

A Mode Control Model of Counting and Timing Processes

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The similarity of animal counting and timing processes was demonstrated in four experiments that used a psychophysical choice procedure. In Experiment 1, rats initially learned a discrimination between a two-cycle auditory signal of 2-sec duration and an eight-cycle auditory signal of 8-sec duration. For the number discrimination test, the number of cycles was varied, and the signal duration was held constant at an intermediate value. For the duration discrimination test, the signal duration was varied, and the number of cycles was held constant at an intermediate value. Rats were equally sensitive to a 4:1 ratio of counts (with duration controlled) and a 4:1 ratio of times (with number controlled). The point of subjective equality for the psychophysical functions that related response classification to signal value was near the geometric mean of the extreme values for both number and duration discriminations. Experiment 2 demonstrated that 1.5 mg/kg of methamphetamine administered intraperitoneally shifted the psychophysical functions for both number and duration leftward by approximately 10%. Experiment 3 demonstrated that the magnitude of cross-modal transfer from auditory signals to cutaneous signals was similar for number and duration. In Experiment 4 the mapping of number onto duration demonstrated that a count was approximately equal to 200 msec. The psychophysical functions for number and duration were fit with a scalar expectancy model with the same parameter values for each attribute. The conclusion was that the same internal mechanism is used for counting and timing. This mechanism can be used in several modes: the "event" mode for counting or the "run" and the "stop" modes for timing.

The purposes of the present study are two-fold: to determine whether animals can discriminate number and duration independently and to determine whether or not the same mechanism is used for the discrimination of the number of sequential events and duration. An animal may be said to be timing if the duration of an event serves as a discriminative stimulus; an animal may be said to be counting if the number of events serves as a discriminative stimulus. The conclusions will be that animals can discriminate number and duration independently, but they use the same mechanism for number and duration discrimination.

In previous research on response counting, the number of responses has often been con-

founded with duration. Mechner (1958) was the first to attempt to identify a criterion number of responses (N) as an effective discriminative stimulus. His procedure was as follows: Following N or more successive right-lever responses by a rat, a left-lever response was reinforced. On different groups of sessions the value of N was 4, 8, 12, or 16 responses. The results showed that the probability of a left-lever response as a function of the number of right-lever responses that had been made was fairly symmetrical on a linear scale with a maximum probability near the criterion N . As the value of N increased, the variability of the distribution also increased. Various investigators have recognized that the effective variable in Mechner's experiment may have been the time that the animal worked on the right lever, not the number of right-lever responses. One way to separate duration and number of responses is to determine the effect of a treatment that changes response rate. Mechner and Guevrekian (1962) found that an increase in water deprivation increased response rate but

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did not affect the function relating the probability of a left-lever response to the number of right-lever responses that had been made. Laties (1972) found a similar result when drugs were used to change the response rate. Another way to separate duration and number of responses is to introduce intervals following each response during which responses do not occur (Wilkie, Webster, & Leader, 1979). With this procedure pigeons had functions that were equivalent when the blackout periods were fixed (so that either duration or number could be used) or when the blackout periods were of random duration (so that only number could be used). Hobson and Newman (1981) provided a good review of these differentiation and discrimination studies (e.g., Rilling & McDiarmid, 1965) based on the number of responses.

There are only a few demonstration experiments that show that the number of successive stimuli can serve as a discriminative stimulus. For example, with an autocontingency, Davis, Memmott, and Hurwitz (1975) showed that rats can discriminate three successive events when time between events is a random variable, but they did not rule out the possibility that rats may have summed the durations of the fixed-duration signals. Fernandes and Church (1982) showed that rats can discriminate between two and four sequential events, even when all temporal cues are counterbalanced or held constant.

In contrast, there are many experiments that show that the duration of a signal can serve as a discriminative stimulus. For example, Meck, Church, and Olton (in press), Roberts (1981), and Roberts and Church (1978) showed that rats are able to sum the durations of successive stimulus components in order to determine their response.

Experiment 1: Training on Compound Signals

In the present experiment, duration and number were totally confounded during training. A left response was reinforced following a two-cycle noise of 2-sec duration and a right response was reinforced following an eight-cycle noise of 8-sec duration. A cycle was defined as sound-on and sound-off periods of equal duration. During testing for

number discrimination, signal duration was held constant at an intermediate value while the number of cycles was varied; during testing for duration discrimination, the number of cycles was held constant at an intermediate value while the signal duration was varied. The logic of holding one of the signal attributes (duration or number) constant at an intermediate value while varying the other was to neutralize one attribute to measure the degree of control by the other.

Method

Subjects

The subjects were 10 male albino Norway rats (Charles River CD), about 190 days old at the start of training. The animals were kept in individual metal cages (Wahmann Mfg. Co., Baltimore, Maryland) and had unlimited access to water. Throughout the experiment, each rat received a daily ration of about 15 g of ground Charles River Rat Formula mixed with about 15 cc of water delivered approximately 15 min. following the end of each session.

Apparatus

Ten lever boxes ($23 \times 20 \times 22$ cm) were used in the experiment. The roof and the two side panels of each box were transparent acrylic; the front and back walls were aluminum; the floor was constructed of 16 parallel stainless steel bars. Two retractable stainless steel levers projected through the front panel on either side of the food cup. The levers in Boxes 1-6 were 1.6×4.6 cm wide and were located 3.8 cm above the grid floor (Gerbrands Model 6311). The levers in Boxes 7-10 were 2.5×5.0 cm and were located 5.0 cm above the floor (BRS/LVE Model 123-07). A pellet dispenser delivered 45-mg Noyes Precision food pellets through an opening in the front panel to a food tray. A 140-ml glass water bottle hung from the back wall of the chamber. Six boxes had a 7.5-W lamp attached to the middle of the back wall of the chamber; four boxes had a 6-W lamp attached to the outside of the roof of the lever box. A noise generator could be used to deliver white noise of about 80 dB (re $20 \mu\text{N/m}^2$; the General Radio Sound Level Meter, Model 1565-D, A scale) above background level through a 4-in. (10.2 cm) speaker mounted inside each chamber. In Boxes 7-10, electric shock could be delivered to the grid floor through an autotransformer, a power transformer, and a 150-k resistor in series with the animal. Each lever box was enclosed in an insulation board chamber designed to minimize outside light and sound. Each chamber was equipped with a fan for ventilation and a small observation window. A PDP-12 computer controlled the experimental equipment and collected the responses.

