance. (c) With procedures that produce a time discrimination where response rate decreases with time since food, the omission of food decreases response rate (Staddon, 1970, 1972). The idea that food resets the clock is not new. Staddon (1974) stated this possibility explicitly and used a variation of it to explain the omission effect and some of the results just described.

When the intertrial interval was reduced from 60 sec (average) to 5 sec (fixed), peak time increased. This suggests that there was something important happening 5 sec after the end of a trial that was no longer happening 60 sec after the end of a trial. Perhaps something caused by the receipt of food delayed the starting of the clock when the next trial began. It was probably not the consumption of the food: Rats appear to eat a 45-mg Noyes pellet in much less than 5 sec.

The difference between the two distributions of peak rates (lower panels of Figure 14) is what would be seen if each observed distribution was actually a mixture of two distributions, call them A and B, and the only difference between the observed distributions was the ratio of A to B. If the baseline distribution is assumed to be 100% A, 0% B, then the omission distribution would be about 85% A, 15% B, and the B distribution would be roughly $P(0) = .40$, $P(1) = .30$, $P(2) = .25$, $P(3) = .05$ (i.e., the probability of a peak rate of 0 resp/bin is .40, etc.). A simple interpretation of this is that the two mixing distributions (A and B) reflect two states of the animal, an A state and a B state: When the animal is in the A state, peak rates come from the A distribution; when it is in the B state, they come from the B distribution. The omission of food sometimes changes the animal from the A state to the B state. The A state is the usual state. In the A state, responses are made on 99% of all trials. The B state is a state of low but not zero responding; responses are made on 60% of all trials. Because responding was not zero, the B state is not so simple as the animal's being away from the lever.

To find out more about the B state, I did two analyses. The first looked at the proportion of peak rates 24 resp/min or less on single days; because low peak rates are rare during the A state, this is a rough guide to the frequency of the B state. This analysis suggested that the probability of entering the B state may have declined over the 10 days of food omission. Data from the first day were lost; on the second day the proportion was 45% (more than any later day); on the third day, 21%; on the last 2 days, 8% and 19%. This may mean that the B state is a state of surprise. The second analysis tried to measure the quality of the time discrimination during the B state. I measured response rate as a function of time on only those omission trials with peak rates of 24 resp/min or less. The response-rate function was almost flat; during the first two bins (Sec 0–10), rates were 1.6 and 1.1 resp/min.; during the middle two bins (Sec 35–45), 2.8 and 2.4 resp/min; during the last two bins (sec 70–80), 1.6 and 1.9 resp/min. This is flatter than the distribution over all omission trials (Figure 12). It is plausible that the B state shows no discrimination at all and that the existence of discrimination in the response-rate function is only the result of some responses coming from the A state. For trials with peak rates of 12 resp/min or less—presumably a purer example of the B state—the response-rate function was apparently flat. Both the time discrimination and overall response rate of the B state are close to what was seen late in the trial with the Sec 20 functions of Experiment 1 (Figure 2)—response rate was flat at about 1 resp/min. These results suggest, in a tentative way, that there are two sources of responses, one source producing responses controlled by time, the other producing responses not controlled by time. During the A state—the normal state—responses come from both sources; during the B state, responses come only from the second source. For another example of the apparent mixture of distributions, with a similar interpretation, see Blough (1978).

The results of this experiment are evidence against the idea that the omission effect is due to frustration. Frustration theory assumes that the omission of an expected

reward has "immediate motivational (energizing) effects" (Amsel, 1962, p. 313). In the context of bar pressing, "energizing" can be interpreted at least two ways: to imply that the animal presses the bar more often (response rate increases) or to imply that the animal leaves the bar and runs around the chamber (response rate decreases). But neither interpretation agrees with what happened: There was little or no change in overall response rate (Sec 0–80). Although the omission of food may have sometimes put the animal into a new state (the B state), there is no clear reason for considering that state a state of frustration. If frustration was produced by the omission of food, it was not detectable in the rate of response.

Experiment 5

Part 1 of Experiment 1 showed that with food primed at Sec 20, the peak in response rate will be near Sec 20 and that with food primed at Sec 40, near Sec 40. Let us assume that the peak in response rate comes when the clock time most closely matches some criterion time. Then there are three simple ways that the time of food could change the time of the peak: (a) by changing the starting time of the clock—the setting of the clock when the interval begins (man-made clocks that measure different intervals this way are said to "time down," e.g., kitchen timers); (b) by changing the rate of the clock; and (c) by changing the criterion time (this is like "timing up"; stopwatches, for example, work this way).

