

Research Report

LEARNING TO TIME (LET) OR SCALAR EXPECTANCY THEORY (SET)?

A Critical Test of Two Models of Timing

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Abstract—Two theories of timing, scalar expectancy theory (SET) and learning to time (LeT), make substantially different assumptions about what animals learn in temporal tasks. In a test of these assumptions, pigeons learned two discriminations: On Type 1 trials, they learned to choose a red key after a 1-s signal and a green key after a 4-s signal; on Type 2 trials, they learned to choose a blue key after a 4-s signal and a yellow key after a 16-s signal. Then, two psychometric functions were obtained by presenting them with intermediate durations (1 to 4 s and 4 to 16 s). The two functions did not superpose, and most bisection points were not at the geometric mean of the training stimuli (*contra* SET); for most birds, the function for Type 2 trials was to the left of the function for Type 1 trials (*contra* LeT). Finally, the birds were exposed to signals ranging from 1 to 16 s and given a choice between novel key combinations (e.g., red vs. blue). The results with the novel key combinations were always closer to LeT's than to SET's predictions. Observations of the birds' behavior also suggest that, more than being a mere expression of an internal clock, behavior constitutes the clock.

During the past 15 years or so, the study of how animals time events has been guided to a large extent by two competing theories, the scalar expectancy theory (SET; Gibbon, 1977, 1991) and the behavioral theory of timing (BeT; Killeen & Fetterman, 1988). The present study reports the results of an experiment for which these two theories make substantially different predictions. However, instead of focusing on BeT directly, we focus on a more detailed version of BeT, a model called *learning to time* (LeT; Machado, 1997; Machado & Cevik, 1998). In what follows, we summarize the major attributes of SET and LeT, derive their predictions for a specific timing task, and then report the corresponding experimental findings.

SET postulates an internal clock whose structure is represented in the left panel of Figure 1: A pacemaker generates pulses at a high rate; an accumulator counts the pulses emitted during the interval to be timed; and a long-term store saves the count obtained at the end of each trial. Because the rate of the pacemaker is assumed to vary across trials, the counts stored in memory will also vary. To time an event, the animal samples a number from its long-term memory at the beginning of the event and then compares continuously the sampled number with the number currently in the accumulator. The ratio between the two numbers controls the instrumental response.

LeT, in contrast, consists of three major components (see the right panel of Fig. 1): a serial organization of behavioral states, a vector of associative links connecting the behavioral states to the instrumental response, and the instrumental response itself. At the onset of the event

to be timed, only the first state is active, but as time elapses, the activation of each state flows to the next state in the series. How fast the activation spreads across states varies directly with the overall reinforcement rate in the situation. Each behavioral state is also coupled with the instrumental response, and the degree of the coupling changes in real time, decreasing during extinction and increasing during reinforcement. Thus, states that are strongly active during extinction will lose their coupling and eventually may not support the instrumental response, whereas states strongly active during reinforcement will increase their coupling and may therefore sustain the response. To paraphrase Hodgson, as quoted in James (1892/1985, p. 150), the behavioral states are the measuring tape, and reinforcement is the dividing engine that stamps its length. Finally, the strength of the instrumental response is obtained by adding the coupling values of the states, each value weighted by the activation of the corresponding state.

Consider now the following temporal discrimination task and how each model conceptualizes what an animal exposed to it learns. A pigeon is presented with one of two signals, for example, a short- or a long-duration light. To obtain food, the animal must then report in a two-choice phase which duration has just occurred: If the stimulus was short, choose the red key; if the stimulus was long, choose the green key. During test trials after the bird learns the discrimination, the experimenter introduces stimuli with intermediate durations and records the proportion of times the animal chooses the red key—what we call “reporting *short*,” abbreviated $P(\text{short})$. The resulting psychometric function relating $P(\text{short})$ to the probe duration has two key features (see, e.g., Catania, 1970; Church & Deluty, 1977; Platt & Davis, 1983; Stubbs, 1968). First, typically the animal is indifferent between the red and green keys— $P(\text{short}) = .5$ —when the probe duration equals the geometric mean of the two training stimuli. Second, the functions obtained for different pairs of short and long training stimuli, but with their ratio held constant, superpose when plotted in relative time. For example, if the short and long stimuli were 1 s and 4 s during Condition A, and 4 s and 16 s during Condition B, then the psychometric functions obtained in the two conditions would superpose when $P(\text{short})$ is plotted against the ratio of probe duration/short stimulus duration. The superposition of the psychometric functions suggests a Weber-like property for temporal discrimination, for equal ratios yield equal discriminabilities.