Procedure

Pretraining. Each rat received two sessions of combined magazine and lever training. A food pellet was

delivered each minute for 60 min. (magazine training) and, in addition, each lever press produced food. The session began with the insertion of the left lever and 10 responses were reinforced, after which the left lever was retracted and the right lever inserted. Ten right lever responses were then reinforced, followed by retraction of the right lever and insertion of the left lever. This alternation between levers continued until the rat had pressed each lever 60 times or when 30 min. had passed, whichever came first. The houselight illuminated the chamber at all times during the session.

Training (Days 1-15). The rats were trained to press the left lever following a one cycle/sec white noise signal of 2-sec duration ("few-short" response) and to press the right lever following a one cycle/sec white noise signal of 8-sec duration ("many-long response"). (The one cycle/sec signal had .5-sec sound-on periods alternated with .5-sec sound-off periods; the number of cycles is equal to the number of sound segments.) These signals differed in two ways: number of sound segments (two or eight) and total signal duration (2 or 8 sec). (See the cells labeled L and R in Table 1 for Experiment 1.) On each trial one of the two signals was randomly presented with a probability of .5. When the signal was turned off, both levers were inserted in the box. If the rat made the correct response, a pellet of food was immediately delivered; if it made the incorrect response, no pellet was delivered. When either lever was pressed, there was a .5-sec delay and then both levers were retracted. Intertrial intervals (ITIs) were 5 sec plus a geometrically distributed duration with a minimum of .1 sec and a mean of 35 sec. On Days 1-5, if an incorrect response had been made on the previous trial, the same signal was presented again on the next trial (correction procedure). From Day 6 until the end of the experiment, there were no correction trials. A daily session began within 30 min of the same time each day and lasted for 3 hr. A record was kept of the number of left and right responses following each of the two signals and the latency of each response.

Testing (Days 16-17). The conditions of training were maintained except that each of the two training signals were presented with a probability of .25 on each trial. On the remaining trials, there were two types of unreinforced test signals. One set of signals held the number of cycles constant at four while varying the total signal duration between 2 and 8 sec (2, 3, 4, 5, 6, and 8 sec).

The other set of test signals held total signal duration constant at 4 sec while varying the number of cycles between two and eight cycles (two, three, four, five, six, and eight cycles). (See the cells labeled X in Table 1 for Experiment 1.) These 12 signal combinations were presented with equal probability. Only the data from Day 16 are presented.

Results

The median performance of the rats during the first test session is shown in Figure 1. Responses with latencies greater than 3 sec are not included in this figure or in any subsequent figures or calculations because previous work has shown that such responses are not well controlled by the reinforced dimension (e.g., Maricq & Church, 1983; Maricq, Roberts, & Church, 1981). A median of $6.7\% \pm 5\%$ of the trials were discarded by the 3-sec latency criterion. For each signal type, the probability of a "long" or a "many" response increased as a function of signal value. The smooth function near the data points is based on a model described in the Discussion section. Similar smooth functions were obtained for each rat, and these were used to estimate the point of subjective equality (PSE), the difference limen (DL), and the Weber fraction (DL/PSE).

The PSE is the signal value that the rat called "long" or "many" on 50% of the trials. The median PSE was $4.07 \pm .17$ (for duration) and $4.02 \pm .15$ (for number), a nonsignificant difference, $t(9) < 1$. For both duration and number, the PSE was close to 4.0, which is the geometric mean between the two extreme signal values. A DL was also estimated from the individual psychophysical

Table 1
Design of Experiment 1: Testing

Total no. of cycles	Total duration (in sec) of signal					
	2	3	4	5	6	8
2	L(1.00)		X(2.00)			
3			X(1.33)			
4	X(.50)	X(.75)	X(1.00)	X(1.25)	X(1.50)	X(2.00)
5			X(.80)			
6			X(.67)			
8			X(.50)			R(1.00)

Note. L = left response reinforced, R = right response reinforced, X = neither response reinforced; each number in parenthesis represents duration in seconds of a single cycle.

functions. From the same smooth theoretical functions used to estimate the PSE, the signal value that the rat called "long" or "many" on 75% of the trials and the signal value that the rat classified as "long" or "many" on 25% of the trials was found. One half of this range of signal values is defined as the DL. The median DL for duration was $.97 \pm .14$, and for number it was $1.04 \pm .27$, a nonsignificant difference, $t(9) < 1$. The median Weber fraction was $.22 \pm .02$ for duration and $.24 \pm .01$ for number, a nonsignificant difference, $t(9) < 1$. The values above refer to the median and plus or minus the median absolute deviation.

Discussion

During original training both duration and number were relevant attributes. The rats learned, apparently, to classify the signals both according to duration and number when they were totally confounded, and the accuracy of the duration and the number

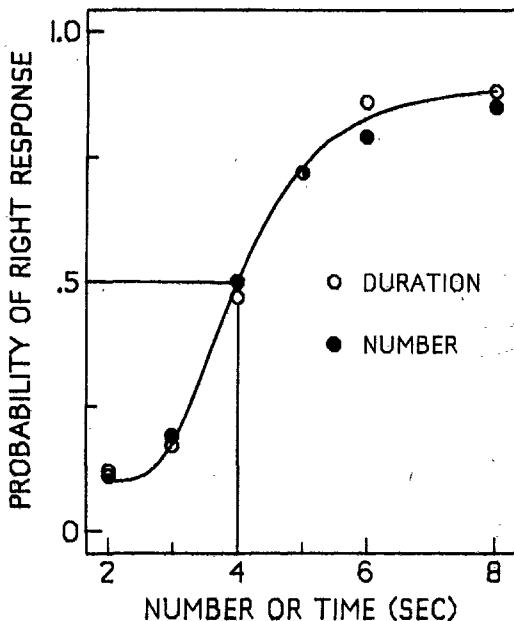


Figure 1. Psychophysical function for duration and number during the first test session. Median probability of a right response as a function of number of cycles or time (in sec). (Open circles represent variation in signal duration and closed circles represent variation in the number of cycles. Smooth function represents the theory fit.)