In order to distinguish these possibilities, this experiment used a procedure similar to Experiment 3 of Roberts and Church (1978). As in Part 1 of Experiment 1, two signals (light and sound) were established: With one, food was primed at Sec 20; with the other, at Sec 40. Then shift trials were added: They began with the Sec 20 signal but soon shifted to the Sec 40 signal; the shift happened at Sec 5, 10, or 15. No food was given on shift trials.

With some assumptions, the different ways of changing peak time make different predictions about the peak time on shift trials. The assumptions are that the two signals (light and sound) are timed by the same clock, a shift does not change the setting of the clock (e.g., does not reset it), and time measured after the shift is added to time measured before the shift. Given this, suppose the time of food sets the starting time of the clock (the first alternative). At the time of a shift at Sec 5, the clock essentially reads "15 sec left," so the peak should happen 15 sec later, at Sec 20. (For simplicity, these predictions assume that the peak time with the Sec 20 signal is 20 sec and that with the Sec 40 signal, 40 sec.) With shifts at Sec 10 or Sec 15, the peak should also be at Sec 20. Or suppose that the time of food sets the rate of the clock (the second alternative). At the time of a shift at Sec 5, the clock essentially reads "25% done" (or "75% left"), so the peak should happen 30 sec later (75% of 40 sec), at Sec 35. With a shift at Sec 10, the peak should be at Sec 30; with a shift at Sec 15, at Sec 25. Suppose, finally, that the time of food sets the criterion time (the third alternative). At the time of a shift at Sec 5, the clock essentially reads "5 sec done," so the peak should happen 35 sec later, at Sec 40. With shifts at Sec 10 or Sec 15, the peak should also be at Sec 40.

Method

Subjects and apparatus. The subjects were the 10 rats used in Experiment 1. For a description of the apparatus, see General Method.

Procedure. During a preliminary phase of the experiment, the conditions of Part 1 of Experiment 1 were reinstated. This lasted 4 days. During the main phase of the experiment, these conditions continued, but with the addition of shift trials. The mix of trials was 70% food (half Sec 20, half Sec 40), 20% empty (half Sec 20, half Sec 40), and 10% shift. A shift trial began with the Sec 20 signal but shifted to the Sec 40 signal 5, 10, or 15 sec later. Shift trials were otherwise the same as empty trials: Measured from the start of the Sec 20 signal, they were the same length; they ended independently of responding; and no food was given. This part of the experiment lasted 15 days. On a given day, all shifts happened at the same time (5, 10, or 15 sec) after the start of the trial. Each of the five 3-day blocks contained 1 day with each shift time, in random order.

Results

The upper panel of Figure 15 shows the response-rate functions from the Sec 20 and Sec 40 signals during the main part of the experiment. The peak time with the Sec 20 signal was 21.8 ± .6 sec; for days with shifts

at Secs 5, 10, and 15, it was 21.8, 21.7, and 21.5 sec, respectively. The peak time with the Sec 40 signal was 42.0 ± .9 sec; for days with shifts at Secs 5, 10, and 15, it was 42.5, 41.7, and 42.1 sec. The difference in peak rates between the Sec 20 and Sec 40 signals was 0% ± 3%. This equality reflects the fact that 7 of the 10 rats had differences ranging from −5% to 10% (positive meaning Sec 20 > Sec 40). The other three, though, had differences of 45%, 30%, and 30%, all reliable across days by the sign test. They account for the apparent difference in peak rate seen in Figures 15 and 16.

The lower panel of Figure 15 shows the response-rate functions on shift trials. (The vertical scale differs from the upper panel.) The peaks are all close to Sec 40. Peak times were computed for shift trials by iterative centering, but the computation differed in two ways from the usual procedure. First, only responses after the shift were used. Second, the centering was done over the interval covered by the responses used, instead of over the interval 0–80 sec; for instance, a peak time of 40 sec for trials with shifts at 10 sec would mean that the number of responses in the interval Sec 10–40 equaled the number of responses in the interval Sec 40–70. Measured this way, the peak time (from the start of the trial) after a shift at Sec 5 was 38.8 ± 1.8 sec; after a shift at Sec 10, 37.8 ± 2.2 sec; and after a shift at Sec 15, 38.8 ± 3.5 sec. While the peak times are all close to the peak time of the Sec 40 signal (42.0 sec), they are all somewhat less. Only the time from the Sec 5 shift is by itself reliably less than the Sec 40 time, $t(7) = 3.0$, $p < .05$. Combining the evidence from the three shifts (Winer, 1971, p. 50), the difference is reliable, $z = 2.2$, $p < .05$.

