

Acquisition versus steady state in the time-left experiment

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Received 19 November 2005; accepted 20 November 2005

Abstract

To test some predictions of scalar expectancy theory (SET) for the time-left procedure, we performed one experiment with two conditions. In Condition A, pigeons were exposed to two fixed-interval schedules, a fixed-interval (FI) 30 s and an FI 60 s, each associated with a distinct key and presented on a separate trial. Subsequently, during test trials, the FI 60-s key was illuminated and then after $T = 15, 30$ or 45 s the FI 30-s key also was illuminated. The main issue was how choice between the two keys varied with T . Condition B replicated Condition A with different FI parameters and T values. The results showed that (a) contrary to SET's predictions, preference changed reliably with testing, which suggests that learning took place during the test trials; (b) within each test trial, pigeons revealed an almost exclusive preference for one of the keys, and (c) at steady state pigeons behaved in the same way as rats. Because SET could not account for these findings we advanced a new descriptive model of performance for the time-left task. The model fit the data well.

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Keywords: Choice; Learning; Scalar Expectancy Theory; Time-left procedure; Timing

1. Introduction

In an attempt to determine whether the subjective time scale is linear or logarithmic, Gibbon and Church (1981) developed the time-left procedure. The fundamental idea explored in the procedure is as follows: if the scale is logarithmic, then the subjective magnitude of the first half of an interval should be larger than the subjective magnitude of the second half of the interval. In contrast, if the scale is linear, then the two subjective magnitudes should be equal. Consider then a choice between two stimuli, one, the Standard, previously associated with a 30 s delay to food, and the other, the Comparison, previously associated with a 60 s delay to food. A trial always starts with the Comparison stimulus alone; sometime later, say at T s into the 60 s delay, the Standard stimulus is introduced and from then on the animal has a choice between the two alternatives. At T s into the trial, the Comparison stimulus signals 60- T s to food, whereas the Standard stimulus signals always 30 s to food. The question is 'How does preference vary with T ?'

To minimize the delay to food, the animal should choose the Standard stimulus when $T < 30$ s and the Comparison stimulus when $T > 30$ s. A critical test occurs when $T = 30$ s: if the sub-

jective scale is logarithmic, then the animal should prefer the Comparison stimulus because the subjective magnitude of the time-left-to-food on the Comparison stimulus (i.e., the second half of the 60-s interval) would be smaller than the subjective magnitude of the 30-s Standard interval. However, if the subjective scale is linear, then the animal should be indifferent between the two keys because the subjective magnitudes of the second half of the 60-s Comparison interval and the 30-s Standard interval would be equal.

Using this procedure, Gibbon and Church (1981, Experiment 1) reported results consistent with a linear subjective time scale. The authors trained four rats on two separate, fixed-interval (FI) schedules. On the Standard (retractable) lever, the FI was 30-s long; on the Comparison (also retractable) lever the FI was 60-s long. After the typical scallop developed on each lever separately (20 sessions), the experimenters introduced combined trials to assess preference. During these trials, the Comparison (C) lever was inserted into the box at trial onset and then at $T = 15, 30$ or 45 s, the Standard (S) lever also was inserted into the box. The trial ended when reinforcement was received on either lever. After 35 sessions of testing, the authors obtained the results displayed in Fig. 1.

The figure shows that the average preference for the C lever equaled 0.25 when $T = 15$ s, 0.50 when $T = 30$ s, and 0.75 when $T = 45$ s. That is, the rats were indifferent between the two levers when $T = 30$ s and their preference was symmetric

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with respect to indifference when $T = 15$ and 45 s. Moreover, while the two levers were simultaneously present, preference remained roughly constant. The authors also showed that scalar expectancy theory (SET) accounted well for these findings.

SET assumes that animals have an internal clock composed of a pacemaker, an accumulator, a memory store and a comparator (Gibbon, 1977, 1991; Gibbon and Church, 1981; Gibbon et al., 1984). The pacemaker emits pulses at a high rate. The accumulator is reset to zero at the beginning of the to-be-timed interval, and then after a short latency (T_0 s) adds the pulses emitted by the pacemaker for the remainder of the interval. At the end of the interval (in the FI schedule, when food is delivered), the number of pulses in the accumulator is first multiplied by a random variable and then transferred to a memory store. Because of this multiplicative random variable, the number of pulses stored in memory will vary across trials even if the interval remains the same. To decide whether to respond or not during the interval, the animal compares the number of pulses currently in the accumulator with a sample extracted from its memory store at the beginning of the interval. It makes a response when the ratio of the two numbers exceeds a threshold.

In the time-left procedure, SET assumes that the animal has formed two memory stores, one associated with the *C* key and containing the distribution of pulses that represent the longer FI schedule, the other associated with the *S* key and containing the distribution of pulses that represent the shorter FI schedule. When the *S* key is illuminated at time T , the animal computes two times-left-to-food, the time-left on the *C* key and the time-left on the *S* key and responds on the *C* key if the ratio between these two times is less than a bias threshold. Given a few additional assumptions (discussed below), SET predicts the straight lines displayed in Fig. 1.

Several questions remain unanswered though. First, are the rats' preferences displayed in Fig. 1 due to the learning that took place when the two levers were presented separately (the first 20 sessions of the experiment) or to the learning that took place when the two levers were presented together (the last 35 sessions)? Scalar expectancy theory presumes the former because

the clock, memory, and decision processes that according to the model generate the animal's choices during testing are all in place at the end of the FI training. Or, to put it differently, no model ingredient necessary to predict the choice results comes from the testing phase of the experiment. But it is also conceivable that the animal needs to experience the two levers together and the new contingencies of reinforcement in order to learn how to choose the best option and thus show the preference functions displayed in Fig. 1. The present study attempted to distinguish these two accounts by comparing the data from the first sessions of testing with the data from the last sessions of testing. If SET is correct, then the results displayed in Fig. 1 should be observed already during the first sessions of testing, but if the other hypothesis is correct then the results displayed in Fig. 1 should emerge gradually during testing. In the latter case, an alternative model of performance for the time-left procedure must be found.

Second, how was the constancy of the three preference functions displayed in Fig. 1 achieved? Consider the case $T = 30$ s: was the 0.5 indifference value obtained because during each test trial the rats switched frequently between the two levers, or because the rats pressed only one lever during a particular test trial, but changed the preferred lever across trials? More generally, we do not know whether the three partial preferences in Fig. 1 stemmed from corresponding within-trial *partial* preferences, or from an appropriate mixture of within-trial *exclusive* preferences for one or the other lever. Gibbon and Church (1981) did not report the data in ways that allow us to decide between the two alternatives—hence the present experiment.

Third, will pigeons in the time-left procedure show the same preference functions as rats? In their 1981 study, Gibbon and Church reported a second experiment with pigeons (see also Gibbon et al., 1984), but that experiment used a modified and more complex testing procedure, a concurrent-chains procedure that other authors have criticized as methodologically inadequate to address timing issues (for details see Cerutti and Staddon, 2004; Preston, 1994; Staddon and Higa, 1999; Staddon et al., 1999). Therefore, in the present study we extend the original and simpler time-left procedure to pigeons.

In summary, the experiment reported below had three main goals: to determine whether choice performance changes during testing and, in the affirmative, to describe how it changes; to determine how aggregate choice proportion relates to within-trial choice performance; and to determine whether pigeons show the same preference functions as rats. On the theoretical side, we show that SET fails to account for the experimental findings reported below and for that reason in the final section of the paper we propose a new descriptive model for the time-left procedure.