How do SET and LeT explain this performance? According to SET, during training the animal forms two memory stores, one containing the counts obtained at the end of the short stimulus, the other the counts obtained at the end of the long stimulus. To decide which key to choose at the end of a signal, the animal compares the number that is in the accumulator when the signal ends (i.e., the number of pulses generated during the signal, X_T) against two samples, one extracted from the memory store for short durations, X_S , and the other from the memory store for long durations, X_L . If the ratio X_S/X_T is

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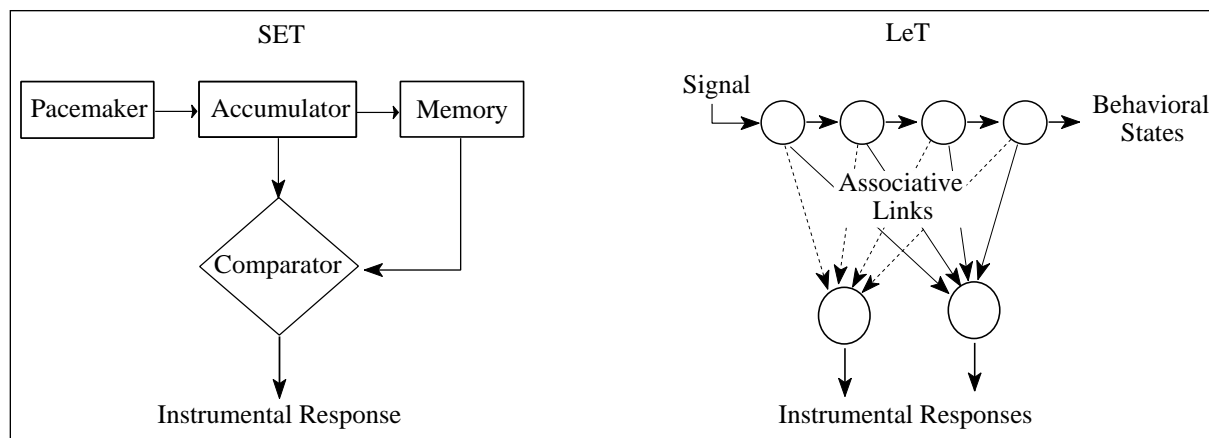


Fig. 1. Structure of the scalar expectancy theory (SET) and learning to time (LeT) models of timing. In SET, a pacemaker generates pulses that are accumulated in the accumulator and stored in long-term memory. A sample extracted from that memory is compared with the number currently in the accumulator, and the ratio between the two numbers determines behavior. In LeT, after a time marker, a series of behavioral states (top circles) is activated. The states may be coupled to various degrees with one or more instrumental responses (bottom circles). The strength of each response is determined by the dot-product between the vectors of state activation and coupling.

greater than the ratio X_T/X_L , then the number is “closer” to the sample extracted from the short stimulus store and the animal is more likely to choose the red key. SET predicts both the superposition of the psychometric functions and indifference at the geometric mean of the training stimuli (see Gibbon, 1981).

LeT’s extension to two-choice situations (see Fig. 1) assumes that the behavioral states will be coupled with the two choice responses. After the short stimulus, only the early states of the cascade are active, and because the choice of the red key is rewarded whereas that of the green key is extinguished, those early states will be coupled mainly with the “short” response. Conversely, following the long stimulus, the later states are the most active, and because the choice of green is rewarded whereas the choice of red is extinguished, those later states will be coupled mainly with the “long” response. LeT predicts an indifference point approximately at the geometric mean of the training stimuli. Furthermore, because the spread of the activation across the behavioral states is proportional to the overall reinforcement rate, the psychometric functions will also superpose (see Machado, 1997).