Response rate after a shift was for a short time influenced by the response rate just before the shift. This is clear from the response-rate function for shifts at Sec 15; the first point after the shift is too high. In order to minimize the effects of prior response rate, peak times were computed by using only responses more than 20 sec after the start of the trial, i.e., at least 5 sec after a shift. Then the peak time after a shift at Sec 5 was 38.6 ± 1.3 sec; after a shift at Sec 10, 38.3 ± 2.2 sec; and after a shift at Sec 15, 41.5 ± 2.7 sec. When comparing these with the peak time of the Sec 40 signal, the probability levels are all the same as before.

Figure 16 shows how peak time and peak rate changed over the 15 days of shifts. The values are for 3-day blocks; each is a median over the three values for the days in the block. (The day values come from the analysis of a 15 days × 10 rats table.) The peak time on shift trials was roughly constant; it was consistently close to the peak time on Sec 40 trials, but also consistently less. The peak rate on shift trials decreased about 60%. Peak times and peak rates on baseline trials changed very little.

Comparison of the baseline peak times with the results of Part 1 of Experiment 1 shows that the introduction of shift trials did not change the peak time on baseline trials. In Experiment 1, the Sec 20 and Sec 40 peak times were 22.0 and 41.3 sec, respectively; in this experiment, 21.8 and 42.0 sec.

The curves fit to the response-rate functions are described in Table 2. The curve for the Sec 40 baseline condition (Figure 15) does not fit as well as the curves for most of the other baseline conditions. Comparing the residuals with the residuals from other base-

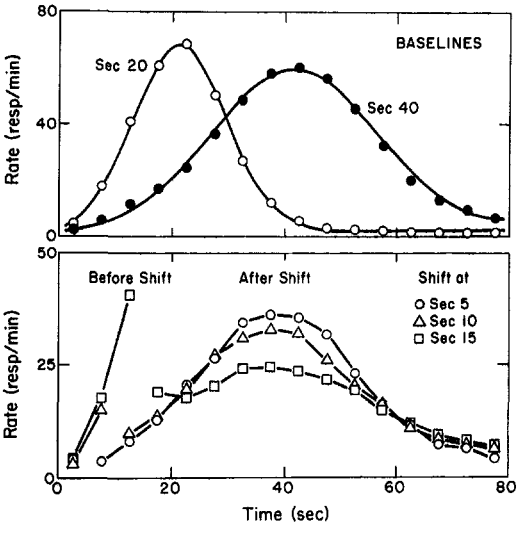

Figure 15. Mean responses per minute as a function of time into the trial on baseline trials (upper panel) and shift trials (lower panel) in Experiment 5. (The fitted curves and the method of fitting are described in Results of Experiment 1.)

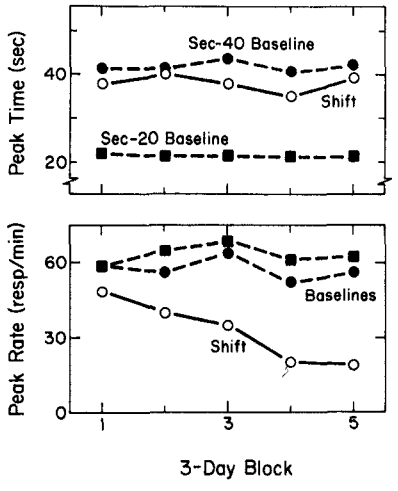

Figure 16. Peak time (upper panel) and peak rate (lower panel) as a function of day in Experiment 5. (Each point is a median over 3 days.)

line fits shows that the discrepancy is due to the three residuals from the first 15 sec of the trial. They are unusually high and suggest some confusion about what the signal was (Sec 20 or Sec 40); this may be due to the fact that shifts could occur at these times.

Discussion

The major result was that the peak time on shift trials was close to the peak time on Sec 40 baseline trials and did not vary with the time of shift. Furthermore, the response-rate functions from the three shift times were aligned over most of the interval, not just at their peaks (lower panel of Figure 15). The results are close to the predictions that assume the time of food sets a criterion time, and far from the predictions of the other possibilities. They suggest that the clock "times up" (starts at the same place when timing the Sec 20 and Sec 40 signals) and times the two signals at the same rate; the difference in peak time between the Sec 20 and Sec 40 signals is due to a difference in the criterion time with which the clock time is compared. Roberts and Church (1978) reached the same conclusions from an experiment that also involved a shift of signal but that did not use the peak procedure.

