

Further tests of the Scalar Expectancy Theory (SET) and the Learning-to-Time (LeT) model in a temporal bisection task

Armando Machado*, Joana Arantes

University of Minho, Portugal

Abstract

To contrast two models of timing, Scalar Expectancy Theory (SET) and Learning to Time (LeT), pigeons were exposed to a double temporal bisection procedure. On half of the trials, they learned to choose a red key after a 1 s signal and a green key after a 4 s signal; on the other half of the trials, they learned to choose a blue key after a 4-s signal and a yellow key after a 16-s signal. This was Phase A of an ABA design. On Phase B, the pigeons were divided into two groups and exposed to a new bisection task in which the signals ranged from 1 to 16 s and the choice keys were blue and green. One group was reinforced for choosing blue after 1-s signals and green after 16-s signals and the other group was reinforced for the opposite mapping (green after 1-s signals and blue after 16-s signals). Whereas SET predicted no differences between the groups, LeT predicted that the former group would learn the new discrimination faster than the latter group. The results were consistent with LeT. Finally, the pigeons returned to Phase A. Only LeT made specific predictions regarding the reacquisition of the four temporal discriminations. These predictions were only partly consistent with the results.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Learning-to-Time model; Scalar Expectancy Theory; Temporal bisection; Timing

The study of how animals time events has made substantial progress during the last three decades and currently there are a few quantitative models that compete to explain the data. Two of these models are Scalar Expectancy Theory (SET), an information-processing model developed by Gibbon and his collaborators (e.g., Gibbon, 1977, 1991; Gallistel and Gibbon, 2002), and Learning to Time (LeT), a behavioral model developed by Machado (1997) on the basis of earlier work by Killeen and Fetterman (1988; also Killeen, 1991). These two models make different assumptions about what animals learn in temporal tasks. The present study reports an experiment that contrasts their predictions.

Consider the temporal bisection procedure and how each model conceptualizes what an animal learns when exposed to it. During training, a pigeon experiences one of two stimuli (for example, a short or a long duration light) and then, in order to get food, it must choose between two keys, one illuminated with red and the other with green light. The choice of the red key is rewarded if the stimulus was short; the choice of the green

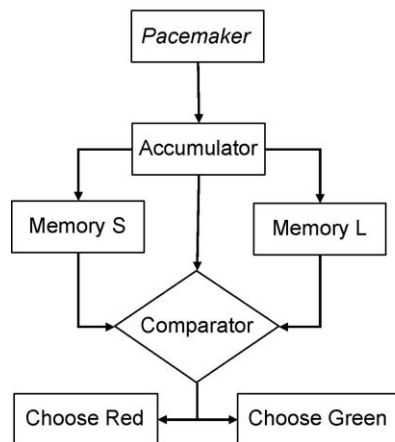
key is rewarded if the stimulus was long. After the bird learns the basic discriminations, the experimenter introduces stimuli with intermediate durations and records the animal's preference for the green key. The curve plotting the proportion of green key choices against stimulus duration is called the psychometric function. In general, as the duration of the test stimulus increases, the psychometric function also increases from about 0 to about 1. Moreover, the point in which the psychometric function equals 0.5 – the point of subjective equality or PSE – tends to occur when the probe duration equals, or is close to, the geometric mean of the two training stimuli (Catania, 1970; Church and Deluty, 1977; Fetterman and Killeen, 1991; Platt and Davis, 1983; Stubbs, 1968).

How do SET and LeT explain the preceding findings? SET postulates an internal clock with a pacemaker that generates pulses at a high and variable rate, an accumulator that counts the pulses emitted during the to-be-timed signal and two memory stores that save the counts obtained at the end of the two training stimuli (see the left panel of Fig. 1). 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 the long durations, X_L . A decision rule based on ratios determines the subject's

* Corresponding author at: Instituto de Educação e Psicologia, Universidade do Minho, 4710 Braga, Portugal. Tel.: +351 253 678 488; fax: +351 253 604 221.

E-mail address: arandom@iep.uminho.pt (A. Machado).

SCALAR EXPECTANCY THEORY (SET)



LEARNING TO TIME MODEL (LET)

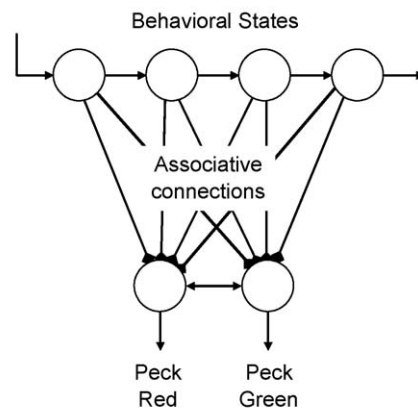


Fig. 1. (Left) Structure of the Scalar Expectancy Theory (SET) model for the bisection procedure. A pacemaker generates pulses which are accumulated in an accumulator. Two memory stores save the counts obtained at the end of the short and long signals. To choose which key to peck, the animal compares the number that is in the accumulator when the test signal ends against two samples, one extracted from each memory store. A ratio similarity rule determines the response. (Right) Structure of the Learning-to-Time (LeT) model. After a time marker, a set of behavioral states (top circles) is activated in series. Through reinforcement and extinction, the states become coupled to various degrees (middle connections) with the two responses (bottom circles). Choice depends on which states are the most active at the end of the test signal and how strongly they are coupled with the responses.

choice. Specifically, if the ratio X_S/X_T is greater than the ratio X_T/X_L , then the animal is more likely to choose the red key and, conversely, if the ratio X_S/X_T is less than the ratio X_T/X_L , then the animal is more likely to choose the green key. During testing, as the signal duration increases from short to long, X_T increases from values close to X_S to values close to X_L ; hence, the probability of choosing the green key increases with signal duration (see Gibbon, 1981; also Gallistel, 1990).

In turn, LeT assumes a serial organization of behavioral states, a vector of associative links connecting the behavioral states to the instrumental responses, and the instrumental responses themselves (see the right panel of Fig. 1). At the beginning of the stimulus, only the first state is active, but as time elapses, the activation of each state spreads to the next state in the series. Therefore, the most active states at the end of the long stimulus will be further down the series than the most active states at the end of the short stimulus. Each behavioral state is also coupled with the operant responses and the degree of the coupling changes with the trial outcome. Thus because the choice of the red key is rewarded and the choice of the green key is extinguished after the short stimulus, the early states will be coupled strongly with the red or “short” response and weakly with the green or “long” response. Similarly, because the choice of green is rewarded and the choice of the red is extinguished following the long stimulus, later states will be coupled strongly with the green or “long” response and weakly with the red or “short” response. During testing, as the signal duration increases, the state most active at the moment of choice also increases. And because later states are coupled mostly with the green, “long” response, the probability of choosing “long” increases with the signal duration.