A simple modification of the task just described allows a clear separation of SET’s and LeT’s predictions. Assume that a pigeon has learned not one but two temporal discriminations within the same session (see Fig. 2, top row). In the presence of two keys, one red (R) and one green (G), the choice of R is rewarded if the preceding signal was 1 s long, and the choice of G is rewarded if the signal was 4 s long; we call these trials Type 1 trials. In the presence of two other keys, one blue (B) and the other yellow (Y), the choice of B is rewarded following a 4-s signal, whereas the choice of Y is rewarded following a 16-s signal; we call these trials Type 2 trials.

Two questions may be asked. First, will the psychometric function obtained by presenting durations from 1 s to 4 s and giving the bird a choice between R and G superpose the function obtained by presenting durations from 4 s to 16 s and giving the bird a choice between Y and B? According to SET, the answer is yes because if the two discriminations are learned, then the process described earlier for simple discrimination is operating, and this process predicts superposition.

SET’s predictions are illustrated in the left panel of the middle row in Figure 2. In contrast, according to LeT, the psychometric functions should not overlap because the overall reinforcement rate remains constant and, consequently, the function for Type 2 trials should be steeper than the function for Type 1 trials (see Bizo & White, 1994, 1995a, 1995b; Fetterman & Killeen, 1991; Morgan, Killeen, & Fetterman, 1993). The right panel of the middle row in Figure 2 illustrates this prediction.

Second, what will a bird do when, following a signal T seconds long, it is presented with a pair of keys that it has never seen together before, for example, the G and B keys? According to SET, the animal should always be indifferent between G and B because in the presence of these keys, the just-experienced test duration would be compared with two samples that came from identical distributions (i.e., G and B are both associated with experienced durations of 4 s). This prediction is illustrated by the horizontal line in the bottom left panel of Figure 2. However, LeT predicts that the animal’s preference for the G key will increase monotonically with the duration of the signal (see the G-vs.-B curve in the bottom right panel of Fig. 2). LeT’s prediction stems from the profile of couplings learned during training. Thus, during Type 1 trials, the initial states become coupled with R, whereas subsequent states become coupled with G, and during Type 2 trials, the initial and subsequent states become coupled with B and Y, respectively. On trials when G and B are presented together, the initial states are coupled mostly with B, whereas later states are coupled mostly with G. Therefore, as the duration of the signal increases, later states exert more and more control at the moment of choice and the probability of choosing G increases.

The remaining curves in the bottom panels of Figure 2 show that SET and LeT also make different predictions for the other three novel key combinations. Whereas the shape of these three curves is the same for SET (in fact, the curves are scale transforms of one another), LeT predicts a U-shaped curve when the choice is between R and B, an inverted U-shaped curve when the choice is between G and Y, and a descending curve when the choice is between R and Y.