This places the time-of-food effect in the comparison stage. The criterion time is some sort of average of the memory of food times. The predictions for the "timing up" case assume that the shift of signal changes the comparison and not the clock; thus their verification supports the idea that the comparison can be changed without changing the clock.

A qualification to these conclusions is that the results were close to, but reliably different from, the predictions based on the assumption of "timing up." In its simplest form, the idea that the time of food sets the criterion time predicts that the peak times on shift trials should be the same as the peak times on Sec 40 trials. In fact, they were about 3 sec less, a difference that was reliable across rats and days (Figure 16). The discrepancy is not easy to explain. It is not due to the peak rate on shift trials because it appears consistently across varying peak rates (Figure 16). It is not due to events near the shift because it persists, for at least two of the three shift times, when data near the shift are excluded. None of the explanations I can think of—e.g., the clock is slower with the Sec 40 signal, or the clock starts more slowly with the Sec 40 signal—seem plausible to me, or are supported by other evidence.

The results are also a guide to what the clock is based on—what it is that changes with time in a regular way. Pavlov (1927, p. 104) explained inhibition of delay by assuming that the neural activity produced by a stimulus decreased during that stimulus; the decrease was the clock that allowed a time discrimination to form. A similar idea is that the start of the stimulus produces a unique impression; as time passes, this impression is forgotten. The memory of the start of the stimulus is the clock. These two ideas can be thought of as specific examples of timing down. Without elaboration, both of them predict that peak time on shift trials, measured from the time of shift, should have been the same as the peak time on Sec 40 baseline trials. Thus they are apparently ruled out.

If the clock measures time by counting or integrating something, the shift results are a guide to what is being counted or integrated. The rate of the event being counted

(or the level of the signal being integrated) can have a positive, negative, or zero correlation with the rate of the recorded response—here, a lever press. At one extreme (perfect positive correlation) is the suggestion of Ferster and Skinner (1957, p. 164) that the clock is an actual count of the responses made. There is some indirect evidence that supports this (Rilling, 1967). At the other extreme (perfect negative correlation) is the suggestion of Staddon (1977) that the clock is a count of "interim activities" (such as drinking) made when the animal is *not* making the recorded response. There is indirect support for this, too (e.g., Glazer & Singh, 1971; see Staddon, 1977, for a full discussion). However, over the course of Experiment 5, response rate on shift trials decreased more than 50% with little or no change in peak time (Figure 16). With a positive correlation between response rate and what the clock counted, peak time should have increased. If the correlation was perfect and the rate of the counted event was zero when response rate was zero, a 50% decrease in response rate should have doubled peak time. With a negative correlation, peak time should have decreased. Thus this result suggests that the rate of what is being counted (if anything) has no necessary correlation with the rate of the recorded response. The results of Experiments 1 and 3, other examples of large changes in rate with little change in peak time, support this conclusion.

This experiment provides more evidence that peak time and peak rate are independent measures. The peak rate on shift trials declined over days, but the peak time on shift trials was roughly constant (Figure 16). Part 2 of Experiment 1 found something similar—peak rate changes, peak time constant—but the example from this experiment is in a way better. In the example from Experiment 1, there was feedback—food was given during both of the conditions being compared. A change in the clock might have been hidden by a compensating change in the comparison. In the example from this experiment, there was no feedback because food was never given on shift trials. The other instance of the independence of the two measures was a repetition of a result of Experiment 1: Peak rates were equal for the Sec 20 signal and the Sec 40 signal in spite of a large difference in peak time. This was not true for all rats, though; three had much lower peak rates during the Sec 40 signal. This is easy to explain. On shift trials, no food was given, and the rats noticed the lack of food during the Sec 40 signal on these trials. If, when a rat noticed the lack of food, it still remembered the shift, it could associate the lack of food with the shift and reduce its rate only on shift trials. But if the rat did not remember the shift when it noticed the lack of food, it would associate the lack of food with the Sec 40 signal and reduce its rate on any trial with the Sec 40 signal.

General Discussion

Main Results and Conclusions

The results suggest some conclusions about the structure of the stimulus-response path used in time discrimination:

First, the stimulus-response path can be divided into a timing system, measured by peak time, and a response system, measured by peak rate. The two systems are separate in the sense that the timing system can be changed without changing the response system and that the response system can be changed without changing the timing system. This is suggested by the independence of peak time and peak rate. In Experiments 1, 3, and 5, peak rate changed substantially, with little or no change in peak time; in Experiments 1 and 2, peak time changed substantially, with little or no change in peak rate. The timing system is apparently sensitive to the time of food (Experiments 1 and 5), blackouts when timing light (Experiment 2), prefeeding (Experiment 3), and the omission of expected food (Experiment 4); each of these changed peak time. It is apparently insensitive to a low probability of food (Experiments 1 and 5); this did not change peak time. The response system is apparently sensitive to a low probability of food (Experiments 1 and 5) and prefeeding (Experiment 3); each of these changed peak rate. It is apparently insensitive to the time of food (Experiments 1 and 5) and blackouts

(Experiment 2); neither of these changed peak rate.