Despite the fact that the two models differ in their conceptualization of temporal learning, both predict monotonic increasing

psychometric functions with the point of subjective equality at (SET), or approximately at (LeT), the geometric mean of the training stimuli. To separate the two models’ predictions, Machado and Keen (1999) modified the basic temporal bisection task. In their experiment pigeons learned two sets of temporal discriminations within the same session (Fig. 2, top). In the presence of two keys, one red and one green, the choice of red was rewarded if the preceding signal was 1-s long, and the choice of green was rewarded if the signal was 4-s long (Trial Type 1); in the presence of two other keys, one blue and the other yellow,

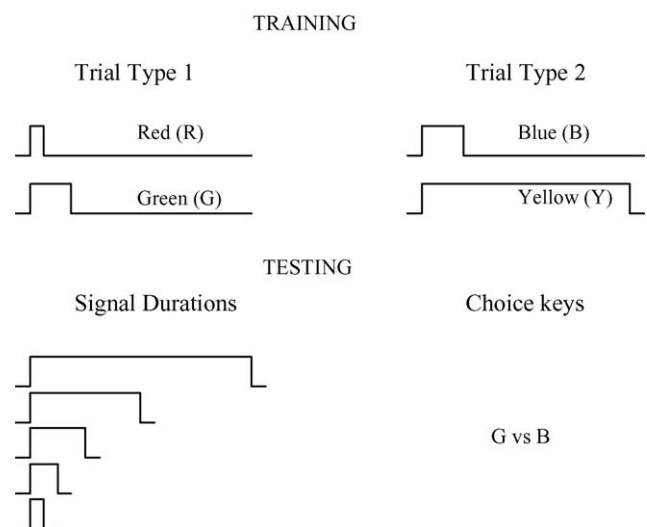


Fig. 2. (Top) Structure of a double bisection procedure. During Type 1 trials, a 1 or a 4-s signal occurs. A red-key choice is rewarded if the signal was 1-s long and a green-key choice is rewarded if the signal was 4-s long. During Type 2 trials, the signal is either 4 or 16-s long. After the former, the choice of blue is rewarded and after the latter, the choice of yellow is rewarded.

the choice of blue was rewarded if the preceding signal was 4-s long, and the choice of yellow was rewarded if the signal was 16-s long (Trial Type 2). Note that the green and blue keys were both associated with the same duration of 4 s. We refer to this task as a double bisection task.

What will a bird do when, following a signal t seconds long, it is presented with the green and blue keys, a pair of key colors it has never seen before simultaneously (Fig. 2, bottom)? According to SET, the animal should always be indifferent between green and blue because in the presence of these keys the experienced test duration would be compared with two samples that came from identical distributions (blue and green are both associated with 4-s signals). Obviously, the animal may be biased for one key, in which case preference will not equal 0.5, but the important feature of SET's prediction is not the absolute value of the preference for the green key, but the absence of any relation between that preference and the duration of the test signal.

In contrast, LeT predicts that the animal's preference for the green key will increase with the duration of the signal. The prediction is derived mathematically in Machado and Pata (2005); here we give only an intuitive account. When the signal duration is 1 s, the pigeon learns through reinforcement and extinction to behave in accord with two rules. First, approach the red key, and second, avoid the green key. In testing, when the signal duration is 1 s and the pigeon sees the green and blue keys, choice cannot accord with the first rule, for the red key is absent, but it can accord with the second—the pigeon avoids the green key and consequently chooses the blue key. Conversely, when the signal duration is 16 s, the animal learns to behave in accord with two other rules: approach the yellow key and avoid the blue key. It follows that, in testing, when the signal duration is 16 s and the bird must choose between the green and blue keys, the pigeon avoids the blue key (in accord with the second rule) and therefore chooses the green key. Thus, as the signal duration increases from 1 to 16 s, the preference for the green key, when the choice is between green and blue, will also increase. Machado and Keen's (1999) and Machado and Pata's (2005) results were always closer to LeT than to SET's predictions. In particular, both studies found that given the choice between the green and blue keys, preference for the green key increased monotonically with stimulus duration.

The present study developed an alternative test of the two models' conceptualizations of learning in the simple bisection and double bisection tasks. To understand the logic of the test, assume that a pigeon has learned the two sets of basic discriminations mentioned above, 1 s versus 4 s and 4 s versus 16 s (see Fig. 2, top). Afterwards, the experimenter attempts to teach the bird a new task involving the green and blue keys only: if the signal is 1-s long, the choice of the blue key is reinforced; if the signal is 16-s long, the choice of the green key is rewarded. According to LeT, the animal should have no difficulty with the new task (i.e., it should make few errors) because the training that preceded it created a tendency to choose that is *consistent* with the new reinforcement contingencies. In fact, as Machado and Keen (1999) and Machado and Pata (2005) showed, the effect of the initial training can be summarized as follows: when the choice is between green and blue, the proba-

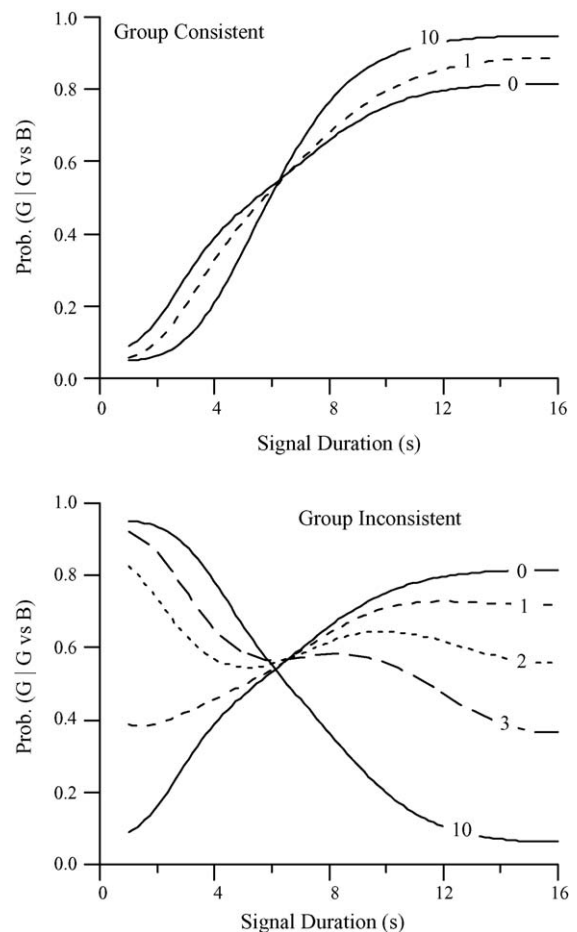


Fig. 3. Predictions of the LeT model for Groups Consistent and Inconsistent (see Appendix A for mathematical details). Each curve shows the probability of choosing green, given a choice between green and blue, $P(G|G \text{ vs. } B)$, as a function of signal duration. The number on each curve identifies the session for which the curve applies (e.g., curve 0 = immediately after double bisection training, curve 1 = after one session with the new discrimination training, etc.).

bility of choosing green increases with the signal duration. This tendency is consistent with a reinforcement rule that associates the choice of blue with 1-s signals and the choice of green with 16-s signals. The top panel of Fig. 3 shows LeT's quantitative predictions: accuracy increases slightly across sessions but it is already high during the first session with the new task. Appendix A may be consulted for the quantitative details of LeT's predictions.

But suppose that the new task were the opposite one: green is correct, and therefore reinforced, after the 1-s signal and blue is correct and reinforced after the 16-s signal. In this case, LeT predicts that the bird should have difficulty with the new task (i.e., make substantially more errors) because the preceding training created a tendency to choose that is *inconsistent* with the new reinforcement contingencies. This tendency must be eliminated before the bird learns the new task. The bottom panel of Fig. 3 shows LeT's quantitative predictions: although the choice of green is reinforced only after 1-s signals, during the first session with the new task the probability of choosing green increases with signal duration. The model also predicts that across sessions, as learning the new associations takes

place, the psychometric function will rotate in a clockwise direction such that, at the steady state, the bird is choosing mostly the green key after 1-s signals, and the blue key after 16-s signals.

To summarize, given the training depicted in Fig. 2, LeT predicts that learning the associations “after 1-s signals, choose green; after 16-s signals, choose blue” will be significantly retarded by comparison with learning the opposite associations “after 1-s signals, choose blue; after 16-s signals, choose green”. However, according to SET there should be no difference in the learning of the two tasks because the memories associated with the blue and green keys would be similar.