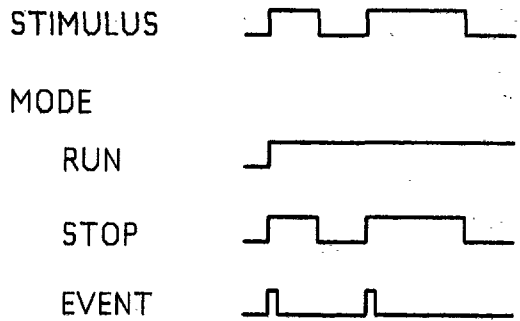


Figure 2. Diagram of three modes of operation of the accumulation process.

classification was equivalent. This became evident when one of the attributes was held constant and the other varied. The geometric mean of the two reinforced values was used as the intermediate value for the attribute held constant, because previous work has shown that this value represents the subjective middle for duration in bisection tasks (e.g., Church & Deluty, 1977).

On any given trial the rat required a representation of the total duration and the number of events. Previous studies have shown that a rat can time two signals simultaneously and independently (Meck & Church, in press). In the present study the rats timed and counted simultaneously in a similar manner.

The psychophysical functions for duration and number were quite similar when the ratio of the extremes was constant. This suggests that either the same mechanism was used for the analysis of duration and number or two different mechanisms were used that, coincidentally, had the same sensitivity. Because it is a simpler proposal, we will explore the possibility that the same mechanism is employed for timing and counting. Perhaps there is an internal mechanism that puts out pulses that can be controlled in several modes, as shown in Figure 2. The top line shows a stimulus that goes on and off several times. The next three lines show how the animal might respond to the stimulus: In the "run" mode the initial stimulus starts a process that continues until the end of the trial; in the "stop" mode the process occurs whenever the stimulus occurs; in the "event" mode each onset of the stimulus produces a relatively fixed duration of the process regardless

of stimulus duration. This is a mechanism that can be used either for the estimation of time (the run and the stop modes) or for the estimation of number (the event mode).

Figure 3 shows the functional units of an information-processing model of timing (Gibbon & Church, in press). A pacemaker puts out pulses. A mode switch can be closed to pass these pulses to an accumulator. The pacemaker-switch-accumulator system may be called either a clock or a counter. It is used as a clock if the switch operates in a run or a stop mode; it is used as a counter if the switch operates in an event mode. In either case, the value in the accumulator may be passed to working memory (e.g., Meck et al., in press). The current accumulator value is compared to the remembered accumulator value at the time of reinforcement of a previous response, a value that is stored in reference memory. The decision process is a response rule that determines the response.

The precise form of the psychophysical function provides evidence for the discrimi-

nation processes involved. In the case of the temporal bisection function, the PSE is near the geometric mean of the two reinforced durations and the Weber fraction is fairly constant over a wide range of signal durations (e.g., Church & Deluty, 1977; Meck, 1983; Stubbs, 1968). Gibbon developed several models of time estimation that are compatible with these results (Gibbon, 1981). The version Gibbon refers to as the "sample known exactly with a similarity decision rule" provides the best fits and the least systematic deviations. In this version, the pacemaker is assumed to emit pulses at some fixed interpulse interval on any given trial. Across trials the interpulse interval is assumed to be normally distributed with some mean and standard deviation. On the basis of experience the animal learns the accumulator value associated with reinforcement of a left or right response. This information is stored in reference memory. On any given trial, the animal has a representation of the current accumulator value. The animal makes

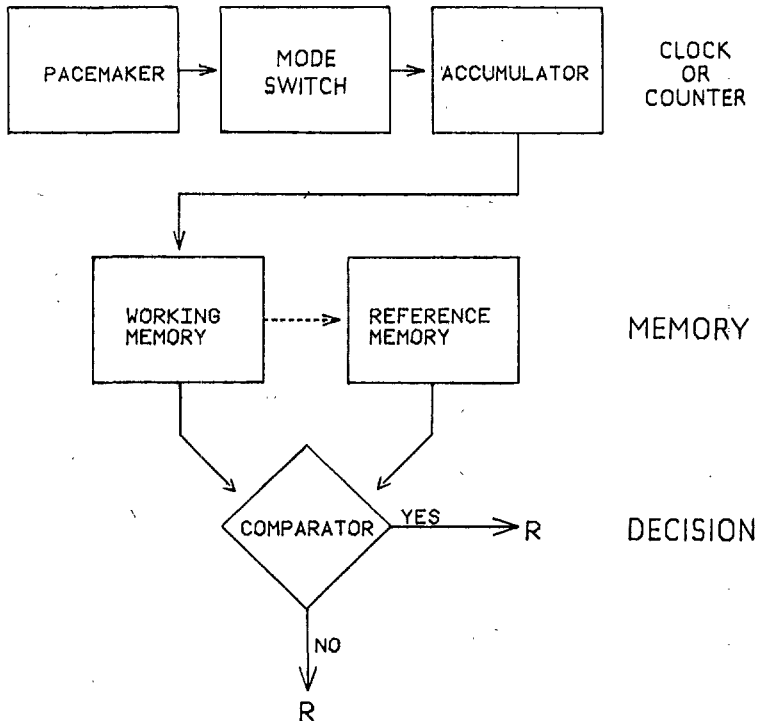


Figure 3. Functional units of an information-processing model of counting and timing. (Adapted from Gibbon & Church, in press).

a left response if this value is closer to the value in reference memory of a reinforced left response; it makes a right response if this value is closer to the value in reference memory of a reinforced right response. The measure of distance is a ratio between the accumulator value and the reference memory values, as described below.

The following account illustrates this process: On a particular trial the signal is presented for t sec, and the animal's pacemaker runs at some rate (λ) that is a normally distributed random variable with a mean (Λ) and some standard deviation (α). Λ_2 , the pacemaker speed at the time of a test, is potentially distinguished from Λ_1 , the pacemaker speed at the time of training. The mode switch is closed for some period of time (d), and pulses from the pacemaker enter the accumulator during this time. The number of pulses in the accumulator is $n_i = \lambda d$. The ratio of the standard deviation to the mean (γ) is called the coefficient of variation. The lower the ratio, the more sensitive the animal is to time. As $\gamma \rightarrow 0$, n_i becomes an increasingly accurate estimate of t .