Second, the timing system can be divided into a clock and a comparison. In Experiment 5, the predictions that turned out to be close to correct assumed that the comparison could be changed without changing the clock. In Experiments 2 and 3, manipulations that changed peak time did not change the spread of the response-rate functions (Figures 6 and 11). Other results suggest that these manipulations changed the clock; given that the spread of the functions is set by the timing system, then these results suggest that the clock can be changed without changing the comparison. The clock is apparently sensitive to blackouts (Experiment 2), prefeeding (Experiment 3), and the omission of expected food (Experiment 4) and insensitive to the time of food (Experiment 5); the comparison is apparently sensitive to the time of food as measured by the clock (Experiments 1, 3, 4, and 5) and insensitive to prefeeding.

These conclusions are not new; they are implicit or explicit in most theories of timing. For example, Gibbon (1977) described a mathematical theory of timing with a motivational parameter (sensitive, for example, to prefeeding) that is assumed to be independent of various timing parameters (sensitive, for example, to time of food). The division of a discrimination system into measurement and memory-comparison components is a feature of most theories of discrimination learning (e.g., Sutherland & Mackintosh, 1971). What *is* new is the precision and directness of the evidence, especially the evidence for separate timing and response systems (e.g., Table 1).

The results also suggest some properties of the internal clock:

First, the clock can be stopped temporarily—in Experiment 2, by blackouts. The main evidence for this is that blackouts increased peak time and that the size of the increase was close to, and varied with, the length of the blackout. Roberts and Church (1978) reached the same conclusion.

Second, the pacemaker of the clock is internal. This is based on the conclusion that prefeeding changed the rate of the clock (Experiment 3); the main evidence for this is that prefeeding increased peak time and that the prefeeding response-rate function overlapped the baseline response-rate function when plotted in terms of percentage of peak time. Maricq, Roberts, and Church (1981) also concluded that the pacemaker of the clock is internal.

Third, the clock is at least partially reset by food (Experiment 4). When food was omitted at the end of one trial, peak time on the next trial was less than usual. Staddon (1974) reached a somewhat similar conclusion.

Fourth, the clock times intervals of different lengths, using the same starting point and rate (Experiment 5). The evidence for this is that the response-rate functions from different shift times all had peaks near Sec 40. Roberts and Church (1978) reached the same conclusion.

Some other important results and conclusions are described below.

Shape of the Response-Rate Functions

There are three main findings about the shape of the response-rate functions:

First, the functions were fit very well by the sum of two curves: one (signal) shaped like a Gaussian distribution, with three free parameters (location, height, and spread); the other (noise) starting at the origin, increasing linearly until Sec 30 and later constant, with one free parameter (final height). Table 2 shows that in 10 of 19 cases, the fitted curve described at least 99.8% of the variance (12 *df*). Others (Killeen, 1975; Lowe & Harzem, 1977; Osborne, 1978) have found that a Gaussian curve fits very well the response-rate functions from an ordinary fixed-interval schedule; these functions resemble the early half of the response-rate functions from the peak procedure. For example, in three of five cases, the fits of Osborne described at least 99.6% of the variance (7 *df*).

Second, the noise parameter did not vary much across fits; in 13 of 19 cases, it was between 1.5 and 2.7 resp/min. For functions with peaks near Sec 40, the noise parameter is not fixed in any obvious way by the data, and its constancy is an important sign of its reality.

Third, the fits fail to describe a slight asymmetry, but otherwise the deviations are not systematic. I looked at the residuals from six Sec 40 conditions: the Sec 40 condition of Experiment 1, the three baseline conditions of Experiment 2, and the two baseline conditions of Experiment 3. These conditions were chosen because their fits were very close, describing at least 99.8% of the variance. The only pattern in the residuals that was consistent across fits was that the first residual, at Sec 2.5, was always negative (range, −.2 to −1.0 resp/min) and the last residual, at Sec 77.5, was always positive (range, .4–1.1 resp/min). The same thing was true for the three well-fit Sec 20 conditions, two from Experiment 1 and one from Experiment 5. The residual at Sec 2.5 was always negative (range, −1.2 to −2.6 resp/min) and the residual at Sec 42.5 was always positive (range, .9–1.7 resp/min).