The present experiment tested the foregoing predictions in an ABA design. During Phase A, a group of pigeons learned the two sets of basic discriminations displayed in Fig. 2. Next, during Phase B, the birds were divided into two groups. Group Consistent was exposed to the task that according to LeT would be easy to master; Group Inconsistent was exposed to the task that according to LeT would be harder to master. Finally, both groups returned to Phase A.

LeT also makes specific predictions about the return to Phase A¹ and these predictions are displayed in Fig. 4 (see Appendix A for quantitative details). For Group Consistent, performance will be disrupted only when the choice is between the red and green keys and the signal is 4-s long (empty circles). The reason for this prediction derives from two model features, *response competition* and *temporal generalization*. By response competition we mean that the effect of reinforcement or extinction on one of the two available choices is the opposite of the effect on the other choice. To illustrate, when the choice is between keys x and y, reinforcement for choosing x increases the tendency to choose x and reduces the tendency to choose y. By temporal generalization we mean that the effects of reinforcement or extinction after signals of a specific duration extend to signals of different duration.

Consider now the effect of these model features as well as the reinforcement contingencies during Phase B on the tendency to peck green after 4-s signals. When the bird receives a reward for choosing green after 16-s signals, the tendency to peck green after 4-s signals *increases* by temporal generalization; but when the bird receives a reward for choosing Blue after 1-s signals, the tendency to peck green after 4-s signals *decreases* by temporal generalization and response competition. Because the generalization from 16 to 4 s is less than the generalization from 1 to 4 s (see Eq. (1) in Appendix A) the net effect of the reinforcement contingencies of Phase B is a decrease in the tendency to peck green after 4-s signals. At the end of Phase B, then, the bird will be less likely to choose green after 4-s signals than it was at the end of the first Phase A—hence the effect displayed in the top panel of Fig. 4.

For Group Inconsistent (see Fig. 4, bottom panel), performance will be disrupted when (a) the choice is between the red and green keys and the signal is 1-s long (filled circles), and

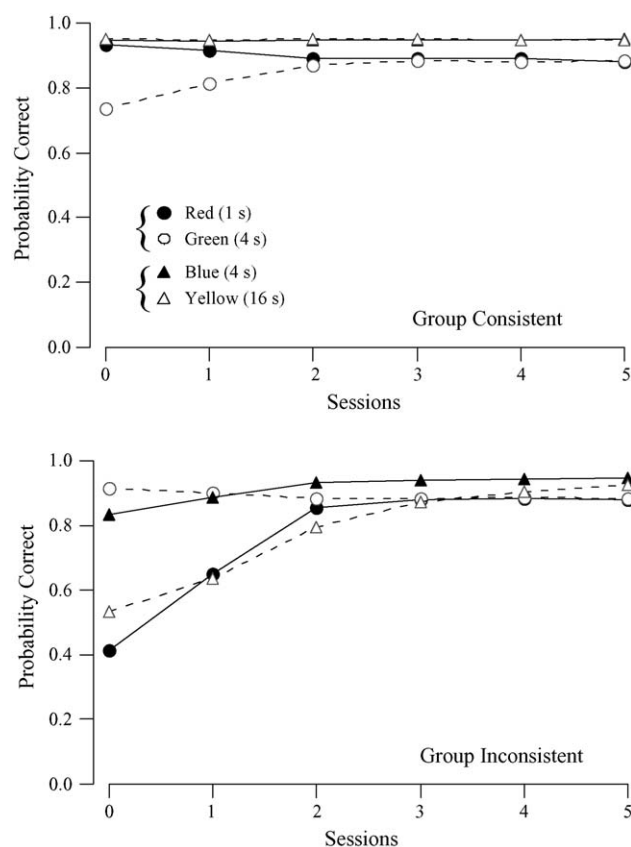


Fig. 4. Predictions of the LeT model for Groups Consistent Inconsistent during the first five sessions of the return to Phase A (see Appendix A for mathematical details). Each curve represents the probability of a correct choice following a particular signal (e.g., the curves with filled circles represent the probability of correctly choosing the red key following 1-s signals).

(b) the choice is between the blue and yellow keys and the signal is 16-s long (empty triangles). The reason for (a) is that during Phase B green becomes associated also with 1-s signals and therefore when the signal is 1-s long during the subsequent Phase A, the tendency to peck green is almost as strong as the tendency to peck red. The reason for (b) is similar: during Phase B blue becomes associated also with 16-s signals and therefore when the signal is 16-s long during the subsequent Phase A, the tendency to peck blue is almost as strong as the tendency to peck yellow. In summary, LeT predicts that overall performance will be disrupted more severely in Group Inconsistent than in Group Consistent, which is to say that Group Inconsistent will relearn the four original associations more slowly than Group Consistent. The experiment reported below also tested these predictions.

1. Method

1.1. Subjects

Ten naïve pigeons (*Columbia livia*) maintained at 80% of their free-feeding body weight participated in the experiment. The pigeons had continued access to water and grit in their home cages. The pigeon colony was under a 12:12 h light–dark cycle.

¹ Because SET has no explicit learning rules, one cannot derive its predictions for the return to Phase A.

1.2. Apparatus

Two standard experimental chambers from Med Associates® were used. The front panel of each chamber contained three keys, 2 cm in diameter. The keys were centered on the wall, 22 cm above the floor, and 8 cm apart, center to center. They 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 cm × 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. A personal computer programmed in C++ controlled all experimental events and recorded the data.

1.3. Procedure

After learning to peck the keys through autoshaping, the birds were exposed to one of the two basic discrimination tasks, “1 s versus 4 s” (Type 1) or “4 s versus 16 s” (Type 2). Half of the birds started with one task and the other half started with the other task. The assignment of keylight colors to signal durations was counterbalanced across birds but with two restrictions: (a) red and green, on the one hand, and blue and yellow, on the other hand, always occurred together; and (b) the two 4-s signals were associated always with the green and blue colors. However, for clarity we describe the procedure and the experimental results as if all birds had the following assignment: the 1 and 4-s signals of Type 1 trials were associated with the red and green keylights, respectively, and the 4 and 16-s signals of Type 2 trials were associated with the blue and yellow keylights, respectively (see top panel of Fig. 2).

Sessions were divided into trials and the following sequence of events happened during each trial: the houselight and the center keylight 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., red and green). A peck at a choice key turned all keylights and the houselight off, and if the choice was correct, the hopper was activated. The hopper duration varied across birds from 2 to 5 s in order to maintain body weight while minimizing extra-session feedings. After feeding a 30-s intertrial interval (ITI) followed. If the choice was incorrect, the ITI started immediately and the trial was repeated (correction method). If the bird made three errors on the same trial, then only the correct key was illuminated during the choice phase. Sessions ended after the bird obtained 60 reinforcements.

When choice performance was above 80% correct for five consecutive sessions, the birds were exposed to the second discrimination task. Once they learned this second task, the two tasks alternated across sessions before they were included into the same session and the experiment proper begun (see below). This preliminary training lasted from 26 to 45 sessions (mean = 34).

The experiment proper followed an ABA design. During Phase A, half of the trials were Type 1 and the other half were

Type 2. Sessions ended after 80 reinforcers were obtained, 40 from each trial type. The two colors presented during each trial type occurred always the same number of times on the left and right keys.