2. Experiment

The experiment was divided into Conditions A and B. In Condition A, pigeons learned to associate one key with an FI 60-s schedule (the Comparison key, *C*) and the other key with an FI 30-s schedule (the Standard key, *S*). After the birds acquired

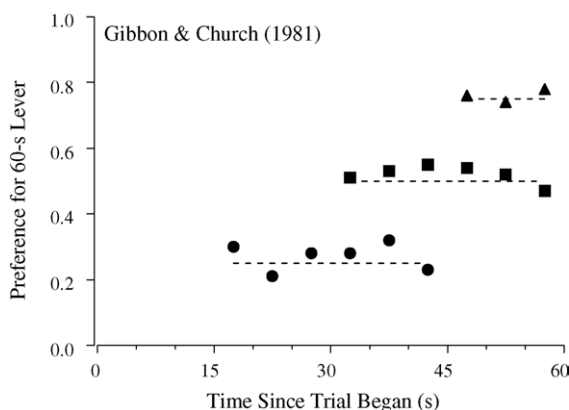


Fig. 1. Proportion of responses for four rats on the Comparison lever as a function of time since the trial began. The parameter is the time the Standard lever is introduced into the trial (circles: $T = 15$ s; squares: $T = 30$ s; and triangles: $T = 45$ s). The horizontal lines show the fits of scalar expectancy theory (SET). Adapted from Gibbon and Church (1981).

the temporal discrimination on both schedules, testing started. Each test trial began with the illumination of the *C* key and then at $T = 15, 30$ or 45 s into the trial, the *S* key also was lit. The test trial ended when the bird collected a reinforcer from either key.

To determine whether the bird's choices change with exposure to the combined trials, we divided testing into three phases. In the first phase, test sessions occurred only once a week and only about 15% of all trials during test sessions were combined trials—the remaining were the regular trials with the separate FIs. In the second phase, test sessions occurred daily but still only 15% of all trials were combined trials. In the third phase, test sessions occurred daily and about 47% of all trials were combined trials. The low frequency of test sessions (Phase 1) or the low number of combined trials per test session (Phases 1 and 2) enabled us to assess how much transfer occurs from the separate FI training to the combined trials while minimizing the effect of learning during the combined trials themselves; the higher frequency of test sessions plus the large number of combined trials (Phase 3) enabled us to determine steady state choice performance.

In Condition B, the procedure remained the same except for the schedule parameters. The FI values were 45 and 90 s for the Standard and Comparison keys, respectively, and T equaled 22.5, 45 or 67.5 s.

2.1. Materials and methods

2.1.1. Subjects

Six experimentally naïve pigeons participated in Condition A and seven pigeons participated in Condition B. Five of the birds in Condition B had participated in Condition A, whereas the other two had participated in a number discrimination experiment. Birds were maintained at 80% of their free-feeding body weights and were housed in individual home cages with water and grit continuously available. A 14:10 h light/dark cycle was in effect in the pigeon colony.

2.1.2. Apparatus

Two standard experimental chambers for pigeons from Lehigh Valley® were used. The front panel of each chamber contained two keys centered on the wall, 2.5 cm in diameter, 23 cm above the floor, and 14 cm apart center to center. The keys could be illuminated from behind with red, green, white or yellow lights. The hopper opening measured 6 cm × 5 cm and was centered on the wall, 8.5 cm above the floor grid. The bird had access to mixed grain when the hopper was raised and illuminated. On the opposite wall of the chamber another white light provided general illumination. The intelligence panels were enclosed by outer boxes equipped with ventilating fans. Two personal computers programmed in C++ controlled the experimental events and recorded the data.

2.1.3. Procedure

The birds were randomly assigned to the two chambers and the naïve pigeons learned to peck the keys using an autoshaping procedure.

2.1.3.1. FI Training. Next all birds were trained on the two FI schedules, FI 30 and 60 s in Condition A, and FI 45 and 90 s in Condition B (these final parameter values were reached progressively during 3 or 4 sessions). In Condition A, the assignment of the FI schedules to the left and right keys and to the red and green light colors was partially counterbalanced across birds. Once made, the assignment did not change until the condition ended (e.g., for one bird the left key, illuminated with red light, was always associated with the FI 30 s schedule, and the right key, illuminated with green light, was always associated with the FI 60 s schedule).

In Condition B, the two FI schedules were also associated with different keys, but to reduce potential carryover effects the keys were illuminated with white or yellow lights. In addition, the left–right assignment of the two schedules was reversed for the five birds that had participated in Condition A (i.e., if a bird experienced the *S* schedule on the left key during Condition A, then it experienced the *S* schedule on the right key during Condition B).

Each training session comprised 60 trials, 30 of each FI schedule, presented in random order. We call these trials *regular* and refer to them individually as *S* trials and *C* trials. At the beginning of each trial, the houselight was turned on and one of the keys was illuminated with the appropriate light color. The first response after the fixed interval elapsed turned the keylight and the houselight off and raised the food hopper for 3 s. During the first sessions, the hopper duration was adjusted for each bird to minimize extra-session feeding. After food there was a 30-s ITI during which all lights were turned off. Training with regular trials continued until the FI scallops were clearly established and did not change systematically across sessions. The number of training sessions ranged across birds from 40 to 44 in Condition A, and from 40 to 49 in Condition B.

2.1.3.2. Testing. Test sessions included three types of trials: regular *S* trials, regular *C* trials, and combined *C + S* trials. The combined trials began with the illumination of the *C* key, but after $T = 15, 30$ or 45 s in Condition A, or $T = 22.5, 45$ or 67.5 s in Condition B, the *S* key also was illuminated. When food became available on one key, the first peck on that key turned the houselight and the keylights off and delivered food. After food, the 30-s ITI began. Note that only one reinforcer was delivered on each trial.

The proportion of each trial type varied across three test phases. Table 1 shows the details. During Phase 1, test sessions occurred once per week and included 50 regular trials (25 *C* and 25 *S*) and 9 combined, *C + S* trials, 3 for each value of T . After each test session, the animals were exposed to five training sessions (see above). This phase continued until six test sessions were completed, yielding 18 test trials at each T value. During Phase 2, the test sessions had the same trial structure as in Phase 1, but they occurred daily. This phase lasted for 6 days, also yielding 18 test trials at each T value. Finally, during Phase 3 the test sessions occurred daily and each session included 30 regular trials (15 *C* and 15 *S*), and 27 combined *C + S* trials, 9 per value of T . This phase lasted for 12 sessions.

Table 1
Trial structure of test sessions

	Regular trials	Combined trials	Periodicity
Phase 1	25 × FI 30 s; 25 × FI 60 s	3 × T=15; 3 × T=30; 3 × T=45	Weekly
Phase 2	25 × FI 30 s; 25 × FI 60 s	3 × T=15; 3 × T=30; 3 × T=45	Daily
Phase 3	15 × FI 30 s; 15 × FI 60 s	9 × T=15; 9 × T=30; 9 × T=45	Daily

Data analyses included all six test sessions of Phases 1 and 2, and the last two sessions of Phase 3. We included only two sessions of Phases 3 to equalize the number of combined test trials across phases (18 for each T value). We chose the last sessions because a preliminary comparison between the results from the first two sessions (capturing the immediate effects of the higher density of test trials introduced in Phase 3) and the results from the last two sessions of testing (capturing steady state choice performance) revealed only small and unreliable differences between them.