When the signal value is S , a left response is reinforced. The mean accumulator value at the time of reinforcement is $N_S = \Lambda D_S$, where capital letters are used for expected values. We assume that this value is remembered accurately. By a similar argument, when the signal value is L , a right response is reinforced, the mean accumulator value at the time of reinforcement is $N_L = \Lambda D_L$, and we assume that this value is remembered exactly.

On a given trial, when the signal value is t , the accumulator value is $n_i = \lambda d_i$. The animal compares the distance of the current accumulator value to two samples of accumulator values that were stored in reference memory, one associated with reinforcement of the "many-long" response m_L^* and the other associated with reinforcement of a "few-short" response m_S^* . The animal responds to the closer one. The specific rule is respond "many-long" if $m_L^*/n_i < n_i/m_S^*$, that is, respond "many-long" if $n_i > \sqrt{m_S^* \cdot m_L^*}$. If the values stored in reference memory are accurate representations of the values in the accumulator, indifference is predicted at the geometric mean of S and L . This process may

be simulated or calculated with equations derived by Gibbon (1981, Equation 17) that, in the special case of the referents known exactly, is given in Equations 45a and 45b. He has shown under these conditions:

$$P(T; S, L) \cong \Phi(\sqrt{C} - \sqrt{\lambda}) \quad (1[17])$$

$$\sqrt{\lambda} = \frac{1}{\gamma} \quad (2[45a])$$

$$C = \frac{1}{\gamma^2} \left(\frac{\sqrt{S \cdot L}}{T} \right)^2 \quad (3[45b])$$

Therefore,

$$P(T; S, L) \cong \Phi \left(\frac{\sqrt{S \cdot L}}{\gamma \frac{\Lambda_2}{\Lambda_1} T} - \frac{1}{\gamma} \right) \quad (4)$$

Subjects may not always attend to the signal value. On such trials, the process described by the above equations cannot apply. It is assumed that on any particular trial the animal is attending to the signal value with some probability, $p(A)$, and its behavior is described by the process described above; however, with probability $1 - p(A)$, the animal is not attending to the signal value, and on these trials its probability of responding "many-long" is some constant bias, $p("R"/\sim A)$. The term $p(A)$ is called *attention* and $p("R"/\sim A)$ is called *responsiveness* or the probability of a "many-long" response given inattention (cf. Church & Gibbon, 1982).

The formal model can be described with T as a continuous variable identified as the time since stimulus onsets, or it can be described with T as a discrete variable identified as the number of events. The smooth function near the data points in Figure 1 has been fit with this model with the following values of the parameters: (a) γ = sensitivity to time (number) = .25, (b) Λ_2/Λ_1 = relative pacemaker speed = 1.0, (c) $p(A)$ = probability of attending to time (number) = .8, and (d) $p("R"/\sim A)$ = probability of a "long" ("many") response given inattention = .5.

These values were found by an exhaustive search of the parameter space (with a step size of .05). The .25 value of γ is similar to

that previously observed as an optimal fit in temporal estimation; the relative speed of the pacemaker is 1.0, as it should be. For both duration and number discrimination, the model accounted for a satisfactory percentage of the variance, $\omega^2 > .99$, and there were no systematic deviations of data from theory.

Although the observed PSE for stimulus duration is consistent with previous work (e.g., Church & Deluty, 1977; Maricq et al., 1981; Meck, 1983; Stubbs, 1968, 1976a, 1976b), the Weber fraction for time is somewhat higher. This is probably due to the instability of the testing procedure, that is, the rats learned that responses were unreinforced following signals of 4 sec or four cycles. By the second test session classification of the unreinforced test signals was no longer strongly related to duration or number.

The observed PSE for number was different from that observed in previous work on response-based counting schedules (e.g., Hobson & Newman, 1981; Fetterman, Stubbs, & Dreyfus, Note 1). Fetterman et al. found that pigeons bisected time-based schedules near the geometric mean but bisected response-based schedules at or below the harmonic mean. The basis for this difference in the PSE on response-based counting schedules is not understood. The investigators did not attempt to rule out the possibility that some time interval, rather than the number of responses, was the controlling stimulus. It is possible that animals sum the durations of individual responses in order to make the discrimination (cf. Church & Meck, in press-b). It is reasonable to assume that rats can sum the durations of discrete stimuli because that is the essential finding of the "gap" experiments in which rats ran their clocks during the stimuli but stopped them during the gaps (e.g., Roberts & Church, 1978). Previous studies of the scaling of number by animals that used stimulus-based schedules have not controlled stimulus duration.

Experiment 2: Training on Disjunctive Concepts

In Experiment 1 it was demonstrated that rats were equally sensitive to a 4:1 ratio of counts (with duration controlled) and a 4:1 ratio of times (with number controlled). This

equivalence suggests that the same pacemaker, but different accumulators, are used for simultaneous timing and counting (cf. Meck & Church, in press). The present experiment provides another test of this single mechanism hypothesis.

When methamphetamine (1.5 mg/kg) is administered intraperitoneally (ip) to rats that are working on a temporal estimation task similar to the one used in Experiment 1, the PSE of the obtained psychophysical functions is shifted leftward by about 10% (e.g., Maricq et al., 1981; Maricq & Church, 1983; Meck, 1983). This shift in the PSE has been interpreted as a consequence of an increase in pacemaker speed. What happens to the psychophysical functions for duration and number in the present procedure when methamphetamine is administered? If the drug affects timing and counting behavior in a similar manner, a single mechanism would be implicated. However, if methamphetamine selectively affects timing or counting, then separate mechanisms must be responsible for the perception of duration and number.

To maintain steady-state performance, the procedure used in Experiment 1 was modified such that a left response was reinforced following a signal that was either two cycles or 2 sec in duration, and a right response was reinforced following a signal that was either eight cycles or 8 sec in duration.

Method

Subjects and Apparatus

The subjects were the same 10 rats used in Experiment 1. The apparatus was also the same.