Initially, all correct choices were reinforced and incorrect choices repeated the trial. We call these regular trials. Then, extinction trials were introduced to adapt the birds to the lower rate of food that would occur during the next phase. Besides not ending with food (even when a choice was correct) extinction trials were not repeated even if the choice was incorrect. The number of extinction trials was initially set at 24 (with 56 regular trials) and then at 40 (with 40 regular trials). This phase lasted until the birds averaged at least 80% correct choices (excluding repeated trials) for five consecutive sessions on each of the four basic signals (range of required sessions: 13–45; mean = 26).

During Phase B, the signal durations were 1, 2, 4, 8 or 16 s and the keylight colors were always green and blue. Half of the animals, randomly selected, were reinforced for choosing the blue key after the 1-s signal and the green key after the 16-s signal (Group Consistent). The other birds were reinforced for pecking the green key after the 1-s signal and the blue key after the 16-s signal (Group Inconsistent). After an incorrect choice, the trial was repeated but at the moment of choice only the correct key was illuminated. This arrangement minimizes not only the effects of extinction, which according to LeT is likely to happen in Group Inconsistent, but also the effects of the correction method. Pecks following the 2, 4 and 8-s signals were never reinforced. Sessions comprised 88 trials, 20 in which the signal was 1-s long, 20 in which it was 16-s long, and 3 × 16 in which the signal was 2, 4, or 8-s long. Phase B lasted for 10 sessions.

When the birds returned to Phase A, all procedural details were the same as in the last sessions of the initial Phase A: each session comprised 40 regular and 40 extinction trials; during the regular trials, the correction method was in effect for a maximum of three errors; after three errors, only the correct key was lit during choice. This phase lasted for 10 sessions.

2. Results

2.1. Phase A

All pigeons learned the two basic discriminations. During the last five sessions of Phase A, overall proportion correct was consistently high both across birds (average = 0.93) and signal durations (range: 0.85–0.99). These results reproduce the earlier findings of Machado and Keen (1999) and Machado and Pata (2005).

2.2. Phase B

Fig. 5 shows the average results from this phase for the first, second, and 10th (last) sessions. Consider the top panel, which illustrates the data from Group Consistent: as the signal duration increased, preference for the green key also increased. In addition, the empirical curves did not change appreciably from the first to the 10th session. The bottom panel shows the corre-

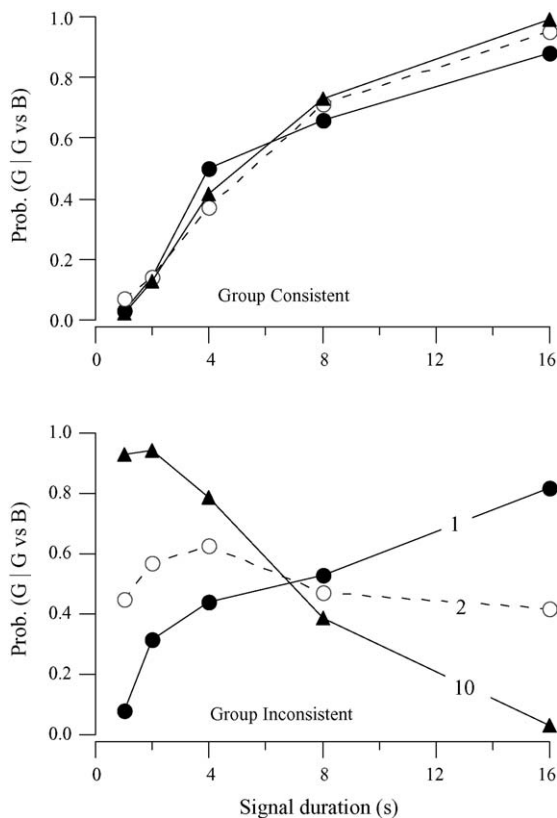


Fig. 5. Each curve shows the average probability of choosing the green key (given a choice between the green and blue keys) as a function of signal duration. The curves represent sessions 1, 2, and 10 of Phase B for Group Consistent (top panel) and Group Inconsistent (bottom panel).

sponding data for Group Inconsistent. During the first session, the preference for green increased monotonically with signal duration even though the choice of green was reinforced only after the 1-s signals. During the second session, average preference did not change systematically with signal duration. Finally, by the last session, preference for green decreased systematically with signal duration. In summary, whereas for Group Consistent performance was at (or close to) the steady state since the first session of Phase B, for Group Inconsistent performance was at the steady state only after a minimum of two sessions. The pattern of change in the curves for the two groups was consistent with LeT's predictions.

To better appreciate the within-group consistency of the foregoing findings, Fig. 6 shows the data for individual birds, from Group Consistent on the left panels and from Group Inconsistent on the right panels. The four curves in each left panel represent the results from the first, second, third, and 10th sessions. In all cases, the probability of choosing green increases with signal duration either in a sigmoid shape or in a negative exponential shape. There were no obvious differences between the curves from the four sessions. On the right panel, the four curves represent either the first, second, third, and 10th sessions, or the first, third, fourth and 10th sessions. These sessions were chosen because they show how the psychometric function rotated across sessions before stabilizing at the steady state. With the possible exception of bird P35, the psychometric functions were

clearly increasing during the first session; for all birds, they were clearly decreasing during the 10th session; and during the second and third or the third and fourth sessions, the psychometric functions rotated clockwise. (A closer analysis of the curves from all sessions revealed that by the fifth session performance was essentially at the steady state.) We conclude that the average curves displayed in Fig. 5 summarize adequately the individual data displayed in Fig. 6.

Fig. 7 allows us to compare the performance of the two groups during the first and last sessions of Phase B. With regard to the first session, the two curves are relatively close to each other, which shows that despite the opposite contingencies of reinforcement, the two sets of birds behaved in similar ways. However, the curve from Group Inconsistent seems to be slightly rotated in a clockwise direction with respect to the curve from Group Consistent, perhaps the effect of the first session itself.

The two curves in the bottom panel show performance during the last session. For Group Consistent the curve represents the probability of choosing green, and for Group Inconsistent the curve represents the probability of choosing blue—in both cases the color associated with the 16-s signals. The two curves show that the two sets of birds performed similarly, although the curve for Group Inconsistent was slightly shifted to the right when compared with the curve for Group Consistent.

To assess the statistical significance of the foregoing results, we conducted a $2 \times 2 \times 5$ ANOVA with Group as a between-subjects factor and Day and Duration as within-subjects factors. The ANOVA was based on the arcsine transform of the individual choice proportions. The results yielded only two significant effects at the 0.05 significance level, the main effect of duration: $F(4,32) = 126$, $p < 0.05$, because the psychometric functions increased reliably with signal duration; and the duration \times day interaction effect: $F(4,32) = 6.7$, $p < 0.05$, because the psychometric functions tended to be steeper on Day 10 than on Day 1.

To summarize, for Group Consistent, learning during Phase A transferred positively to Phase B such that the performances during the first and 10th sessions of Phase B were similar. In contrast, for Group Inconsistent, learning during Phase A transferred negatively to Phase B such that the performances during the first and last sessions were opposites, as it were: preference for green following 16-s signals was strong during the first session but weak during the last session, whereas following 1-s signals it was weak during the first session but strong during the last one. The rotation of the psychometric curves meant that Group Inconsistent required at least three sessions to learn the new discrimination; Group Consistent required none.