2.2. Results

We divide the experimental findings into three parts. The first includes steady state performance during the combined test trials of Phase 3 and it allows us to determine whether pigeons show preference functions similar to those reported by Gibbon and Church (1981) for rats. The second includes the preference data from all three test phases and it allows us to determine if and how preference changed with testing. The third includes response rate data and it allows us to compare schedule performance when the keys were presented separately and in combination.

2.2.1. Steady state: did pigeons reproduce the results obtained by Gibbon and Church (1981) with rats?

Condition A: Preference for the C key was measured in 5-s bins by the ratio of the total number of pecks on that key to the total number of pecks on both keys, provided the latter number exceeded five. If the bird pecked less than five times on both keys, preference was undefined at that bin. Fig. 2 shows the steady state preference for the C key.

In general, all pigeons favored the key associated with the shortest delay to food, the S key when it was introduced at $T=15$ s, and the C key when the S key was introduced at $T=45$ s. Both when $T=15$ s and when $T=45$ s, decreasing and flat curves were obtained. When the S key was lit at $T=30$ s, pigeons showed initially a clear preference for the C key, but as the trial continued their preference for that key decreased. The mean curves show a clear pattern of preference, particularly at the end of the test trials: almost exclusive preference for S at $T=15$ s and for C at $T=45$ s, and about indifference between the two keys at $T=30$ s.

Condition B: Fig. 3 shows preference for the C key during the last two sessions of Phase 3. To measure preference, the trial was divided into six periods, three 7-s long, and three 8-s long. For all birds, the average preference for C increased with the moment the S key was introduced. Thus, when the S key was introduced at $T=22.5$ s all birds preferred the S key on the average, but when it was introduced at $T=67.5$ s all birds preferred the C key. When

the S key was lit at 45 s, there were no consistent findings across subjects: two birds preferred the S key (s21, s23), one bird was indifferent (s20), and four birds preferred the C key (s8, s15, s19, and s24). The shape of the curves showed substantial variation across birds: some curves were flat, others decreased, and still others were bitonic.

The bottom right panel shows averages across birds. The three preference functions are similar to those obtained in Condition A (compare with the bottom panel of Fig. 2) except that in Condition B the average preference for S at $T=22.5$ s and for C at $T=67.5$ s were less extreme than the corresponding preferences in Condition A.

These results obtained with pigeons reproduce the findings obtained with rats by Gibbon and Church (1981), but with two exceptions. First, and particularly in Condition A, pigeons showed stronger preferences than rats for the S key at $T=15$ s and for the C key at $T=45$ s. And second, whereas rats had shown roughly constant preference curves, the pigeons showed both constant preference curves and decreasing preference curves.

2.2.2. Did preference change during testing?

Condition A: The top panel in Fig. 4 shows how the average preference for the C key changed during the three test phases. For all T values, the mean data represent well the individual data. When $T=15$ s, the birds favored the S key strongly, and that preference remained strong at the steady state. To assess the statistical significance of the differences among the three curves, we performed a two-way, repeated-measures ANOVA with phase and time bin as factors. Because some pigeons did not peck a minimum of five times during the first two bins, the ANOVA included only the last four bins. The results revealed no significant differences at the 5% level, but the effect of phase approached significance—phase: $F(2, 10)=3.67, p=0.06$; time: $F(3, 15)=0.3$; phase × time: $F(6, 30)=0.6$.

When $T=30$ s, the average curves showed a clear preference for the S key during Phase 1, but this preference was reduced in Phase 2, and reversed in Phase 3. Within trials, preference for the C key decreased, most noticeably during Phases 2 and 3. A two-way, repeated-measures ANOVA yielded significant effects of phase [$F(2, 10)=7.9, p<0.01$], time [$F(5, 25)=27.5, p<0.001$], and their interaction [$F(10, 50)=4.4, p<0.001$].

When $T=45$ s, the average curves showed a slight preference for the C key during Phase 1 but a strong preference for that key during Phases 2 and 3. Moreover, preference for the C key tended to decrease with time into the trial, particularly during Phase 1. A two-way, repeated ANOVA yielded significant effects of phase [$F(2, 10)=34.1, p<0.001$], time [$F(2, 10)=16.9, p=0.001$], and their interaction [$F(4, 20)=7.62, p=0.001$].

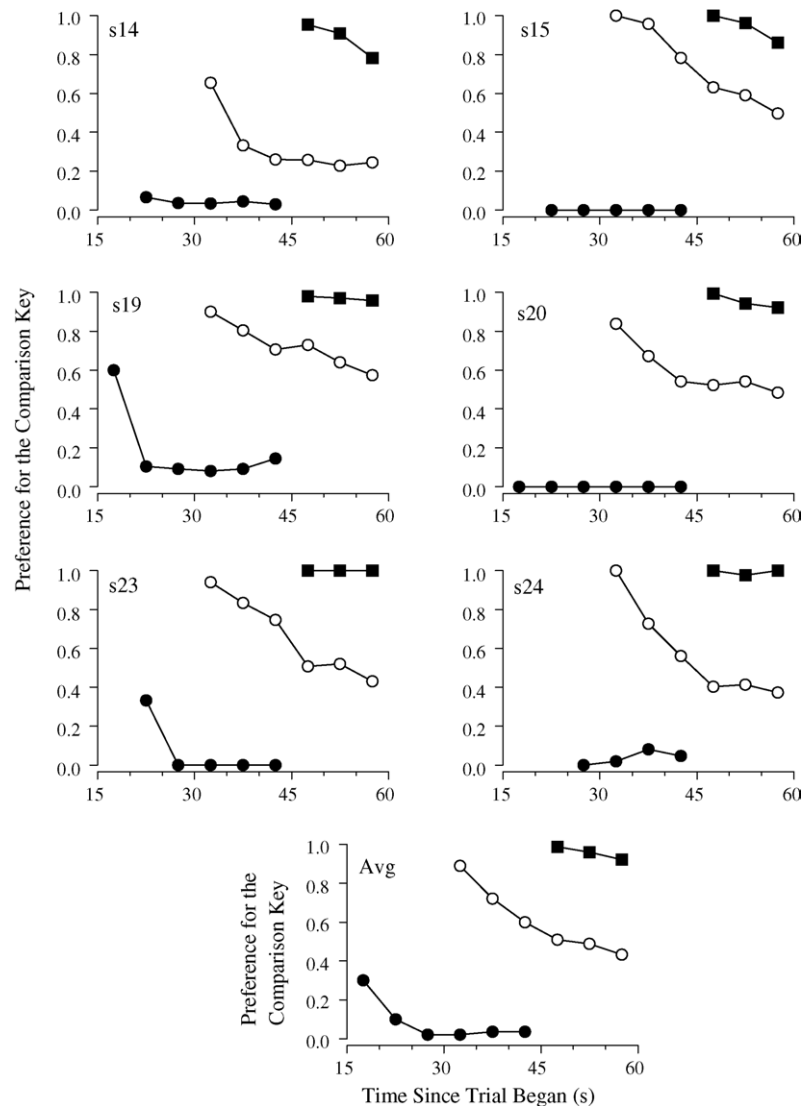


Fig. 2. Preference for the Comparison key during the last two sessions of Condition A (Phase 3, steady state). The parameter is the time the Standard key was illuminated into the trial (filled circles: $T = 15$ s; empty circles: $T = 30$ s; and squares: $T = 45$ s).