These findings lead to several conclusions:

1. Observed responding was probably a mixture of responses from two sources (distinct in the sense that one can be changed without changing the other). The response-rate function of one source (signal) had a Gaussian shape, whereas the response-rate function of the other (noise) was almost flat. These conclusions are supported by four lines of evidence: (a) The shape of the Sec 20 distributions (Figure 2). Before about Sec 50, response rate changes with time; after that, it does not. The tail seems to be a direct observation of the noise. (b) The quality of the fits, described above. (c) The constancy of the noise parameter, described above. (d) A decrease in the probability of food had a large effect on the fitted level of signal and little or no effect on the fitted level of noise (Table 2). In Part 2 of Experiment 1, signal (peak rate) decreased 72% from baseline (from 55 to 15 resp/min), whereas noise decreased 4% (from 2.6 to 2.5 resp/min). (e) The results from Experiment 4 (Figure 14) that suggest that food omission can sometimes shut off the signal source, leaving just noise. The details of the argument are described in Discussion of Experiment 4.

Others have concluded that they observed two types of responses, different in a sense close to what is meant here. Blough (1963), using pigeons in a variety of free-operant procedures, found that the probability of short interresponse times was unchanged by many variables that changed the probability of longer interresponse times. Schwartz and Williams (1972) found that long-duration key pecks were sensitive to differential reinforcement but that short-duration pecks were not; Schwartz (1977b) found that only long-duration pecks were sensitive to differential punishment. There are other qualitative differences between short- and long-duration pecks (Schwartz, 1977a; Schwartz & Williams, 1972; but see also Ziriax & Silberberg, 1978). Using a wavelength discrimination task, Blough (1978) concluded that some responses were controlled by wavelength and some were not. The two types of responses had very different (but slightly overlapping) latency distributions. In the work of Blough and of Schwartz, the two types of responses were "physically" different (different in duration, latency, etc.); in these experiments, the two types may not have been physically different.

The following conclusions assume that the signal function had a shape very close to a Gaussian distribution.

2. The scale of the rat's clock is probably linear, i.e., equal differences on the scale correspond to equal differences in seconds. The signal function has a simple (easily described) shape on a linear stimulus scale. The observed simplicity is really a combination of two things: a simple shape (Gaussian) and a simple stimulus scale (linear). Both are important. Any unimodal function will be Gaussian on some transformation of the stimulus scale, and any function will have some shape on a linear stimulus scale. The same argument could also be made using only the symmetry of the response-rate functions (which does not depend on the response scale) rather than their Gaussian shape (which does). Another simplicity is that a linear stimulus scale gives the Sec 20 and Sec 40 functions the same shape. If the rat's clock does not have a linear scale, then the observed simplicities are hard to explain.

Church and Deluty (1977) concluded that the scale of the rat's clock was logarithmic, or at least that such a scale was consistent with their results. They trained rats to press one lever after one duration and a second

lever after another duration. Then they exposed the rats to intermediate durations and found that the geometric mean of the two training durations produced equal choice of the two levers. Their conclusion was based on this finding and on the assumption that the point of equal choice is equidistant from the two training durations on the scale of the rat's clock. However, I know of no support for this assumption. Later work with choice procedures suggests a linear scale (Gibbon & Church, 1981; Church & Gibbon, Note 2). For example, with a procedure that produces a temporal generalization gradient with two sides (like the peak procedure), the function is close to symmetrical on a linear scale of time (Church & Gibbon, Note 2).

3. The error in the clock is small relative to other error ("error" meaning variance). The total error in performance is measured by the spread of the response-rate functions. Because the response-rate functions were averaged over trials and rats, "error" as used here includes not only within-trials variation but also between-trials and between-rats variation.

The conclusion that the clock error is small is based on the symmetry of signal function and four assumptions: (a) The scale of the clock is linear. (b) The clock error is proportional to the clock time (Weber's law applied to the clock). (c) Response rate is a measure of how well the rat discriminates the clock time from the peak time. The better the discrimination, the lower the rate. Equal discriminations will lead to equal rates. (d) The discrimination between clock time and peak time is a function of two things: the difference (on a linear scale) between clock time and peak time, and the total error. The more difference, the better the discrimination. The more error, the worse the discrimination. Suppose that the peak of a response-rate function is at Sec 40. The symmetry means that the response rate at Sec 20 will equal the response rate at Sec 60. Equal response rates implies equal discrimination. Because the discriminations are equal and the differences are equal (both Sec 20 and Sec 60 are 20 sec different from Sec 40), the total error must be equal at the two times. However, the clock error is three times larger at Sec 60 than at Sec 20. Therefore the clock error is zero at both times, and therefore zero throughout. The same argument holds, of course, with other assumptions about the clock error—for example, if the clock error is proportional to the square root of the clock time (Creelman, 1962).