2.3. Return to the Phase A

Fig. 8 shows the average results from the last phase. The top panel corresponds to the birds from Group Consistent. On average, proportion correct following the 1 and 16-s signals was high on the first session and remained high throughout the 10 sessions. In contrast, proportion correct following the two 4-s signals was close to indifference during the first session, increased during the second session, and remained high during the last eight ses-

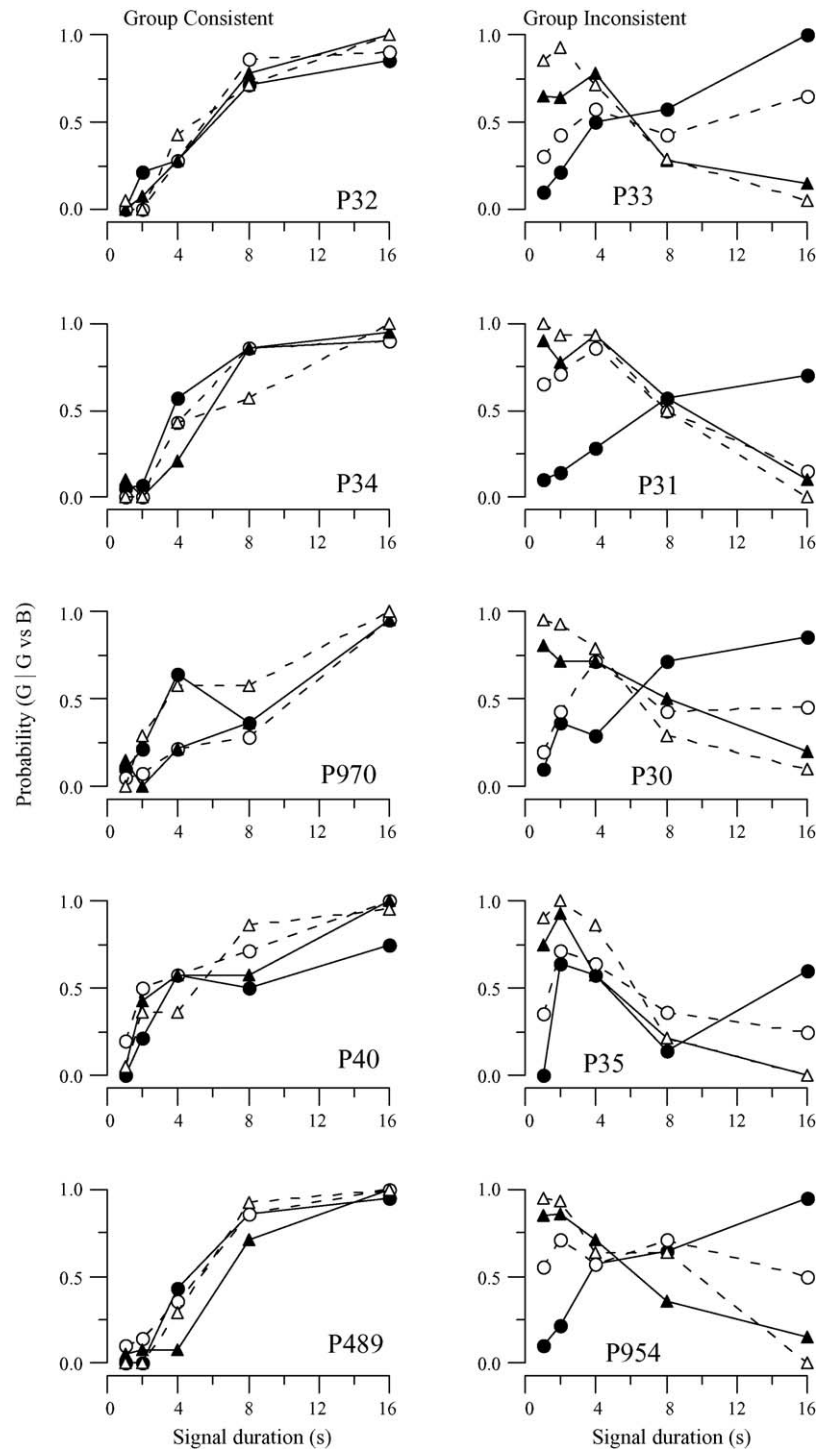


Fig. 6. Each curve shows the probability of choosing the green key as a function of signal duration for a single bird and session. For all birds of Group Consistent (left panels) the curves represent sessions 1 (filled circles), 2 (empty circles), 3 (filled triangles), and 10 (empty triangles). For Group Inconsistent (right panels) the curves represent sessions 1, 2, 3, and 10 (birds P31, P30, and P954) or sessions 1, 3, 4, and 10 (birds P33 and P35).

sions. We conclude that the birds from Group Consistent had difficulties mainly with the 4-s signals but relearned the original discriminations in about 2 days.

The bottom panel corresponds to Group Inconsistent. Initially, the birds from this group had difficulty with all four discriminations. On the average, performance following all signals was initially close to, or slightly below, chance, and then

it improved with training. However, the choice of red following the 1-s signal never reached the average accuracy observed during the initial Phase A. In addition, the improvements across sessions were slower than for Group Consistent.

The individual data are plotted in Fig. 9. Group Consistent (left panels) showed little between-subjects variability. For all birds, worst performance during the first session followed the

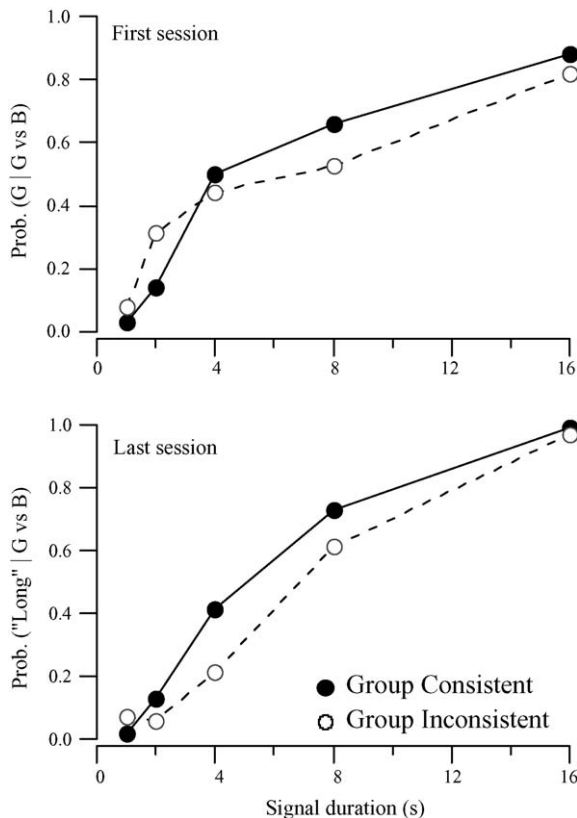


Fig. 7. The top curves show the average probability of choosing the green key as a function of signal duration during the first session of Phase B. The filled and empty symbols correspond to Group Consistent and Group Inconsistent, respectively. The bottom curves show the probability of choosing the key associated with the long duration during the last five sessions of Phase B. For Group Consistent "long" meant the green key and for Group Inconsistent it meant the blue key.

two 4-s signals; after the first or second sessions, accuracy on the four signals was roughly comparable. Group Inconsistent (right panels) showed greater between-subjects variability. Over the 10 sessions, worst performance followed the 1-s signal for four birds and the 16-s signal for one bird (P954). For two birds (P954 and P33) the two most disrupted choices were red following the 1-s signal and yellow following the 16-s signal; for one bird (P35) the two most disrupted choices were red following the 1-s signal and green following the 4-s signal; for the other two birds (P31 and P30), the choices following the two 4-s signals and the 16-s signal were equally affected. By the last sessions, only one bird (P954) had reached the accuracy levels observed during the first Phase A.