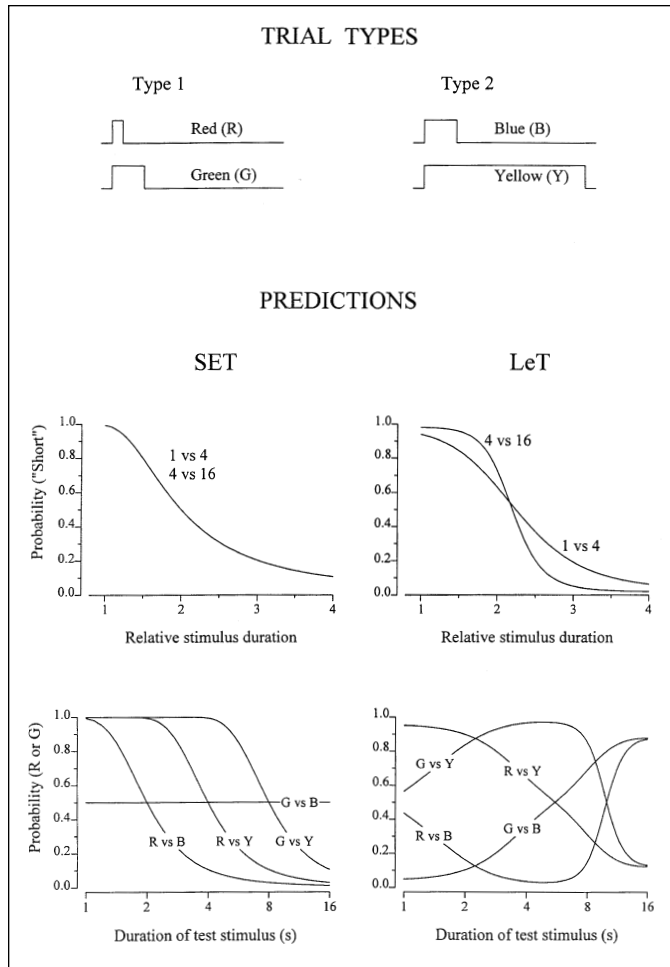


Fig. 2. Structure of regular trials (top panel) and predictions of SET and LeT for stimulus generalization test trials (middle panel) and test trials with new key combinations (bottom panel). During Type 1 trials, a 1-s or a 4-s signal occurred. A red-key choice was rewarded if the signal was 1 s long, and a green-key choice was rewarded if it was 4 s long. During Type 2 trials, the signal was either 4 s or 16 s long. After the former, the choice of blue was rewarded; after the latter, the choice of yellow was rewarded. In the middle panel, the proportion of "short" responses is plotted against relative stimulus duration. The geometric mean of the training stimuli equals a relative stimulus duration of 2. In the bottom panel, the proportion of choices of the red or green key is plotted as a function of stimulus duration. Note the logarithmic scale on the x-axis.

METHOD

Subjects

Eight pigeons (*Columba livia*) maintained at 80% of their free-feeding body weight participated in the experiment. Each bird was included in each experimental condition. The birds had no previous experience with time-related tasks.

Apparatus

Two standard experimental chambers for pigeons from Med Associates© were used. The front panel of each chamber contained three keys centered on the wall. The keys were 2 cm in diameter, 22 cm above the floor, and 8 cm apart, center to center. The keys could be illuminated from behind with red, green, blue, yellow, or white lights. Directly below the center key and 4 cm above the floor was a hopper opening measuring 6 × 7 cm. The bird had access to mixed grain when the hopper was raised and illuminated with a 7.5-W white light. On the back wall of the chamber another 7.5-W house light provided general illumination. An outer box equipped with a ventilating fan enclosed the experimental chamber. All events were controlled by a Dell© 386 computer.

Procedure

The general structure of a regular training trial was as follows: At the beginning of the trial, the house light and the center key were illuminated with white light. After the signal duration elapsed (e.g., 4 s), the center key light was turned off and the side keys were illuminated with different colors (e.g., R and G). A peck at a choice key turned all key lights and the house light off, and if the choice was correct, it activated the hopper for 3 s; after food, a 20-s intertrial interval (ITI) followed. If the choice was incorrect, the ITI started immediately and the trial was repeated.

During training there were two types of trials: On Type 1 trials, the signal was either 1 s or 4 s long; on Type 2 trials, the signal was either 4 s or 16 s long. The assignment of light colors to the choice keys was counterbalanced across birds except that one pair was always R and G, and the other was always B and Y. In the end, a unique combination of signal duration and correct key color was used for each bird. However, for clarity, we describe the procedure and the experimental results as if all birds had the assignment shown in the top panel of Figure 2. The two colors presented during each trial type always occurred the same number of times on the left and right keys.