In fact, even allowing for noise, the response-rate functions were slightly asymmetrical (shown by the residuals from the fitted curves); the asymmetry is in the direction predicted if the clock error were more than zero. To judge the meaning of the observed asymmetry, it is helpful to know how much asymmetry would be expected if all the error were due to the clock. To make exact predictions, it is necessary to be more explicit about the relation between discrimination, difference, and error. An assumption that seems as plausible as any other is that discrimination is a function of difference divided by error. This is a sort of *z*-score approach: If the error is doubled, to produce equal discrimination the difference must be doubled. An assumption like this is a consequence, for example, of signal-detection theory. Again consider a distribution with a peak at Sec 40. When will response rate after the peak equal response rate at Sec 20? As explained above, if none of the error is in the clock, the answer is Sec 60. If all of the error is in the clock, the answer depends on the relation between clock error and clock time. If the clock error is assumed to be a constant fraction of the clock time, the answer is Never. At Sec 100, for instance, the difference between clock time and peak time is three times more (compare $100 - 40$ to $40 - 20$), but the error is five times more (compare 100 to 20). If the clock error is assumed to be proportional to the square root of the clock time, the answer is Sec 80. If timing is based on counting, this is a likely lower limit (Creelman, 1962). What was observed is clearly much closer to Sec 60 than Sec 80 or never and thus suggests that the clock error is small relative to other error.

The Sec 20 functions (high food) from Experiments 1 and 5 have Weber fractions (standard deviation/peak time) of .44, .38, and .39; the Sec 40 functions from the same experiments have fractions of .39 and .35. So (overall) accuracy in this situation at

least roughly obeys Weber's law. This agrees with other work on animal timing (e.g., Church & Deluty, 1977; Church, Getty, & Lerner, 1976; Gibbon, 1977). Both the Sec 20 and Sec 40 distributions are nearly symmetrical and the arguments of the preceding paragraphs suggest that their spread is due almost entirely to sources other than the clock. It is therefore these nonsensory sources that are obeying Weber's law. One source of Weber's law in this situation could be the memory—longer times are remembered less accurately.

These conclusions contradict common assumptions about the accuracy of timing. For example, Church et al. (1976) compared two models of timing; both models assumed that the nonsensory error was constant with changes in interval length and that differences in accuracy were due entirely to differences in the accuracy of perceived time. Gibbon derived the conclusion that the accuracy of discrimination followed Weber's law from the assumption that perceived time followed Weber's law. The usual assumption of signal-detection theory (e.g., Green & Swets, 1966) is that differences in accuracy between conditions are due entirely to differences in the accuracy of the sensory signal.

4. Response rate was a multiple of the response probability of some internal event. Just as the observation of a simple shape (Gaussian) on a simple stimulus scale (untransformed seconds) is remarkable, the observation of a simple shape (Gaussian) on a simple response scale (untransformed responses/minute) is also remarkable.

Functions with a shape close to Gaussian are empirically common (e.g., Tukey, 1977), but in all the cases I know of outside these experiments the functions are frequency distributions. The response-rate functions of these experiments, of course, are not frequency distributions, but it seems likely that they have Gaussian shapes because they are really frequency distributions in disguise; that is, response rate is a multiple of the probability that some (internal) response has a given value, where different values correspond to different times, and the distribution of values is Gaussian on a linear scale. To make this more concrete, suppose that the clock measures time without error, i.e., for each physical time there corresponds one clock time. Throughout the trial, say once a second, a time is taken from memory. The memory times have a Gaussian distribution with the same location and spread as the response-rate function. When the clock time is within a second of the memory time, a response is made. This shows how a frequency distribution could be turned into a response-rate function with the same shape.

The conclusion (from these data) that response rate was a multiple of the response probability of some internal event depends entirely on the assumption that the only way to produce a Gaussian shape is by a frequency distribution. If there are other ways of producing Gaussian shapes, the conclusion might be wrong. However, on the basis of much different data and reasoning, Roberts (Note 3) also concluded that response rate was a multiple of the response probability of some internal event.