Procedure

Training (Days 1-5). During training there were two types of sound signals: count relevant and time relevant. The count relevant signals were 4 sec in duration and were either two or eight cycles in number. The time relevant signals were four cycles in number and were either 2 or 8 sec on duration. On each trial one of these four signals was randomly selected with equal probability. The other aspects of training were similar to Experiment 1 except that no correction trials were given.

Testing under saline (Days 6, 8, and 10). Fifteen minutes prior to the experimental session each rat received an ip injection of .2-cc physiological saline. The conditions of training were maintained except that on a random half of the trials one of the four training signals

was randomly selected for presentation, each with equal probability. On the remaining trials, one of eight unreinforced test signals was presented, each with equal probability. There were two types of test signals. (See Figure 4 for a diagram of the signal types.) There were two types of test signals. One set of signals held the number of cycles constant at four while varying total signal duration between 3 and 6 sec (3, 4, 5, and 6 sec). The other set of test signals held total signal duration constant at 4 sec while varying the number of cycles between three and six cycles (three, four, five, and six cycles). The logic of holding one of the signal dimensions constant was similar to that of Experiment 1.

Testing under methamphetamine (Days 7, 9, and 11). Fifteen minutes prior to the experimental session each rat received an ip injection of 1.5 mg/kg methamphetamine in .2-cc physiological saline. The conditions of training were maintained except that on a random half of the trials one of the four training signals was randomly presented with equal probability and the value of the time constant changed as described below. On the remaining trials, one of eight unreinforced test signals was presented, each with equal probability. There were two types of test signals. One set of signals held the number of cycles constant at four cycles while varying the total signal duration between 3 and 6 sec (3, 4, 5, and 6 sec). The other set of test signals held the total signal duration constant at 3.6 sec while varying the number of cycles between three and six cycles (three, four, five, and six cycles). The physical duration of the constant time was decreased by 10% (from 4 to 3.6 sec), because 1.5 mg/kg of methamphetamine administered under similar conditions has been found to increase subjective duration by about 10% (e.g., Maricq et al., 1981).

Results

The median performance of the rats during the test sessions is shown in Figure 5. The left panel shows variation in signal number, and the right panel shows variation in signal duration. The smooth functions near the data points are based on the scalar expectancy model previously described. For each signal type, under each condition, the probability of a right response ("many" or "long") increased as a function of signal value. The PSE and the Weber fraction were obtained using the same methods as in Experiment 1. For number, the median PSE for rats tested under saline was $4.02 \pm .16$, and the median PSE for rats tested under methamphetamine was $3.73 \pm .23$. For duration, the median PSE for rats tested under saline was $4.05 \pm .15$, and the median PSE for rats tested under methamphetamine was $3.68 \pm .18$. There was a significant difference between saline and methamphetamine treatments for the PSE for both number and duration, $t_s(9) > 2.91$, $p < .02$. There were no significant differences in the median Weber fractions, which ranged from $.25 \pm .01$ to $.26 \pm .01$ in the four groups, $t_s(9) < 1$.

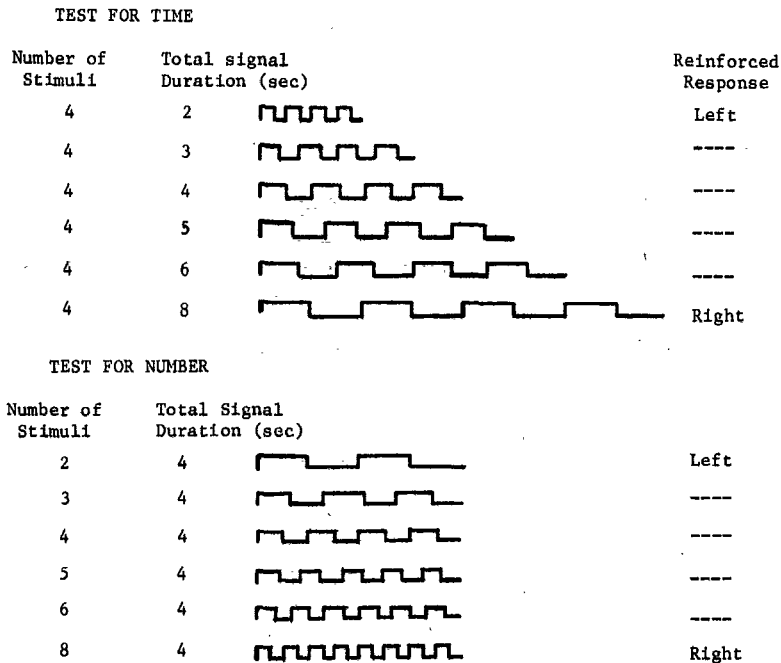


Figure 4. Diagram of signal types for Experiment 2.

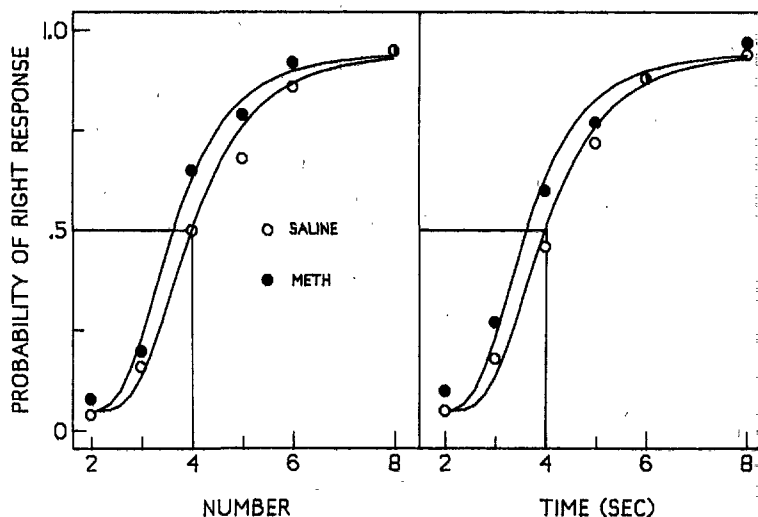


Figure 5. Psychophysical functions for number and duration with methamphetamine and saline during the three saline and the three methamphetamine test sessions. (Median probability of a right response as a function of number [left panel] or duration [in sec, right panel]. Open circles represent saline test sessions and closed circles represent methamphetamine [METH] test sessions. The smooth functions represent the theory fits.)