Condition B: The bottom panel in Fig. 4 shows the three preference functions during each phase of testing. The pattern of results was similar to that obtained in Condition A. Thus, in most cases the preference curves decreased with time into the trial; preference for C increased significantly from Phase 1 to Phase 3 when $T = 67.5$ s ($p = 0.02$), tended to increase with Phase when $T = 45$ s although the effect only approached statistical significance ($p = 0.065$), and did not change reliably with phase when $T = 22.5$ ($p = .4$).

In summary, when preference was measured by the relative rate of responding in successive bins, we found that preference changed systematically across phases although in different directions depending on T . At the largest T , the change was from about indifference to a strong preference for C , whereas at the intermediate T , the change was from a strong preference for S to indifference; at the smallest T , the preference for S remained strong through the end of testing. These changes show that the birds started the test trials with a strong overall bias for the S key, but at the steady state showed no overall bias for either key.

A close analysis of within-trial performance revealed that on most trials the pigeons chose one key and stayed on that key till the trial ended. In other words, they rarely switched between keys. This fact suggested a second way to measure preference. We classified each combined trial as “Standard”, “Comparison”, or “Mixed” according to the distribution of pecks *when both keys were illuminated*. A trial was classified as “Standard” if at least 80% of the total pecks were on the S key; it was classified as “Comparison” if at least 80% of the total pecks were on the C key; and it was classified as “Mixed” in all other cases. Notice that the total pecks did not include any pecks on the C key emitted before the S key was illuminated. Because most trials were either “Comparison” or “Standard” trials, “Mixed” trials were not further analyzed. In Condition A, for five birds “Mixed” trials accounted for less than 5% of all the combined trials of each phase; the exception was bird s14 for which “Mixed” trials accounted for 22, 15, and 7% of all the combined trials in Phases 1, 2 and 3, respectively. In Condition B, for six birds only 7.25% of all trials were “Mixed”. Bird s8 was the exception because

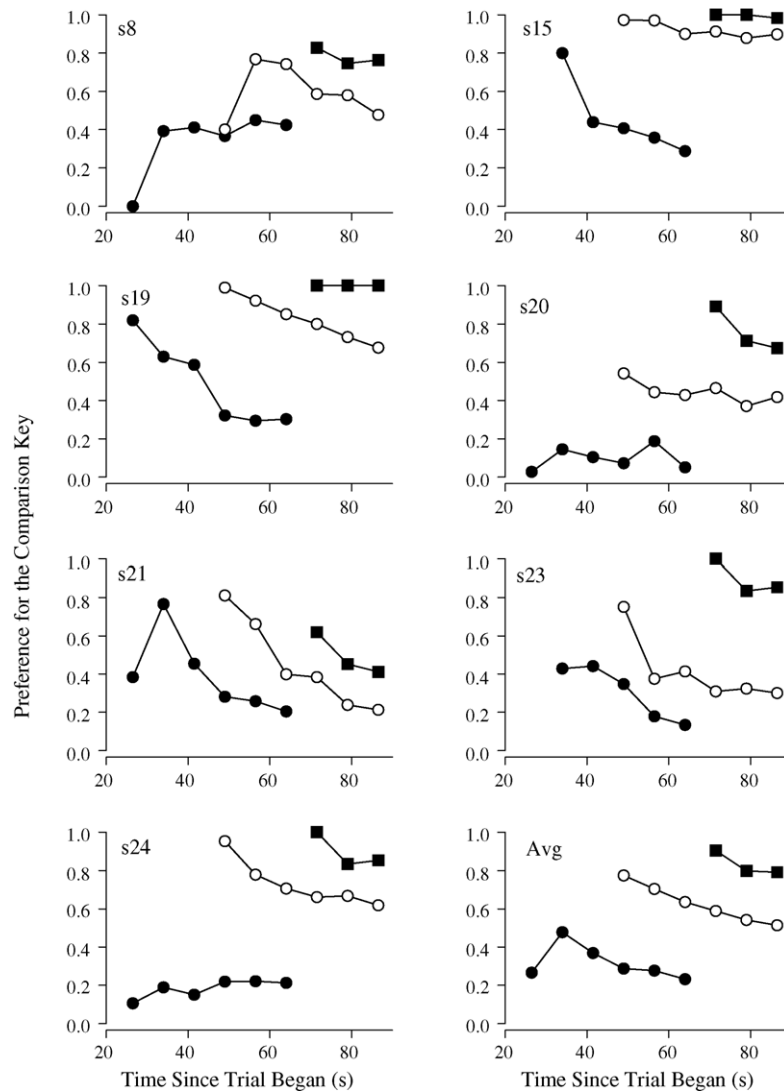


Fig. 3. Preference for the Comparison key during the last two sessions of Condition B (Phase 3, steady state). The parameter is the time the Standard key was illuminated into the trial (filled circles: $T = 22.5$ s; empty circles: $T = 45$ s; and squares: $T = 67.5$ s).

57% of its trials were “Mixed”; data from this bird were excluded from the analysis that follows.

The top panel in Fig. 5 plots the mean preference for the C key (proportion of “Comparison” trials) as a function of testing phase in Condition A. When the S key was introduced at $T = 15$ s into the trial, very few combined trials were “Comparison”, which means that the birds preferred the S key strongly. This preference remained strong across phases. When the S key was introduced at $T = 30$ s, preference for the C key was below indifference during Phase 1 (0.21), but it increased during Phases 2 and 3 to 0.30 and 0.49, respectively. Finally, when the S key was introduced at $T = 45$ s, preference was at indifference during Phase 1 (0.53), but it increased to 0.85 and 0.87 during Phases 2 and 3, respectively.

A two-way, repeated-measures ANOVA yielded a significant effect of Phase [$F(2, 10) = 8.4$, $p = 0.007$] because the overall bias for the S key was reduced across phases, a significant effect of T [$F(2, 10) = 86.1$, $p < 0.001$] because overall preference for C increased with T , and a significant effect of their interaction

[$F(4, 20) = 8.2$, $p < 0.001$] because the effect of Phase varied with T .

The bottom panel in Fig. 5 shows the data for Condition B. When the S key was introduced at $T = 22.5$ s, the birds preferred the S key strongly and their preference remained roughly constant across phases. When the S key was introduced at $T = 45$ s into the trial, average preference for C was below indifference during Phase 1, but it increased in Phases 2 and 3. Finally, when the S key was introduced at $T = 67.5$ s into the trial, preference was above indifference during Phase 1 and increased in Phases 2 and 3. A two-way, repeated-measures ANOVA with phase and T as factors yielded no effect of phase [$F(2, 10) = 1.82$, $p = .21$], a significant effect of T [$F(2, 10) = 21.75$, $p < 0.001$], and a significant interaction [$F(4, 20) = 4.64$, $p = 0.008$].