When one considers how response rate is measured, this conclusion may seem either obvious or amazing. Response rate is a multiple of the response probability of an external event, namely, a switch closure. It will be a multiple of the response probability of an internal event if there is a one-to-one relation (or two-to-one, or one-to-two, etc.) between the internal event and the external event. If this seems likely, then the conclusion may seem obvious. However, one should consider, among other things, that there are many ways to close a switch, that many muscles are involved, and that there is a vast physical difference between a switch closure and anything that happens in the nervous system.

The Peak Procedure

The independence of peak time and peak rate can be important apart from any deep concern about what they measure. In the second half of Experiment 3, for example, prefeeding did not change peak time. To interpret this, it is helpful to know that prefeeding did change peak rate; this shows the potency of the manipulation. From a more theoretical view, however, the independence of the two measures is important because it

suggests that each measure isolates part of the stimulus-response path. ("Isolate" is used here in the following way: A measure isolates some part of the stimulus-response path if (a) a change in the measure implies a change in the part and/or (b) no change in the measure implies no change in the part.) The extent to which peak time isolates the clock depends on the extent to which a change in peak time implies a change in the clock and no change in peak time implies no change in the clock.

A change in peak time implies a change in the clock. This is supported, of course, by the observation of a change in peak time when there is (other) evidence that the clock has changed; it is contradicted by the observation of a change in peak time when there is evidence that the clock has not changed. Evidence supporting this statement comes from Experiments 2, 3, and 4. In Experiment 2, for example, blackouts changed peak time. The conclusion that blackouts changed the clock is supported by the invariance of the spread of the response-rate functions; by the sizes of the changes in peak time; and by the results of Roberts and Church (1978). Outside support for this statement comes from the work of Maricq et al. (1981). With the peak procedure, they found that methamphetamine injections change peak time; with a choice procedure, they found evidence supporting the conclusion that methamphetamine injections change the clock.

Evidence against this statement comes from Experiment 5, whose main conclusion was that the time of food changed peak time by changing the comparison rather than the clock. But this conclusion is not surprising, and it can be seen as a special case. All results so far are consistent with the idea that response rate peaks when the clock time is closest to the memory of the times when food has been received. With this idea, a change in peak time implies a change in the clock only if the memories are constant. Changing the time of food is an obvious way, and probably the only obvious way, of changing the memories of time of food. This shows that the statement should be limited: A change in peak time implies a change in the clock when the physical time of food is constant.

No change in peak time implies no change in the clock. In Experiment 1, changing the probability of food did not change peak time. The best evidence that changing the probability of food did not change the clock seems to come from the many signal-detection-theory experiments that have concluded that changes in payoffs do not affect sensory processes, or at least the sensory processes that determine sensitivity; an example from the study of timing in pigeons is Stubbs (1976). Although the evidence for the statement is not strong, it should be recognized that it has a lot of a priori plausibility. A rewording of the statement is "a change in the clock will produce a change in peak time." If peak time is at least in part determined by the similarity of clock time and memory times, then a change in the clock will change peak time unless there is some sort of cancellation.

Unfortunately, cancellation can happen. During the second half of Experiment 3, prefeeding did not change peak time; the best explanation of this result seems to be that prefeeding changed the clock but that the change in the clock was canceled by a compensating change in the comparison. The possibility of cancellation creates problems for any interpretation of no change in peak time. The mechanism that produced cancellation in Experiment 3 will presumably operate whenever the treatment changes the clock on food trials and the rat can discriminate the treated (e.g., prefed) state from the baseline state. Then the rat can adopt different criteria for the two states, and eventually the treatment will not change peak time. But there are a number of ways one can get evidence for or against the existence of cancellation: (a) Cancellation should take time to develop, on the order of days. Thus it will not be present on the first day, and it will produce changes in peak time over days. In Experiments 3 and 4, the treatment presumably altered the clock on food trials, and peak time changed over days. In Experiments 2 and 5, the treatment presumably did not change the clock on food trials, and peak time did not change over days. (b) Unless the discrimination of the treated and baseline states is perfect, the conditions that produce cancellation should change the peak

time on baseline trials. In Experiments 3 and 4, the treatment changed the peak time on baseline trials; in Experiments 2 and 5, it did not. (c) The mechanism of cancellation proposed here is similar to the mechanism of morphine tolerance proposed by Siegel (e.g., 1975). Experiments parallel to Siegel's could provide evidence for or against cancellation.

Maybe the most important conclusion from these experiments is that the peak procedure is useful. For the most part, the experiments of this study asked questions that had been asked before, and found the same answers. This is a sort of validation of the procedure. Other work (Maricq et al., 1981; Roberts, Note 4) used the peak procedure to ask new questions; the basic assumption of this work is that when the time of food is constant, a change in peak time implies a change in the clock.

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