Initially, only one discrimination was trained. After the birds learned the discrimination (at least 80% correct choices, excluding repeated trials, for five consecutive sessions), they received training on the other discrimination. After the second discrimination was learned, the two types of trials alternated across sessions. Finally, both types of trial were presented during the same session. This preliminary training lasted from 29 to 34 sessions. Next, the experiment proper began. There were six conditions:

- **Condition 1: Regular plus extinction trials.** During the first 10 sessions, all trials were either Type 1 or Type 2, correct choices were reinforced, and incorrect choices led to a repeated trial. Sessions ended after 64 reinforcers were obtained, 32 from each trial type. Then, during 10 sessions, extinction trials were introduced to adapt the birds to the lower rate of food that would occur during the subsequent testing phases. Besides not ending with food—even when a choice was correct—extinction trials were not repeated if the choice was incorrect. Sessions comprised 80 trials, 56 regular and 24 extinction trials.
- **Condition 2: Stimulus generalization.** Each session comprised 56 regular trials and 24 stimulus generalization test trials. Two sets of logarithmically spaced durations were used during the test trials: 1.41 s, 2 s, and 2.83 s for Type 1 test trials, and 5.66 s, 8 s, and

11.31 s for Type 2 test trials. In each set, the middle duration corresponds to the geometric mean of the training durations. Each test stimulus occurred four times in a session, twice for each left-key/right-key color assignment. Test trials were never followed by food. This phase lasted for 16 sessions.

- **Condition 3: Regular plus extinction trials.** This condition lasted for five sessions and was identical to Condition 1.
- **Condition 4: Response generalization.** Each session comprised 56 regular trials and 24 response generalization test trials. The stimulus durations were the same during regular and test trials, namely, 1 s, 4 s, or 16 s. The difference between the two kinds of trials was that new pairs of key colors were presented during the test trials. Specifically, during the regular trials, the pairs were always R-G and B-Y, but during the test trials, they were R-B, R-Y, G-B, and G-Y. Four new key combinations at three test durations yielded 12 different kinds of test trials. Each of these trials was presented twice per session, once for each left-key/right-key color assignment. This condition lasted for 20 sessions.
- **Condition 5: Regular plus extinction trials.** This condition lasted for five sessions, and all details were as in Condition 1 except that the number of extinction trials increased from 24 to 32.
- **Condition 6: Stimulus-response generalization.** Each session comprised 56 regular trials and 32 test trials. During the test trials, the signal was either 2 s or 8 s long, and each signal was followed by a choice between the pairs R-B, R-Y, G-B, or G-Y, for a total of 8 different test trials. Each of these 8 test trials was presented four times in a session, twice for each one of the left-key/right-key color assignments. This condition lasted for 16 sessions.

In summary, the first, third, and fifth conditions maintained the basic discriminations and constituted an attempt to reduce any carryover effects from preceding conditions. The other, critical conditions tested for stimulus generalization (same choice keys, new signal durations), response generalization (same signal durations, new choice keys), and stimulus-response generalization (new signal durations and choice keys).

RESULTS

All pigeons learned the basic discriminations. At the end of the training conditions (i.e., 1, 3, and 5), proportion correct averaged across birds and over the last five sessions was above .92 for all stimulus durations (range: .77–1.0).

Stimulus Generalization

The psychometric functions obtained during the stimulus generalization condition are shown in Figure 3. Four findings are noteworthy. First, for all birds and types of test trials, $P(\text{short})$ decreased monotonically with signal duration. Second, the geometric mean of the training stimuli did not always predict the bisection point. In fact, if .5 were the true probability of choosing “short” when the test duration equaled the geometric mean, then the 95% confidence interval for $P(\text{short})$ would range from .375 to .625 (normal approximation to the binomial). In Figure 3, this interval is shown by the short vertical bar at the center of each panel. Of the 16 cases, only 5 were within that interval. Third,