In summary, the two measures of preference, one based on the relative rate of responding and one based on the classification of combined trials, revealed the same general trend across phases. In Condition A, the birds initially prefer the S key at $T = 15$ and 30 s and are indifferent between the two keys at $T = 45$ s. This

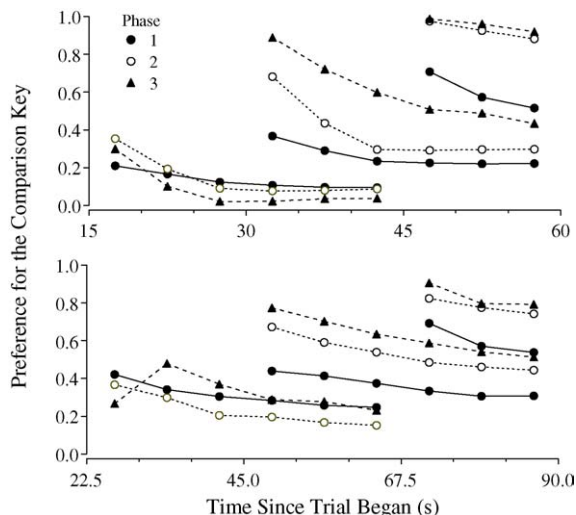


Fig. 4. Average preference for the Comparison key during the three phases. The top and bottom panels correspond to Conditions A and B, respectively. The three sets of curves correspond to the three moments the Standard key was illuminated into the trial ($T = 15, 30$ and 45 s in Condition A and $T = 22.5, 45$, and 67.5 s in Condition B).

pattern of preference changes during testing such that at the steady state the birds prefer the key associated with the shortest delay to food and are indifferent between the two keys when they signal the same delay to food. In a word, choices change during

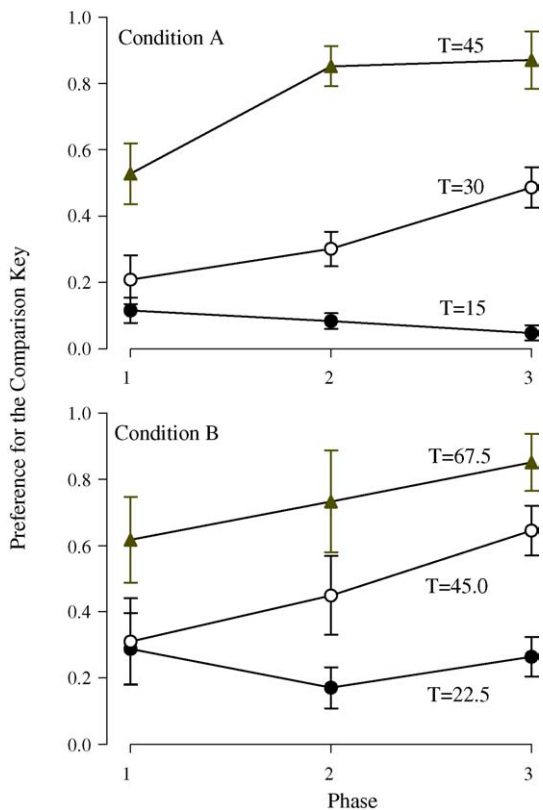


Fig. 5. Proportion of trials classified as “Comparison” (mean \pm S.E. of the mean) during the three phases of Condition A (top panel) and Condition B (bottom panel). The three curves correspond to the three moments the Standard key was illuminated into the trial.

testing from non-optimal to optimal. Condition B revealed a pattern of changes in preference similar to the pattern observed in Condition A, although with greater between-subjects variability.

2.2.3. Did schedule performance change during testing?

The stimulus conditions during combined trials (both keys on) differ from the stimulus conditions during the regular trials (only one key on). It is therefore conceivable that the response rate curves on either the *C* or *S* keys—henceforth called schedule performance—differ between combined and regular trials, and that these differences change with testing.

Condition A: To determine whether schedule performance changed during testing, we compared the rate curves from the two regular trials with the corresponding rate curves from the choice trials. Specifically, the average curve from the FI 30-s regular trials was compared with the average curves generated during choice trials when the bird chose the *S* key—the trials classified above as “Standard”. Similarly, the average curve from the FI 60-s regular trials was compared with the curves generated during choice trials when the bird chose the *C* key. Fig. 6 shows the results.

Consider the top left panel: The empty squares show the average response rate curve in Phase 1 during the trials in which only the *S* key was illuminated. This curve was obtained as follows. First, for each bird we averaged the response rate data from all *S* trials. Next, we divided each point along the individual average curve by the maximum value of that curve. This transformation forced all curves from regular *S* trials to be in the interval from 0 to 1 and facilitated the comparison of curves with different terminal rates. And finally we averaged the individual curves to obtain the group curve (the average curves represent well the individual data). As the figure shows, the average curve during the *S* trials had the typical sigmoid shape—response rate was close to zero immediately after the time marker (due to the post-time-marker pause) and increased monotonically until the end of the trial.

The remaining three curves in the top left panel show the group averages during the combined trials in which the bird preferred the *S* key. Before averaging across birds, each individual average curve was divided by the value used to normalize the curve for the regular trials (i.e., the maximum response rate value during the regular *S* trials for each bird). The three curves show that the main effect of introducing the *S* key during a test trial was to elevate response rate. The post-time-marker pause was greatly reduced (cf. the first data point of each curve) and the terminal rate increased (cf. the last data point of each curve). The shape of the three curves was similar to the right half of the regular trials curve (cf. empty squares curve from 10–15 to 30 s), which suggests that these curves may correspond to the regular curve shifted leftwards, perhaps by different amounts. We return to this suggestion below.

The top right panel shows the response rate data for Phase 3. The post-time-marker pause is again clear during the $T = 15$ and 30 s trials. However, the remaining data points still show an elevated response rate with respect to the (baseline) regular curve (compare filled and empty circles with empty squares;

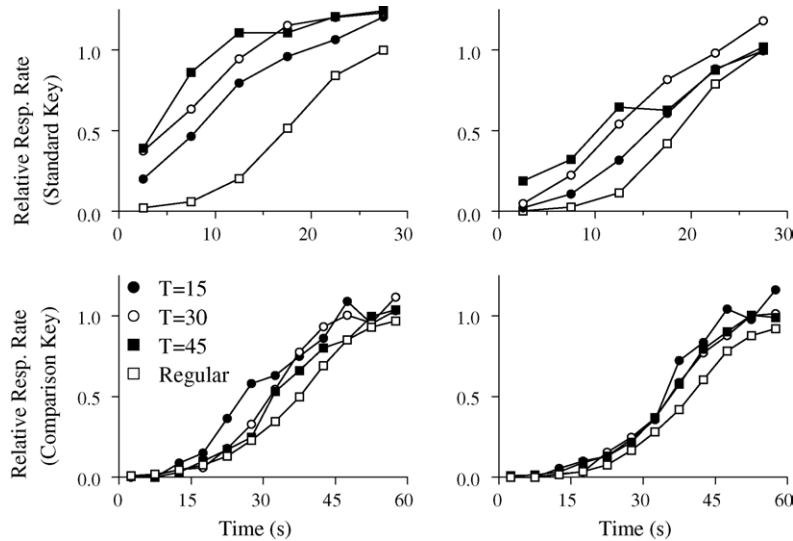


Fig. 6. Average response rate curves during the regular and combined trials of Condition A. The left and right panels correspond to Phases 1 and 3, respectively; the top and bottom panels correspond to the response rate curves on the *S* and *C* keys, respectively.

because all birds preferred strongly the *C* key when $T = 45$ s, the filled squares curve has little reliability).