The smooth functions near the data points in Figure 5 are based on the model described previously. The sensitivity to number and duration remained at $\gamma = .25$, and again there was no reliable bias for one response or the other, $p("R"/\sim A) = .5$. With additional training the probability of attention increased, $p(A) = .9$. Most important, with methamphetamine (1.5 mg/kg) the leftward shift of the psychophysical function suggests that the speed of the internal mechanism was increased by about 10%, $\Delta_2/\Delta_1 = 1.1$, and the same increase was found for number and duration. The fits again were satisfactory ($\omega^2 \geq .99$), and there were no systematic deviations.

Discussion

This experiment demonstrates the equivalence of the effect of methamphetamine (1.5 mg/kg) on timing and counting behavior. The observed leftward shift in the PSE of the psychophysical function for duration by about 10% is similar to previous findings (Maricq & Church, 1983; Maricq et al., 1981; Meck, 1983). The finding that the same dose of methamphetamine produces a leftward shift in the PSE of the psychophysical function for

number by about 10% is a new result. The similar effect of methamphetamine on both duration and number further supports the suggestion that the same internal mechanism is used to process both of these stimulus attributes. Such leftward shifts of the psychophysical function are not obtained for all stimulus attributes. For example, pigeons trained on a wavelength discrimination do not show a horizontal shift of the psychophysical function when amphetamine is administered (Hayes, 1981). The fact that leftward shifts of similar magnitudes occurred for both number and duration suggests that there is a fundamental similarity between counting and timing processes and that the speed of the internal pacemaker involved in counting and timing is determined, at least in part, by the effective level of brain dopamine (e.g., Maricq & Church, 1983; Meck, 1983).

Experiment 3: Cross-Modal Transfer

It is possible that a discrimination learned in one modality can be transferred to another modality without additional training. The demonstration of this type of transfer is evidence that animals are capable of abstracting

amodal stimulus attributes (e.g., duration, intensity, location, and number) from specific modalities. Cross-modal transfer of duration and number has previously been demonstrated in isolation (Church & Meck, in press-a; Meck & Church, 1982a, 1982b; Roberts, 1982). The present question was whether rats would transfer both numerical and temporal attributes from auditory signals to cutaneous signals simultaneously and to a similar degree.

During training each stimulus cycle was composed of two equal time segments with noise on for one segment and noise off for the next. Subjects could have been counting and/or timing the sound-on segments, the background segments (sound off), all segments, or the entire cycle as a single unit. If for the cross-modal test the sound-on segments were simply replaced by shock-on segments, the subjects could have appeared to transfer a duration or number discrimination from one modality to another but, in fact, merely continued to time or count the common repeating background segments. To eliminate possible mediation by experimenter-controlled bridging stimuli that would be present both during training and testing phases, the sound-on, sound-off signal cycle was modified. During cross-modal testing the stimulus cycle on test trials was composed of white noise for a fixed time followed by an equal time of electric shock. Thus, the background segments present during training were replaced with electric shock segments. Cross-modal transfer would be demonstrated if rats counted and/or timed both the white noise and the electric shock segments during the unreinforced test trials.

Method

Subjects and Apparatus

The four subjects from Experiment 2 trained in Boxes 7-10 continued training. The apparatus remained the same, but only Boxes 7-10 were used.

Procedure

Training (Days 1-5). Subjects were retrained as described in Experiment 2.

Testing (Day 6). During the test session, a random half of the signal presentations were training signals and the remaining signal presentations were unreinforced test signals. There were two types of test signals, each

composed of alternating white noise and electric shock (.15 mA) segments (with order of occurrence counter-balanced). In one set of test signals the number of cycles was held constant at two (four segments), and the total signal duration was either 2 or 8 sec. In the other set of test signals the total signal duration was held constant at 4 sec, and there were either one or four cycles (two or eight segments).

Results

During training the median probability of a "many" response for the two-cycle signal was $.06 \pm .03$, and for the eight-cycle signal it was $.93 \pm .05$. The median probability of a "long" response for the 2-sec signal was $.05 \pm .03$, and for the 8-sec signal it was $.95 \pm .02$, a significant difference for both number and duration, $t(3) > 17.6$, $p < .01$.

During testing the median probability of a "many" response for the one-cycle (two segment) signal was $.08 \pm .05$, and for the four-cycle (eight segment) signal it was $.85 \pm .06$. The median probability of a "long" response for the 2-sec signal was $.06 \pm .04$, and for the 8-sec signal it was $.89 \pm .05$, a significant difference for both number and duration, $t(3) > 15.7$, $p < .01$.

Discussion

In the first two experiments an auditory signal was used that was on in one segment of a cycle and off in the next. These experiments demonstrated that rats learned to discriminate both the number of segments or cycles and the signal duration. In the present experiment another signal type was added. This was a combined auditory-cutaneous signal in which an auditory stimulus was on in one segment of a cycle and an electric shock stimulus was on in the next. The probability of a right ("long") response when the number of cycles was constant was controlled by the total duration of all segments (auditory and cutaneous); the probability of a right ("many") response when signal duration was constant was controlled by the total number of all segments (auditory and cutaneous).

Thus, there was substantial simultaneous cross-modal transfer of signal duration and number from auditory segments to cutaneous segments. Such transfer is evidence that rats can abstract these stimulus attributes from the modality-specific aspects of

a signal. The observed cross-modal transfer of number cannot be attributed to simple generalization of auditory signal values used in training to the auditory signal values used in testing, because it was shown in Experiments 1 and 2 that a signal composed of four auditory segments is classified as intermediate between signals with two and eight auditory segments. In the present experiment a signal composed of four auditory and four cutaneous segments was classified as "many" 89% of the time. This indicates that rats were counting segments from both modalities. A similar explanation applies to the duration attribute.

If there was cross-modal transfer of only one of the two attributes (number or duration) or if the magnitude of cross-modal transfer was different for the two attributes, different mechanisms for the perception of number and duration would have been implicated. The fact that the quantitative translation of number and duration from auditory to cutaneous stimulation was similar for both attributes adds additional support to the hypothesis that the same internal mechanism is used for timing and counting.