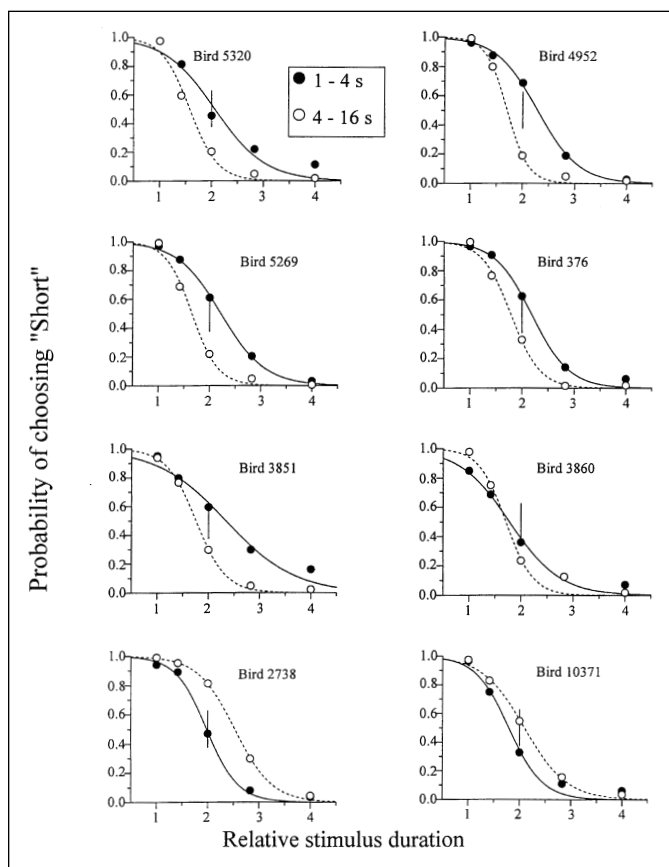


Fig. 3. Proportion of “short” responses during stimulus generalization test trials for each of the 8 birds. Filled and unfilled circles correspond to Type 1 and Type 2 trials, respectively. The end points of each curve correspond to the training stimuli. The geometric mean of the training stimuli equals a relative stimulus duration of 2. The data are based on all sessions of Condition 2. The curves are the best fitting, two-parameter logistic functions $P(\text{short}|T) = 1 / \left[1 + \exp\left(\frac{T - \mu}{0.55\sigma}\right) \right]$, where T is the signal duration, μ is the average, and σ is the standard deviation of the function. The vertical bar shows the 95% confidence interval if $P(\text{short})$ equaled .5 at the geometric mean.

the two curves did not overlap clearly for any bird. In the top six panels, the curve for the Type 2 test trials decreases significantly faster than the curve for the Type 1 test trials; in the bottom two panels, the opposite is the case. Fourth, these findings are also illustrated by the best fitting logistic curves, which accounted always for more than 96% of the variance ($M = 99\%$ on both types of trials): In the top six panels, the average and the standard deviation of the curves for Type 2 trials are smaller than those for the curves for Type 1 trials, whereas in the bottom two panels, these parameters are larger for the curve for Type 2 trials.

Response Generalization and Stimulus-Response Generalization

Figure 4 combines the results from the response generalization and the stimulus-response generalization conditions. Because the results