The bottom panels display the corresponding data for the FI 60 s regular trials (empty squares) and for the choice trials in which the birds preferred the *C* key (remaining symbols). During both Phase 1 (left panel) and Phase 3 (right panel), when the *C* key was presented alone the birds generated the typical sigmoid response rate curve; when the two keys were presented together and the birds preferred to stay on the *C* key, response rate was slightly greater than during baseline (compare remaining symbols with empty squares). However, these slight differences in rate must be interpreted with caution for the following two reasons: (a) to assess the effect of introducing the *S* key on *C* key performance, the comparison between the baseline curve and each one of the other curves must be restricted to the moments in which both keys were present (i.e., $t > 15$ s for the filled circles,

$t > 30$ s for the empty circles, and $t > 45$ s for the filled squares) and (b) the curves for $T = 15$ s in both Phases 1 and 3 (filled circles) and the curve for $T = 30$ s in Phase 1 (empty circles) have little reliability because on those trials the birds preferred the *S* key strongly. In any event, note that the differences between the baseline and the choice curves do not change appreciably from Phase 1 to Phase 3 and are much smaller than in the top panels.

Condition B. Fig. 7 shows the rate curves for Condition B. The pattern of results was the same as in Condition A. When the *S* and *C* keys were presented alone during the regular trials, the birds generated the usual sigmoid rate curve. When the two keys were presented together and the birds chose the *S* key (top panels), the rate curves were initially elevated with respect to baseline (left panel) and the deviation from baseline increased with T . At the steady state (right panel) the deviations from baseline were reduced, particularly during the first bin, but they

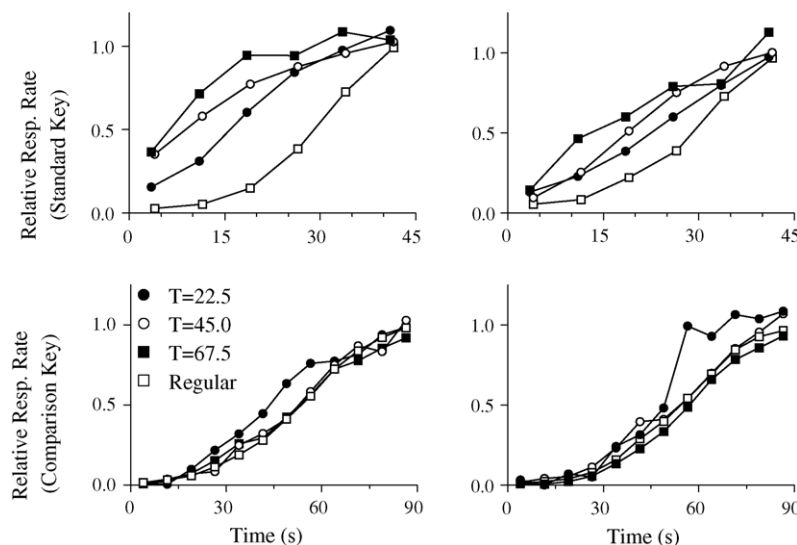


Fig. 7. Average response rate curves during the regular and combined trials of Condition B. The left and right panels correspond to Phases 1 and 3, respectively; the top and bottom panels correspond to the response rate curves on the *S* and *C* keys, respectively.

were still noticeable. When the two keys were presented together and the birds chose the *C* key (bottom panels), the rate curves for $T=45$ and 67.5 s did not change appreciably, but the curve for $T=22.5$ s was slightly above baseline. However, this last result must be interpreted with caution because the filled circles curve was based on the fewest number of trials (at $T=22.5$ s, the birds preferred strongly the *S* key).

The rate curves on Figs. 6 and 7 reproduce some, but not all, major findings reported by Gibbon and Church (1981) with rats at the steady state. According to these authors, the rat curves on the regular trials (one lever only) had the same shape than the curves on the combined trials (two levers), except that the latter had lower terminal rates. In the present experiment, although the rate curves do seem to approach comparable shapes at the steady state, the curves from the combined trials had similar or higher terminal rates than the curves from the regular trials (compare the last data point of each curve) contrary to Gibbon and Church's (1981) results.

In summary, in both conditions, when the *S* and *C* keys were presented alone, the birds showed the typical FI performance. When the two keys were presented together, response rate varied with the pigeon's choices. When the pigeon remained on the *C* key, response rate increased only slightly with respect to the baseline rate on that key. When the pigeon switched to the *S* key, response rate increased appreciably with respect to the baseline rate on that key, but that increase was attenuated during testing.

3. Discussion

In the time-left procedure pigeons behave at the steady state in the same way as rats: they prefer the key associated with the shortest delay to food. However, their preference and schedule performance changes with testing. Concerning preference, when the combined trials are first introduced after separate FI training, pigeons show an overall bias for the *S* key, although this bias is smaller the later the *S* key is illuminated. With further testing, the overall bias for *S* is greatly reduced such that at the steady state no appreciable bias for either key is visible. Thus, choices become more optimal with testing. Concerning schedule performance, initially when the birds choose the *S* key during a combined trial, they respond at a higher rate than during the regular *S* trials (assuming the comparison is done at corresponding moments since the time maker). With more testing, the rate curves during combined trials approach the rate curve during regular trials. The data also showed that within combined trials, pigeons rarely switch between the two keys.

The changes in preference observed from Phase 1 to Phase 3 are correlated with two variables, the absolute number of combined trials and the relative number of combined trials per session; both variables increased during testing (see Table 1) and in principle either one or both could drive the changes in preference. Consider the absolute number of combined trials. As that number increases, the experience with the contingencies of reinforcement and time markers operative during combined trials also increases and this increased experience may explain the changes in preference. Now consider the relative number of combined trials. As this number increases, the influence of per-

formance during combined trials on the overall reinforcement rate also increases. Sensitivity to changes in overall reinforcement rate could be the process underlying the changes in preference. Both accounts involve some form of learning, but whereas the former account stresses *within-trial learning* of reinforcement contingencies and time-markers, the latter account stresses *across-trials learning* of how changes in behavior correlate with changes in overall reinforcement rate. One account is relatively local, the other is relatively global.

Although both accounts are reasonable, the following analysis suggests that in our experiment the global account is less plausible. The overall reinforcement rate during the training sessions of Condition A was approximately 0.8 rewards per minute, a number obtained by dividing 60 rewards by the time required to obtain them, 75 min (i.e., 60 trials \times 30 s of ITI + 30 trials \times 30 s of FI 30 s + 30 trials \times 60 s of FI 60 s; we have excluded the reward duration). During testing sessions overall reinforcement would be highest if the bird chose always the key that signaled the shortest delay to food, and lowest if the bird chose always the key that signaled the longest delay to food. When combined trials were rare (Phases 1 and 2), the highest and lowest overall reinforcement rates equaled 0.78 and 0.77 rewards per minute, respectively, and when combined trials were frequent (Phase 3) the corresponding numbers equaled 0.75 and 0.71. Although we cannot rule out the effect of these differences in overall reinforcement rate, it seems to us that they are too small to account for the observed changes in preference during testing.

Be that as it may be, our main goal was to investigate if the preferences displayed during combined trials were due to the learning that took place during training (hypothesis A) or to the learning that takes place during testing (hypothesis B). Our results are inconsistent with hypothesis A. Left with hypothesis B, we can divide it into several sub-hypotheses: within-trial learning (hypothesis B1), across-trial learning (hypothesis B2), or a combination of both (hypothesis B3). Regardless of which of these sub-hypotheses turns out to be true, our results show that it is unlikely that the preferences originally observed by Gibbon and Church (1981) were due exclusively to the learning that took place during training.