Experiment 4: Mapping Number Onto Duration

Animals can be trained to respond differentially to signals that vary along some stimulus dimension. In the case of the training procedures used throughout this study for number or duration discrimination rats must learn which stimuli are relevant for predicting reinforcement (e.g., noise signals) and to classify some attribute(s) of these stimuli in order to determine their response (e.g., number or duration). We assume that it is not necessary to train animals to count or time; they are able to do this naturally, and although we observe them to be timing, they may also be counting and vice versa.

If the accumulation of pulses from the same internal pacemaker is used by animals to discriminate the attributes of number and duration, it should be possible to establish the quantitative equivalence between an increment of one count and a unit of time. The working hypothesis is that the same internal pacemaker described in the Discussion sec-

tion of Experiment 1 is used for counting and timing, but the accumulation process operates in different modes: the event mode for counting and the run and the stop modes for timing. This implies that if an animal has learned a response rule for one of these stimulus attributes (number or duration) it should then be able to transfer the use of that response rule to the other attribute without additional training because there is no difference between the final accumulations that are being classified. That is, if an animal has learned to classify accumulations obtained with the run mode, it should then be able to immediately use the same response rule to classify accumulations obtained with the event mode if pulses from the same internal pacemaker are used for estimation of both attributes.

Thus, in the present experiment rats were trained to classify noise signals according to their durations, which presumably required the use of the run mode. Unreinforced test signals were then presented that would produce subjective values (accumulations) *similar* to the accumulations produced by training signals if the event mode were used but would produce *dissimilar* accumulations if the run mode were used. If rats used the event mode to determine their response in this test condition, it would be possible to determine the quantitative equivalence between an increment of one count and a unit of time.

Method

Subjects and Apparatus

The subjects were six male albino Norway rats (Charles River CD), about 190 days old at the start of training. The rats were maintained in a manner similar to that described in Experiment 1. The apparatus used was the same as in Experiment 1 (Boxes 1-6).

Procedure

Pretraining. A pretraining procedure similar to the one described in Experiment 1 was used.

Two-signal training (Days 1-10). Half of the rats were trained to press the stationary lever following a white noise signal of 2-sec duration ("short" response) and to press the lever that was inserted and retracted at .5-sec intervals (moving lever) following a white noise signal of 4-sec duration ("long" response). The other half of the rats had this response rule reversed. On each trial one of the two signals was randomly presented with a probability of .5. When the signal was turned off, both levers

were inserted into the box. Random selection determined whether the left lever or the right lever would be stationary with each lever having a probability of .5. The remaining lever was moved in and out of the lever box with the cycle described above. If the rat made the correct response, a pellet of food was immediately delivered; if it made the incorrect response, no pellet was delivered. When either lever was pressed, there was a .5-sec delay, and then both levers were retracted. ITIs were 5 sec plus a geometrically distributed duration with a minimum of .1 sec and a mean of 35 sec. On Days 1-10, if an incorrect response had been made on the previous trial, the same signal was presented again on the next trial (correction procedure). A daily session began within 30 min of the same time each day and lasted for 3 hr. A record was kept of the response choice following each of the two signals.

Seven-signal training (Days 11-15). The conditions of training were maintained except that each of the two extreme signals (2 and 4 sec) was presented with a probability of .25 on each trial. On the remaining trials, one of five signals of intermediate duration was randomly presented, each with an equal probability. The signal durations were spaced at equal logarithmic intervals between the two durations used in training (2.0, 2.2, 2.5, 2.8, 3.2, 3.6, and 4.0 sec). Neither the left nor the right response was followed by food in the case of these intermediate signals.

Testing (Days 16-17). The conditions of seven-signal training were maintained during a random half of the trials. On the remaining trials, one of five test signals was randomly presented with an equal probability. These test signals were composed of repeating cycles of white noise. White noise was on for 1 sec, off for 1 sec, on for 1 sec, and so forth. The independent variable was the number of noise cycles (1-sec noise on, 1-sec noise off). The test signals were composed of 10, 12, 14, 16, or 20 noise cycles. These signal values were selected on the basis of a pilot study that provided an indication of the signal range necessary to have the probability of a "long" response range from 0 to 1.0. The noise-on segments of the test signals could be classified by total segment duration (sum of all noise-on durations) or by total segment number (sum of all noise-on segments). These different classifications are outlined in Table 2.

Results

The median performance of the rats during the 5 days of seven-signal training is shown in Figure 6. The proportion of "long" responses increased as a function of signal duration. The median PSE was $2.83 \pm .20$ sec, which is close to the geometric mean of the two extreme signal values (2.8 sec). The median/DL was $.42 \pm .09$ sec and the median Weber fraction was $.15 \pm .02$. The smooth function near the data points is based on the timing model described in the Discussion section of Experiment 1. The best fit using this model was obtained with the following

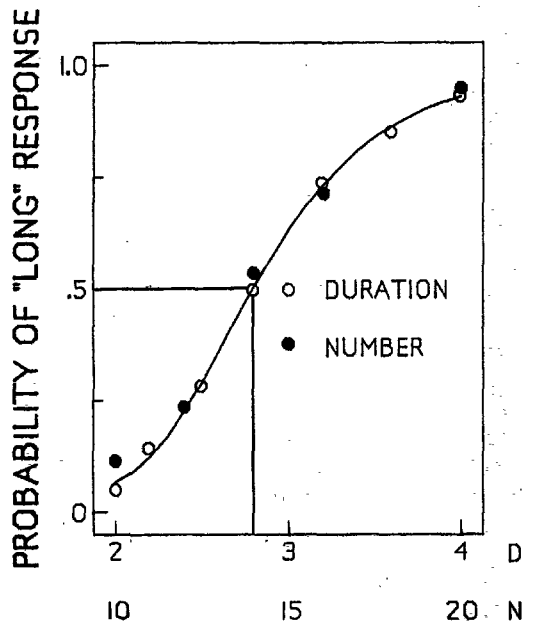
Table 2

Design of Experiment 4: Unreinforced Test Signals

Total no. of sound segments	Total duration (in sec) of sound segments	Total duration (in sec) of signal
10	10	20
12	12	24
14	14	28
16	16	32
20	20	40

Note. Each sound segment was 1 sec in duration.

values of the parameters: γ = sensitivity to time = .2, Λ_2/Λ_1 = relative pacemaker speed = 1.0, $p(A)$ = probability of attending to time = .95, and $p("R"/\sim A)$ = probability of a "long" response given inattention = 1.0.