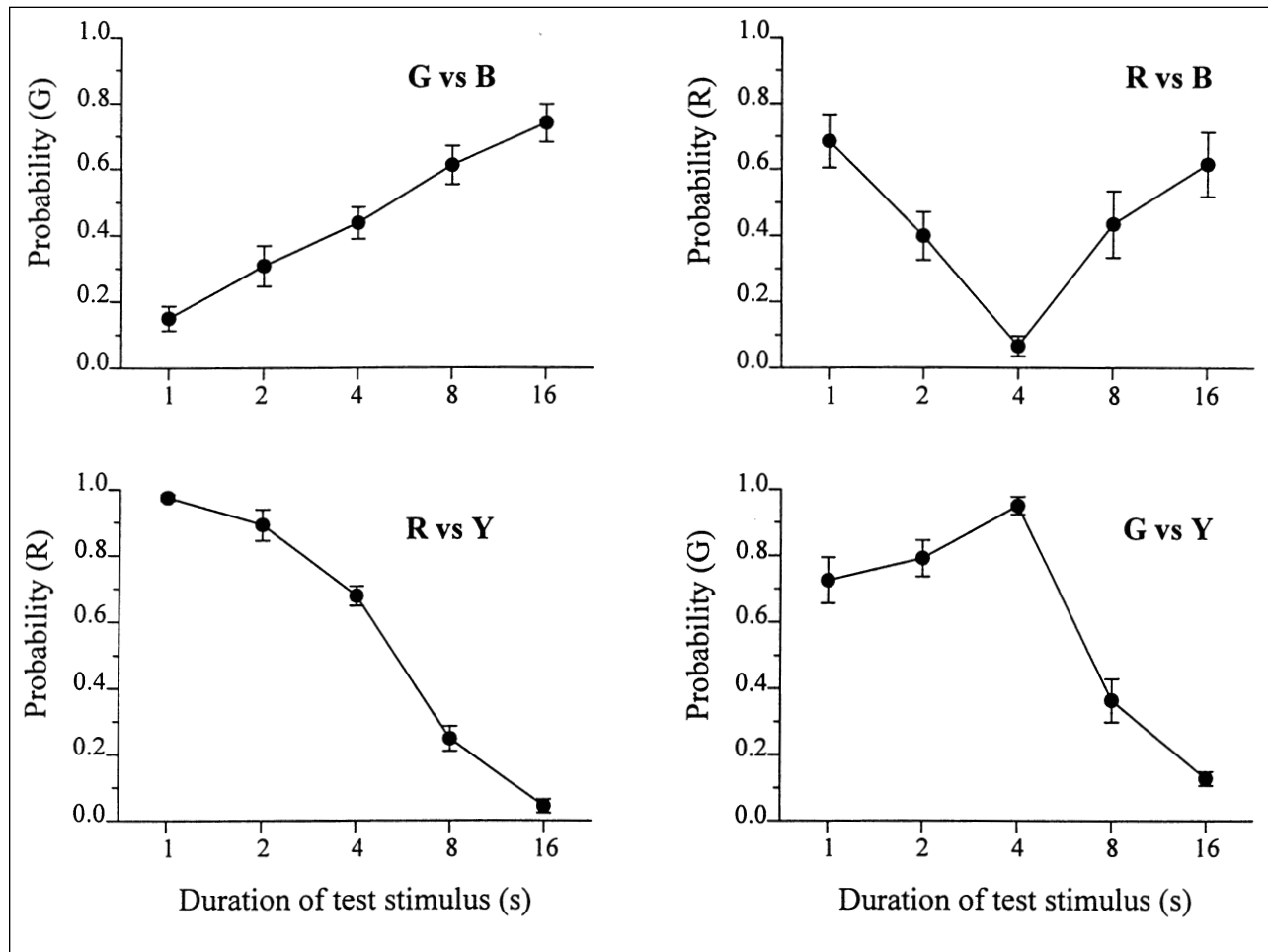


Fig. 4. Mean proportion of choices of the key from the Type 1 trials (i.e., red, R, or green, G) as a function of stimulus duration. Each of the four panels corresponds to a new key combination. The vertical bars show the standard error of the mean. The data came from all sessions of Conditions 4 and 6. Note the logarithmic scale on the *x*-axis. B = blue key; Y = yellow key.

were similar across birds, they were averaged. Consider the top left panel, which shows results for the choice between G and B, the keys paired with the 4-s stimulus duration. For all birds, as the test duration increased, the preference for G increased. This result is consistent with LeT but not with SET.

The bottom left panel shows that when the choice was between R and Y, the keys paired with 1-s and 16-s durations, respectively, the preference for R decreased with stimulus duration. This result is consistent with both SET and LeT. However, the preference for R at the 4-s duration, the geometric mean of 1 s and 16 s, was generally above .5, a result predicted by LeT but not by SET.

The top right panel shows the choice between R and B, the keys paired with 1-s and 4-s durations, respectively. Although there were some individual differences, all birds showed the U-like pattern displayed in the figure. That is, the preference for R first decreased and then increased. This result is qualitatively consistent with LeT but not SET.

Finally, the bottom right panel shows the results for the choice between the G and Y keys (paired with 4-s and 16-s durations, respectively). Qualitatively, the data resemble the pattern predicted by LeT because the preference for G increases with signal durations from 1 to

4 s, and then decreases. However, LeT always predicts a preference for G at the 8-s signal duration, whereas the data show a preference for Y. SET, however, does not predict the initial increase in preference for G.