Our findings have some implications for theories of timing, in particular for the dominant model in the field, scalar expectancy theory (SET). In what follows we show that SET cannot account properly for our findings, perhaps not even for the original findings reported by Gibbon and Church (1981) and which the authors claimed SET could account for. Given the shortcomings of SET, we then propose a new *descriptive* model of performance in the time-left task and fit the model to the data.

3.1. Theoretical analysis I: scalar expectancy theory

According to SET, during the combined trials the animal compares the time-left on the *C* key with the time-left on the *S* key and chooses the *C* key if the ratio between these two values is less than a bias threshold, b . Let x_C be the sample extracted from the *C* store, x_S the sample extracted from the *S* store, and x_t the number of pulses currently in the accumulator. SET assumes that the animal compares $x_C - x_t$, the time-left on the *C* key, with

$x_S - x_{t-T}$, the time-left on the S key. The probability of choosing “ C ”, $P(\text{“}C\text{”})$, at time t and when the S key is illuminated at time T , for $T < t$, equals

$$P(\text{“}C\text{”}) = P\left(\frac{x_C - x_t}{x_S - x_{t-T}} < b\right) \quad (1)$$

In SET, x_C and x_S are independent normal variates with constant coefficient of variation (i.e., $\gamma = \sigma/\mu$). Gibbon and Church (1981) show that if x_t has no variance, then Eq. (1) is equivalent to

$$P(\text{“}C\text{”}) = \Phi[z(t; T)], \quad t \geq T > T_0, \quad (2)$$

in which Φ is the unit normal distribution function and $z(t, T)$ equals

$$z(t; T) = \frac{(1-b)(t-T) + T - C + bS}{\gamma\sqrt{(C-T_0)^2 + b^2(S-T_0)^2}} \quad (3)$$

Eq. (3) has three key properties. First, it uses three parameters, the coefficient of variation γ , bias b , and the refractory period T_0 . However, when, as in the present study, T_0 is small compared to C and S , it has negligible influence and the model becomes effectively a two-parameter model. Second, the denominator in Eq. (3) is independent of t , the time into the trial. In the absence of bias (i.e., $b = 1$), also the numerator of Eq. (3) will be independent of t . In this case, $P(\text{“}C\text{”})$ will be constant throughout the trial and symmetric around indifference, as Gibbon and Church (1981) reported—see Fig. 1. And third, when there is bias, Eq. (3) predicts negative sloping preference curves when $b > 1$ (favoring C) and positive sloping preference curves when $b < 1$ (favoring S).

Eq. (3) could not fit the preference functions from conditions A or B, either Phase 1 or Phase 3. To illustrate, Fig. 8 shows the best-fitting curves to the average data from Condition A, Phase 1. To obtain the average theoretical curves we fit the individual data (thus obtaining three curves per bird) and then averaged the individual curves. (The average curves represent well the individual curves.) The severe misfits stem mainly from the fact that the birds showed a strong overall bias for S , which forces $b < 1$ in Eq. (3), but also downward sloping curves, which is incompatible with $b < 1$. The misfit identifies a structural limitation of the model.

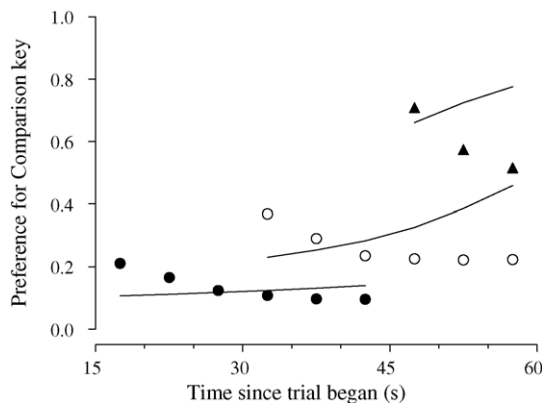


Fig. 8. Best fit of scalar expectancy theory (SET). The symbols show the average data from Condition A, Phase 1. The lines show the average of SET's best-fitting curves (Eq. (3)) of the individual data.

On a more conceptual level, SET's assumptions for the time-left task seem contradictory. On the one hand, Eq. (3) and the reasoning that led to it (see also the Appendix A in Gibbon and Church, 1981) suggest that the animal is sampling its memories as the trial proceeds and choosing according to the results of the sampling. But this interpretation predicts a large proportion of “Mixed” trials, in clear contrast with the data. To illustrate, suppose that the animal's memories are such that sampling from them yields always a 0.5 probability of choosing the C key, as in Fig. 1, $T = 30$ s condition. Because overall response rate is reasonably high, often more than one peck per second, one would expect frequent switching between keys and therefore a high frequency of “Mixed” trials (e.g., if a bird chooses the C key with probability 0.5 and makes 10 choices, the probability of no switching is less than 0.002). However, the majority of the birds rarely switched between keys and most trials were either “Comparison” or “Standard”. On the other hand, one could conceive of the animal as deciding only once whether to stay on the C key or switch to the S key. Having made its decision according to Eq. (3), the animal would then simply stay on the chosen key until the end of the trial. In this view the animal samples its memories only once per trial and all trials are either “Standard” or “Comparison”. The problem with this interpretation is twofold. First, when there is bias (i.e., $b \neq 1$) Eq. (3) predicts an increasing ($b < 1$) or decreasing ($b > 1$) preference function, which means that to apply the equation to a particular data set one would need to know also the time of the bird's decision, for that time will determine the probability of staying on C or switching to S . The model provides no such information. Second, and more generally, if Eq. (3) applies only once per trial, then it ceases to define preference functions measured by the ratio of pecks on the two keys. Some other equation or equations must specify the rates of pecking the two keys and without these equations the preference functions cannot be determined. Gibbon and Church (1981) were not clear on this issue: They seemed to have in mind the second alternative when deriving Eq. (3), but the first alternative when applying Eq. (3) to the preference functions illustrated in Fig. 1. Given SET's failure to account for the data, we propose a new descriptive model of performance in the time-left task.

3.2. Theoretical analysis II: a descriptive model of performance

An alternative description of performance in the time-left procedure starts with the distinction between choice and schedule performance. When the pigeon sees the two keys illuminated simultaneously during the combined trials, it chooses according to some probability value p whether to stay on C or switch to S . Having made its choice, the bird then responds on the chosen key according to another process. These two processes, one yielding p the other yielding response rate, are sensitive to the moment the S key is illuminated, that is, they are influenced by the time since the onset of the trial. For example, p differs if the S key is illuminated close to the beginning or close to the end of the trial (cf. Fig. 5) and the same happens to response rate immediately after the two keys are illuminated (cf. Figs. 6 and 7, first bin of