DURATION OR NUMBER

Figure 6. Psychophysical function for duration during the 5 days of seven-signal training and number during the first test session. (Median probability of a "long" response as a function of duration [in sec] or number [200 msec/count]. Open circles represent variation in signal duration and closed circles represent variation in segment number. The smooth function represents the theory fit, D = duration, N = number.)

These values were found by an exhaustive search of the parameter space (with a step size of .05). The model accounted for a satisfactory percentage of the variance, $\omega^2 = .992$, and there were no systematic deviations of the data from theory.

The median performance of the rats during the first test session is also shown in Figure 6. The equivalence between number and duration was analyzed as follows: A straight line relating the percentage of "long" responses for training signals and the percentage of "many" responses for testing signals to the three most central signal values (2.5, 2.8, and 3.2 sec for training conditions; 12, 14, and 16 segments for testing conditions) was fit by the method of least squares for each rat (see Church & Deluty, 1977). From these straight lines number and duration equivalents in terms of response probability were determined. The median signal value associated with 50% "many" responses estimated from these straight lines for test signals was 14.1 segments, and the median signal value associated with 50% "long" responses for training signals was 2.84 sec. The ratio of 2.84 sec to 14.1 segments gave 200 msec as an estimate of the time equivalent for each count (segment). The median estimate across rats was 200 ± 10 msec. Figure 6 shows the median percentage "many" response as a function of segment number with the independent measure scaled as 200 msec/count. Given the assumption of 200 msec/count the same theory used to fit the seven-signal timing data presented in Figure 6 accounted for greater than 99% of the variance for the counting data, and there were no systematic deviations of data from theory.

Discussion

This experiment further established the similarity between the processes of counting and timing used in the discrimination of sequential stimuli. This was done by estimating the quantitative equivalence between an increment of one count and a unit of time while also extending the similarity of counting and timing processes to a 2:1 ratio of reinforced values. The mapping of response probabilities for number onto the response probabilities for duration led to an estimation of 200

msec as the time unit for one count. Alternatively, the rats could have counted the total number of segments (sound on and sound off) with 100 msec as the time unit for one count. Finally, the present experiment does not rule out the possibility that each cycle initiated a latent period of about 800 msec followed by a run of the clock for the rest of the cycle (200 msec). This would be ruled out if an increment of one count of a longer or shorter cycle also was equivalent to about 200 msec of time.

Massaro (1976) had human observers count sequences of 20-msec tones. Counting accuracy increased with increases in the silent interval between tones, which was presumably related to the time required for an increment of an individual count. Maximal performance occurred when the silent intervals were between 185 and 225 msec. This period may have represented the unit of time equivalent to one count. Klahr (1973) found that the time required by adults to accurately estimate visual numerosities greater than five in simultaneous displays increased with a slope of approximately 300 msec. This suggests that the counting mechanism humans use accumulates a value equivalent to about 300 msec for each count. Whether or not any significant difference exists between the increment associated with auditory and visual counts is uncertain, and such values may vary with the procedure used.

In the studies of human counting behavior outlined above, it was possible that the counting mechanism was simply active for a period of time (185–300 msec) and did not actually accumulate a value equivalent to this time period. The present experiment provides more direct evidence that a count, as used by rats, is equivalent to a unit of time (approximately 200 msec). Human counting performance may involve additional processes such as the labeling or the tagging of each increment (e.g., Gelman & Gallistel, 1978). Such labels may be used instead of the pacemaker accumulations described here because they, lacking the variability associated with the accumulation process, may lead to a more accurate discrimination of number. Some investigators have reserved the term *counting* to describe this labeling behavior and have termed the sort of behavior ana-

lyzed in this report as *number discrimination*, considered to be a more primitive form of number-related ability (e.g., Davis & Memmott, 1982). Whether or not animals can apply symbolic labels to the numerical attributes of stimuli remains uncertain.

General Discussion

The major findings can be summarized as follows:

1. The total number and duration of successive events can serve as an effective stimulus for behavior even when all other cues are held constant. The psychophysical functions for number and duration were indistinguishable when the ratio of the extreme signal values was constant, although both attributes had previously been confounded.

2. Both the number and the total duration of events can be retained simultaneously.

3. With the administration of methamphetamine (1.5 mg/kg), the sensitivity to number and duration remained the same but the speed of the internal mechanism increased by about 10% for both attributes, suggesting that the same pacemaker is used for both discriminations.

4. The simultaneous cross-modal transfer of number and duration from auditory signals to cutaneous signals was of a similar magnitude.

5. One count was approximately equal to a 200-msec unit of time when the response probability for number was mapped onto the response probability for duration.

To produce these five results, the rats may have used the same mechanism for counting and timing, or they may have used two different types of mechanism that, by coincidence, had the same sensitivity. The fact that rats acquired both number and duration information during a single trial and then decided which to use requires parallel processing, that is, a single pacemaker, but separate mode switches and accumulators. The type of mechanism proposed is one that can be used either for counting (the event mode) or for timing (the run and the stop modes). When the number of responses is the discriminative stimulus, it is normally impossible to distinguish between the stop and the event modes, because the responses are usu-

ally brief and relatively constant in duration. When the number of experimenter-controlled stimuli is the discriminative stimulus, however, it is possible to distinguish between the stop and the event modes because the duration of each stimulus can be varied or their total duration held constant while their number is varied.

A one-mechanism proposal is simpler than a two-mechanism proposal with a specialized clock and counter, so it is the preferred proposal unless inconsistent data are found. There is some evidence that the same neural net can be activated in either the run, the stop, or the event mode (Swigert, 1970). These neural modes may have some relationship to the behavioral evidence for an internal mechanism that can be operated in several modes. We have discussed elsewhere further implications of the one-mechanism hypothesis and how a single mechanism might be observed to operate simultaneously in different modes in order to discriminate stimulus rate (Meck et al., in press; Church & Meck, in press-b). The main conclusion from the present study is that an animal is able to utilize different modes of operation of an internal accumulation process, according to the needs of the task.

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