3. Discussion

The present study used a variation of the temporal bisection procedure to contrast the predictions of two models of timing, SET and LeT. During Phase A of an ABA design, 10 pigeons learned 2 temporal discriminations, to choose a red key after a 1-s signal and a green key after a 4-s signal, and to choose a blue key after a 4-s signal and a yellow key after a 16-s signal. During Phase B, the pigeons were exposed to signals ranging from 1 to

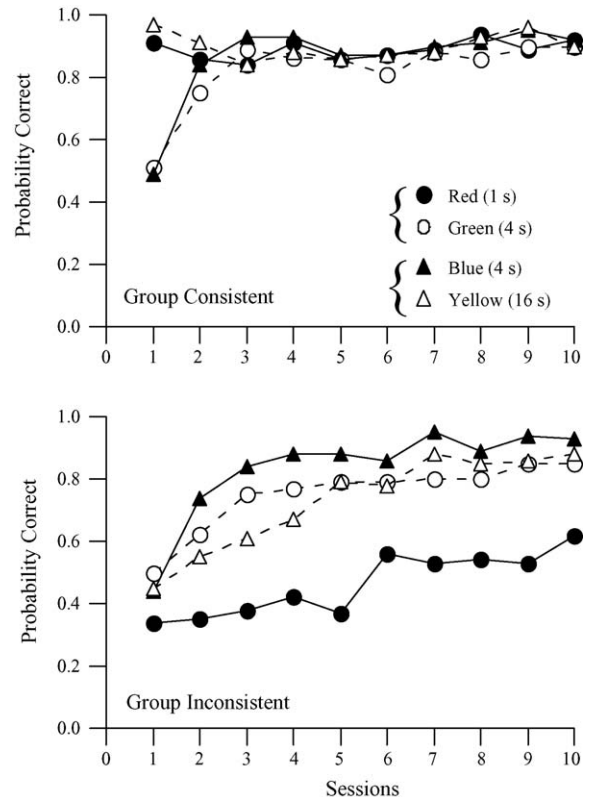


Fig. 8. The four curves show the average probability of a correct choice following the four signal durations across the 10 sessions of the last Phase A.

16 s and at the end of the signal they chose between the green and the blue keys. In addition, the 10 birds were divided into two groups. Group Consistent received food for choosing the blue key after the 1-s signal and the green key after the 16-s signal. LeT predicted that this group would perform accurately since the first session of Phase B because, according to the model, the response tendencies acquired during Phase A would be consistent with the reinforcement contingencies of Phase B. Group Inconsistent received food for choosing the green key after the 1-s signal and the blue key after the 16-s signal. LeT predicted that this group would perform poorly during the first session because the tendencies to respond acquired in Phase A were inconsistent with the reinforcement contingencies of Phase B. According to SET, however, the two groups should perform equally because the memories associated with the blue and green keys would be identical, for each would hold the values in the accumulator at the end of 4-s signals.

The data confirmed LeT's predictions. All birds from Group Consistent performed accurately since the first session, whereas the birds from Group Inconsistent needed from two to five sessions to reach comparable levels of accuracy. In fact, despite the opposite contingencies, the two groups of birds behaved similarly during the first session of Phase B (see Fig. 7, top), a strong corroboration of LeT (see Machado and Keen, 1999; Machado and Pata, 2005).

In the last part of the experiment the animals returned to Phase A. LeT predicted that (a) the two groups would differ in terms of which performances would be disrupted and (b)

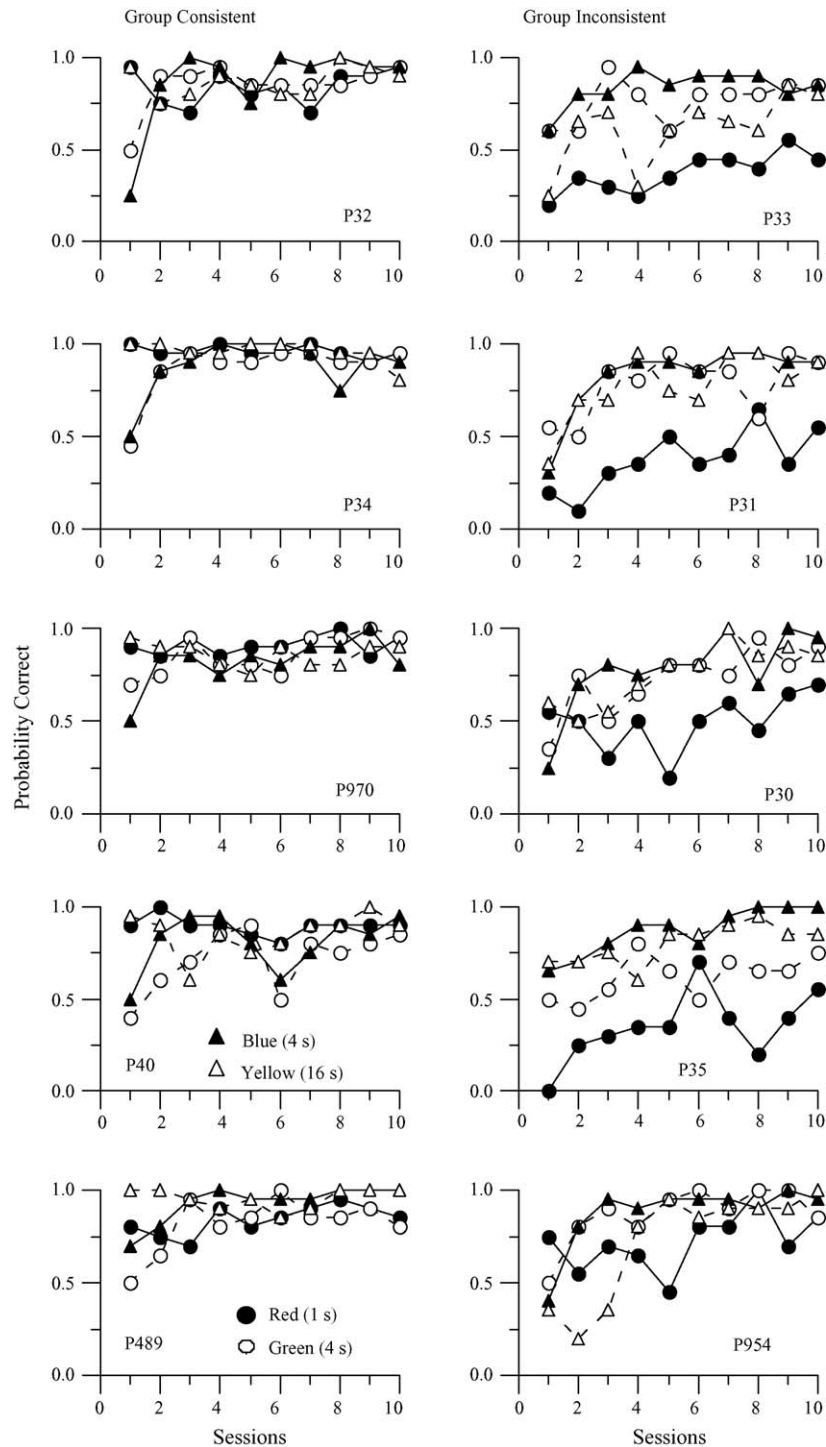


Fig. 9. The four curves on each panel show the probability of a correct choice following the four signal durations across the 10 sessions of the last Phase A. Each panel corresponds to a different bird from Group Consistent (left panels) or Group Inconsistent (right panels).