DISCUSSION

The present study used a variation of the temporal bisection procedure to contrast the predictions of two major models of timing, SET and LeT, the latter a derivative of BeT. During one type of trial, pigeons learned to choose a red key after a 1-s signal and a green key after a 4-s signal; during another type of trial, they learned to choose a blue key after a 4-s signal and a yellow key after a 16-s signal. The results of stimulus generalization tests did not support SET's predictions because the two psychometric functions did not overlap and only in 5 out of 16 cases was the geometric mean of the training stimuli close to the bisection point. In contrast, these outcomes were somewhat more consistent with LeT because 6 birds yielded steeper psychometric functions during Type 2 test trials. In addition, even in those 5 cases in which the geometric mean was close to the bisection point, the average of the bisection points estimated from the logistic fits

equaled 2.14 s, which is close to the 2.16-s value predicted by LeT (see Machado, 1997). However, without further ad hoc assumptions, neither SET nor LeT could account for the occurrence of bisection points substantially below the geometric mean and for the individual differences in the relative positions of the two psychometric functions.

During a second set of tests, new combinations of choice keys were introduced, and preference for a particular key was assessed as a function of signal duration. In one of the tests, the birds chose between the keys that had been associated with the same reinforced duration (i.e., 4 s for G and B). In this case, SET predicted indifference for all test durations, but LeT predicted a systematic increase in the preference for G as the test duration increased. The data from all birds confirmed LeT's predictions. For the remaining novel key combinations, the observed pattern of preferences was also closer to LeT's than to SET's predictions. Thus, whereas SET failed to predict well the data from all conditions, LeT failed to predict well only the data from the stimulus generalization condition.

Why did the psychometric function for Type 2 trials decrease faster than the function for Type 1 trials for 6 birds, but decrease slower for 2 others? To try to answer this question, we started to observe the birds after the first five stimulus generalization sessions. These observations revealed for each bird a set of behavioral patterns that was highly consistent across trials, sessions, and conditions (see also Richelle & Lejeune, 1980). In other words, these patterns had been acquired early in training and were maintained throughout the experiment. Moreover, the differences in the behavioral patterns among the birds were correlated with the differences in their psychometric functions.

All 6 birds that showed a steeper function during the Type 2 trials than during the Type 1 trials behaved in the following way. At trial onset, the bird approached the center key. If the trial ended shortly afterward (i.e., the signal was 1 s long), then the bird pecked the R key; if not, then the bird started to peck the center key or direct pecks at the key but not actually strike it ("air-peck" the key). It emitted this behavior until either the trial ended or approximately 6 s had elapsed. In the former case (i.e., the signal was 4 s long), the bird then pecked either G or B. In the latter case (i.e., the signal was 16 s long), the bird then stopped pecking, or air-pecking, the key and at the end of the trial chose Y. (What each bird did from the moment it stopped pecking until the end of the 16-s trial varied: Some birds oriented toward the house light, others moved around the box, and others simply faced the side keys.) If, as LeT assumes, the bird's behavior at the end of the signal cues the choice response, then the preceding pattern could explain the left shift of the psychometric function for Type 2 test trials and their bisection points close to 6 s: The birds tended to choose Y after signal durations greater than 6 s because by then they had entered a behavioral state coupled mostly with Y.

Bird 2738, however, showed a different, and in a sense a reversed, behavioral sequence: During the 16-s trials, this bird approached the key panel and started to air-peck, but approximately 12 s into the trial it started to actually peck the edges of the center key. Hence, the choice of Y was cued by a behavior (pecking) that occurred very late into the trial. Hence, for this bird, the psychometric function for Type 2 trials shifted significantly to the right, and its bisection point equaled

10 s. Bird 10371 also showed a similar shift, but the behavioral observations did not reveal as clear a pattern; this bird air-pecked throughout the interval, and, on occasion, the rate of pecking increased toward the end of the trial. Perhaps some response-rate modulation cued this bird's choice behavior.

Perhaps the most important message of the preceding findings is that the behaviors observed during temporal cues are not unrelated to, or a mere expression of, an internal clock. Rather than being an extraneous accoutrement as it were, they constitute the clock. Hence, the origins, functions, and dynamic properties of these behaviors must be interpolated in any comprehensive theory of timing. To fail to do so and to persist in dissociating what an animal does from its judgment of time may be equivalent to dismantling a clock to grasp the essence of time.

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