Group Consistent would relearn the four associations faster than Group Inconsistent. The results were mixed. On the one hand, the groups did differ in the pattern of disrupted performances. In Group Consistent, performance was disrupted reliably after the 4-s signals, whereas in Group Inconsistent performance was disrupted reliably after the 1-s signals. In addition, Group Consistent relearned the original discriminations faster than Group Inconsistent. These two sets of findings agree with the LeT

model. On the other hand, the specific pattern of disruptions observed in each group did not match LeT's predictions. In Group Consistent, LeT could not predict the disruption of blue choices following 4-s signals, and in Group Inconsistent, LeT could not predict the disruption of green and blue choices following the 4-s signals. In addition, LeT also could not predict the *degree* of difficulty in relearning to choose the red key following the 1-s signals (see Fig. 8).

Occasional observations throughout the experiment (each bird was observed for about three sessions during each phase) revealed for most birds a set of behavioral patterns that may have mediated the temporal discrimination (see Fetterman et al., 1998; Machado and Keen, 1999; Machado and Pata, 2005; Richelle and Lejeune, 1980). Moreover, the stability of these patterns across phases seemed to differ between the two experimental groups, being greater in Group Consistent than in Group Inconsistent. To illustrate, bird P34 from Group Consistent behaved regularly in the following way: at trial onset, it approached the center key. If the trial ended shortly afterwards because the signal was 1-s long, then the bird pecked the red key; if not, the bird started to peck the center key but without actually striking it (“air peck” the key). It emitted this behavior until the signal ended at 4 s or approximately 6 s had elapsed. In the former case, the bird pecked either the green or the blue key, whichever was presented and in the latter case (i.e., the signal was 16-s long), the bird continued to peck but now around the center key, and at the end of the trial it chose the yellow key. Thus if we consider only the longest, 16-s trials we identify three classes of behavior, Class 1 (‘approach center key’) from approximately 0 to 1 s, Class 2 (‘air peck at center key’) from approximately 1 to 6 s, and Class 3 (‘peck at center key’) from approximately 6 s to the end of the trial.

In addition to bird P34, three other birds from Group Consistent also showed stable patterns across phases. The exception was bird P40 for whom Classes 1 (facing the front panel) and 3 (moving the head up and down in the front left corner of box) remained stable across phases, but Class 2 changed from pecking the center key during Phase A to head bobbing around the feeder during Phase B to pecking at the left (unlit) key upon returning to Phase A.

In contrast, the birds from Group Inconsistent seemed to change their behavior more significantly with the phase of the experiment. For example, bird P954 showed the following three-class pattern during the initial Phase A: ‘facing the keys’ (Class 1), ‘pecking at a salience in the ceiling of the box with a topography that resembled biting (when the beak closes the head pulls back)’ (Class 2), and ‘pecking the center key’ (Class 3). During Phase B, Class 2 changed to simply standing still until approximately 6 s elapsed. On its return to Phase A, the animal resumed the initial behavioral sequence. Other birds (P31, P33, P35) changed their behaviors across phases but did not resume the initial pattern when returning to Phase A. The observations of bird P30 were less clear because the patterns were more variable; for this bird, without more systematic data no reliable statements about changes across phases can be made.

The foregoing findings suggest one way to partly explain the difficulty of Group Inconsistent in relearning the basic discriminations upon its return to Phase A: if temporal discrimination is mediated, or at least influenced, by the acquisition of a behavioral pattern as Killeen and Fetterman’s (1988) behavioral theory of timing suggests and LeT presupposes, and if during Phase B the behavioral pattern acquired during Phase A is disrupted (the pattern may be weakened or replaced by another), then upon returning to Phase A the bird has to (re)learn a pattern supporting the four original discriminations, which relearning takes

time and leads to a slower acquisition curve. However, without an explicit, quantitative theory of how behavioral patterns are learned and unlearned, the preceding account cannot explain the *much* slower relearning of the correct choice following 1-s signals in Group Inconsistent.

The findings reported above reproduce and extend the findings reported by Machado and Keen (1999) and Machado and Pata (2005). Together, the three studies suggest that LeT captures one key aspect of learning in the temporal bisection task, namely, that preference for one key following a signal with duration t_1 depends also on the duration t_2 associated with the other key. To illustrate, preference for green following 4-s signals is affected by the fact that the green key was paired with the red key which was associated with 1-s signals. This context effect, which LeT predicts (see also Machado and Pata, 2005), cannot be derived from SET because SET assumes *independence* among the temporal memories associated with the keys. The reason for SET’s failure to predict the double bisection findings should be taken into consideration when other models (e.g., Multiple Time Scales model, see Staddon and Higa, 1999; Packet Theory, see Kirkpatrick, 2002; Kirkpatrick and Church, 1998) are extended to temporal bisection.

Acknowledgements

The authors thank students Paulo Pata and Paula Magalhães for their help in running the experiment. Research supported by a grant from the Portuguese Foundation for Science and Technology to the first author.

Appendix A

A.1. LeT-simple bisection

In what follows, we assume that the two signals occur with equal probability, 0.5, and that the correct choices following the short (S) and long (L) signals are, respectively, the red (R) and green (G) keys. Correct choices may be reinforced only intermittently.

LeT has three components, the behavioral states, their couplings with the operant responses, and the strength of the operant responses (see Fig. 1). According to the model, the onset of the training stimulus triggers the transitions across the behavioral states. When the stimulus ends the subject responds R or G. If the response is reinforced, then the association between each state and the choice response increases and the association between each state and the other response decreases; if the choice response is incorrect, then the association between that response and each state decreases and the association between the other response and each state increases (see Machado, 1997, for details).

To generate LeT’s predictions for each trial, we need the expression for the activation of state n after a signal of t seconds, $X(n,t)$, the expressions for the change in the couplings between state n and the R and G responses, $\Delta WR(n)$ and $\Delta WG(n)$, respectively, the initial values $WR(n)$ and $WG(n)$, and the probability of choosing one of the responses, say G , after a

Table A.1

The equations describe how the connections between state n and the red and green responses, $WR(n)$ and $WG(n)$, respectively, change during one trial in which the short signal occurred. Although red is the correct choice, it may not be reinforced. Green, however, is never reinforced after the short signal

Choice	Reinforcement	Extinction
Red	$\Delta WR(n) = \beta X(S, n)[1 - WR(n)],$ $\Delta WG(n) = -\beta X(S, n)WG(n)$	$\Delta WR(n) = -\alpha X(S, n)WR(n),$ $\Delta WG(n) = \alpha X(S, n)[1 - WG(n)]$
Green		$\Delta WR(n) = \alpha X(S, n)[1 - WR(n)],$ $\Delta WG(n) = -\alpha X(S, n)WG(n)$

signal t -s long, $P(G|t)$. We consider each of these elements in turn.

In LeT, $X(n, t)$ follows the Poisson distribution:

$$X(n, t) = \frac{\exp(-\lambda t)(\lambda t)^n}{n!} \quad (1)$$

where $\lambda > 0$ is a parameter that controls how fast the activation spreads across the states. In the simulation reported below, $\lambda = 1.5$. We also assumed that n ranged from 1 to 60 states.

The model's learning equations are displayed in Table A.1. Assume the short stimulus occurs on the current trial. Then, if the subject chooses red and receives food, the association between state n and the red response changes by the positive amount $\Delta WR(n) = \beta X(S, n)[1 - WR(n)]$, where $0 \leq \beta \leq 1$ is a reinforcement parameter. The association between state n and the green response changes by the negative amount $\Delta WG(n) = -\beta X(S, n)WG(n)$ —see the top left cell of Table A.1. If the subject responds red but does not receive food, then $\Delta WR(n)$ decreases and $\Delta WG(n)$ increases according to the equations displayed in the top right cell of the table where $0 \leq \alpha \leq 1$ is the extinction parameter. If the bird chooses green after the short stimulus, then its response is always extinguished (hence the empty bottom left cell) and the equations for this case are displayed in the bottom right cell of the table. Table A.2 shows the equations that apply when the long stimulus occurs.

The preceding equations for $\Delta WR(n)$ and $\Delta WG(n)$ plus the initial values of $WR(n)$ and $WG(n)$ fully determine the dynamics of $WR(n)$ and $WG(n)$. In the simulations to be reported, we assumed initial values of 0.5 for all $WR(n)$ and $WG(n)$, which means that, regardless of stimulus duration, the subject was always indifferent between red and green at the beginning of the simulation. To reduce the number of free parameters, we also assumed that extinction had negligible effects compared with reinforcement. Specifically, we set $\alpha = 0$ and $\beta = 0.5$. Extensive simulations showed that the model's predictions do not change substantially if $\alpha > 0$ or if, as in previous studies (Machado, 1997; Machado and Pata, 2005), we let $\alpha = \beta$.

From the values of $X(n, t)$, $WR(n)$, and $WG(n)$ one gets the strengths of the red and green responses after a signal of duration t , $RR(t)$ and $RG(t)$, respectively:

$$RR(t) = \sum_n X(t, n)WR(n), \quad RG(t) = \sum_n X(t, n)WG(n) \quad (2)$$

Note that the strength of a particular response, say red, after a signal of duration t depends on the activation of the behavioral states at that time, $X(t, n)$, and on their links with the red response, $WR(n)$. Whereas $X(t, n)$ expresses the behavioral clock, $WR(n)$ reflects the animal's reinforcement history.

Finally, the probability of choosing the green key at time t (important to determine the trial outcome and therefore which equations from Tables A.1 and A.2 apply) depends on the difference of response strengths. Specifically,

$$P(G|t) = \frac{\exp[\delta RG(t)]}{\exp[\delta RR(t)] + \exp[\delta RG(t)]} = \frac{1}{1 + \exp\{\delta[RR(t) - RG(t)]\}} \quad (3)$$

where $\delta > 0$ is a sensitivity parameter related to factors such as the distance between the choice keys or color discriminability. Parameter δ was set to 3.0 in the simulations to be reported. Concerning Eq. (3) note that if the response strengths are equal, $P(G|t) = 0.5$; if response strength of red is much greater than response strength of green [i.e., $RR(t) \gg RG(t)$], then $P(G|t)$ is close to 0, but if $RG(t) \gg RR(t)$, then $P(G|t)$ is close to 1.

In summary, LeT's predictions are based on Eq. (1), which describes the temporal activation of the behavioral states and uses parameter λ , the learning equations displayed in Tables A.1 and A.2, which use parameter β (we let $\alpha = 0$), and Eq. (3), which yields choice probability on the basis of the two response strengths given by Eq. (2), and which uses parameter δ .

Table A.2

The equations describe how $WR(n)$ and $WG(n)$ change during one trial in which the long signal occurred

Choice	Reinforcement	Extinction
Red		$\Delta WR(n) = -\alpha X(L, n)WR(n),$ $\Delta WG(n) = \alpha X(L, n)[1 - WG(n)]$
Green	$\Delta WR(n) = -\beta X(L, n)WR(n),$ $\Delta WG(n) = \beta X(L, n)[1 - WG(n)]$	$\Delta WR(n) = \alpha X(L, n)[1 - WR(n)],$ $\Delta WG(n) = -\alpha X(L, n)WG(n)$

Although green is the correct choice, it may not be reinforced. Red, however, is never reinforced after the long signal.

A.2. LeT-double bisection simulation

The simulations used the same number of trials, trial structure and phases as the real experiment. In addition to $WR(n)$ and $WG(n)$ defined above, we also defined $WB(n)$ and $WY(n)$ as the couplings of state n with the blue and yellow responses, respectively, and also initiated them to 0.5. During the simulation of Phases A, all four W values ($WR(n)$, $WG(n)$, $WB(n)$ and $WY(n)$) changed, but during Phase B only $WG(n)$ and $WB(n)$ changed. Finally, unlike the experiment, the simulations did not include correction trials. Fig. 3 shows the results of Phase B, before the first trial (curve 0), after the first session (curve 1), and so on until the 10th and last session (curve 10). Fig. 4 shows the results upon returning to Phase A, from the moment before the first trial (session 0) and until the end of the fifth session.

References

- Catania, A.C., 1970. Reinforcement schedules and the psychophysical judgments: a study of some temporal properties of behavior. In: Schoenfeld, W.N. (Ed.), *The Theory of Reinforcement Schedules*. Appleton-Century-Crofts, New York, pp. 1–42.
- Church, R.M., Deluty, M.Z., 1977. Bisection of temporal intervals. *J. Exp. Psychol.: Anim. Behav. Process.* 3, 216–228.
- Fetterman, J.G., Killeen, P.R., 1991. Adjusting the pacemaker. *Learn. Motiv.* 22, 226–252.
- Fetterman, J.G., Killeen, P.R., Hall, S., 1998. Watching the clock. *Behav. Process.* 44, 211–224.
- Gallistel, C.R., 1990. *The Organization of Learning*. Bradford Books/MIT Press, Cambridge, MA.
- Gallistel, C.R., Gibbon, J., 2002. *The Symbolic Foundations of Conditioned Behavior*. Lawrence Erlbaum, Mahwah, NJ.
- Gibbon, J., 1977. Scalar expectancy theory and Weber's law in animal timing. *Psychol. Rev.* 84, 279–325.
- Gibbon, J., 1981. On the form and location of the psychometric bisection function for time. *J. Math. Psychol.* 24, 58–87.
- Gibbon, J., 1991. Origins of scalar timing theory. *Learn. Motiv.* 22, 3–38.
- Killeen, P., Fetterman, J.G., 1988. A behavioral theory of timing. *Psychol. Rev.* 95, 274–295.
- Killeen, P.R., 1991. Behavior's time. In: Bower, G. (Ed.), *The Psychology of Learning and Motivation*, vol. 27. Academic Press, New York, pp. 294–334.
- Kirkpatrick, K., Church, R.M., 1998. Are separate theories of conditioning and timing necessary? *Behav. Process.* 44, 163–182.
- Kirkpatrick, K., 2002. Packet theory of conditioning and timing. *Behav. Process.* 57, 89–106.
- Machado, A., 1997. Learning the temporal dynamics of behavior. *Psychol. Rev.* 104, 241–265.
- Machado, A., Keen, R., 1999. Learning to Time (LET) or Scalar Expectancy Theory (SET)? A critical test of two models of timing. *Psychol. Sci.* 10, 285–290.
- Machado, A., Pata, P., 2005. Testing the Scalar Expectancy Theory (SET) and the Learning to Time model (LeT) in a double bisection task. *Learn. Behav.* 33, 111–122.
- Platt, J.R., Davis, E.R., 1983. Bisection of temporal intervals by pigeons. *J. Exp. Psychol.: Anim. Behav. Process.* 9, 160–170.
- Richelle, M., Lejeune, H., 1980. *Time in Animal Behavior*. Pergamon Press, Oxford, UK.
- Staddon, J.E.R., Higa, J.J., 1999. Time and memory: towards a pacemaker-free theory of interval timing. *J. Exp. Anal. Behav.* 71, 215–251.
- Stubbs, D.A., 1968. The discrimination of stimulus duration by pigeons. *J. Exp. Anal. Behav.* 11, 223–238.