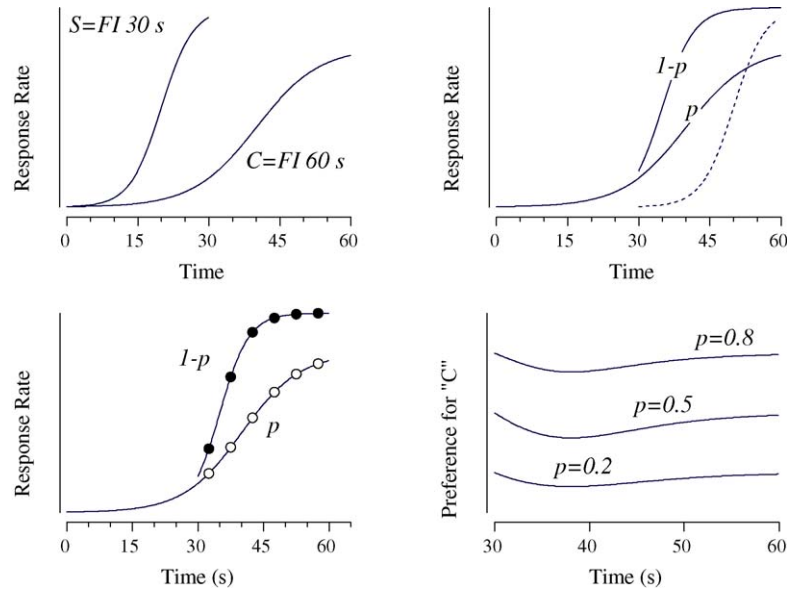


Fig. 9. Structure of the new descriptive model of performance in the time-left procedure. Top left panel: response rate curves during the S and C regular trials. Top right panel: when the S key is illuminated at $T=30$ s, the bird switches to the S key with probability $1-p$ and stays on the C key with probability p . If the bird switches, then it pecks on the S key according to the original response rate function (dotted line) shifted left by s seconds (solid line starting at 30 s). Bottom left: the symbols show how the preference function predicted by the model is computed. Preference for C at time t equals relative response rate at that time (i.e., rate on C key divided by the sum of the rates on the C and S keys) but with each rate weighed by p or $1-p$. Bottom right: depending on p , the model predicts different preference functions for C .

response rate curves in top left panel). In addition they *change with testing* such that p in the middle or at the end of the trial increases with testing (see Fig. 5, Phases 2 and 3) and response rate on the S key decreases with testing (cf. Figs. 6 and 7, top left versus top right panels).

Fig. 9 illustrates the model. Assume that the birds learned to respond on the two separate FI schedules and that their performance is well represented by the curves in the top left panel. The two curves in the figure are logistic functions but only their sigmoid shape matters—they could be cumulative normal distributions or even more complex functions such as those assumed by Machado's (1997) learning-to-time model. They are characterized by three parameters each, the asymptotic response rate parameter, A_S or A_C , the location parameter, m_S or m_C , and the scale parameter, λ_S or λ_C . Their equations are

$$R_C(t) = \frac{A_C}{1 + \exp[-\lambda_C(t - m_C)]} \quad (4)$$

and

$$R_S(t) = \frac{A_S}{1 + \exp[-\lambda_S(t - m_S)]} \quad (5)$$

for the C and S keys, respectively. When the S key is illuminated at, say, $T=30$ s, the bird stays on the C key with probability p , and switches to the S key with probability $1-p$ (see top right panel). If the bird stays on C , then it ignores the S key and continues to behave as if the trial were a regular C trial—hence the similarity between the curve from the regular C trials on the one hand and the curves from the combined trials classified as “Comparison” on the other hand (see bottom panels of Figs. 6 and 7). But if the bird switches to S , then it changes its behavior with respect to the regular S trials. Instead of responding as if a regular trial

had just started with the illumination of the S key (in which case it would produce the dotted line in top right panel), the bird responds according to the regular curve shifted to the left (the solid curve in the middle of the figure). The equation for the rate curve shifted s seconds to the left when the S key is introduced at T s into the trial is

$$R_S(t - T - s) = \frac{A_S}{1 + \exp[-\lambda_S(t - T - m_S - s)]} \quad (6)$$

One reason for the leftward shift may be that the time marker for the 30-s interval on the combined trials (i.e., the illumination of the S key when both the C keylight and houselight are illuminated) differs from the time marker on the regular S trials (ITI darkness followed by illumination of S key only). Stimulus generalization decrement is expected to reduce the post-time-marker pause or, in other words, to elevate response rate (Staddon, 1969). As testing proceeds, the birds learn about the new time marker and therefore reduce response rate at the onset of the interval—the post-time-marker pause returns (compare the left and right top panels in Figs. 6 and 7).

On the basis of the probability of staying on the C key and the two response rate curves (one for C and one, shifted, for S), the model predicts a specific preference function. Assume the S key is illuminated at $T=30$ s and consider the first time bin, from 30 to 35 s: on a proportion p of the trials, the pigeon stays on C and responds at the rate x given by the first empty circle in the bottom left panel of Fig. 9; on a proportion $1-p$ of those trials, the pigeon switches to S and responds at the rate y given by the first filled circle. Therefore, the preference function at that bin will equal $px/(px + (1-p)y)$. More generally, the preference function at time t given that key S was illuminated at T s is given

Table 2
Equation and parameters used to fit each data set

Data set	Equation	Parameters
Curve for <i>C</i> regular trials	4	A_C, m_C, λ_C
Curve for <i>S</i> regular trials	5	A_S, m_S, λ_S
Curve for “Standard” combined trials, $T = 15$ s	6	A_S, m_S, λ_S, s_1
Curve for “Standard” combined trials, $T = 30$ s	6	A_S, m_S, λ_S, s_2
Curve for “Standard” combined trials, $T = 45$ s	6	A_S, m_S, λ_S, s_3
Preference curve, $T = 15$ s	7	$A_C, m_C, \lambda_C, A_S, m_S, \lambda_S, s_1, p_1$
Preference curve, $T = 30$ s	7	$A_C, m_C, \lambda_C, A_S, m_S, \lambda_S, s_2, p_2$
Preference curve, $T = 45$ s	7	$A_C, m_C, \lambda_C, A_S, m_S, \lambda_S, s_3, p_3$

by

$$P(C'') = \frac{p \times R_C(t)}{p \times R_C(t) + (1 - p) \times R_S(t - T - s)} \quad (7)$$

The bottom right panel illustrates three preference functions, each corresponding to a different value of p . Note that if one ignores the few combined trials classified as “Mixed” in the experimental data, then the estimated probabilities p and $1 - p$ should match the proportions of trials classified as “Comparison” and “Standard”, respectively.

In summary, to fit the two response rate curves from the *C* and *S* regular trials, we use Eqs. (4) and (5); to fit the three rate curves corresponding to the three moments the *S* key is illuminated and the bird switches to *S*, we use Eq. (6) but we allow the shift parameter s to vary across curves. Finally, to fit the three preference curves corresponding to the three values of T , we use Eq. (7) but we allow the p parameter to vary across curves. The model uses twelve parameters to fit eight distinctive curves simultaneously, but note that the three rate curves for the combined trials must each be fit with only one extra parameter, s ,

and similarly, the three preference curves must each be fit with only one extra parameter, p . Table 2 shows the equations and parameters used to fit each data set.

To test the model, we fit the equations simultaneously. Using Mathcad®, we searched for the set of twelve parameters that minimized the sum of squared deviations between observed and predicted values. To give similar weights to the rate and preference data, the latter were multiplied by 10 to bring them to approximately the same scale range as the rate curves.

Table 3 shows the best-fitting parameters and the variance accounted for (VAC). From the best-fitting individual curves we computed the average rate and preference curves and then compared them with the average data. Fig. 10 shows the results for Condition A, Phase 1 (top) and Phase 3 (bottom). In general the model fitted the data well (average VAC equaled 0.98 in Phase 1 and 0.97 in Phase 3). In particular, the curve for the regular *S* trials when simply shifted was able to fit the data from the “Standard” combined trials. In addition, a weighted ratio of the regular *C* curve and the curve from the “Standard” combined trials was able to fit the preference data. The Appendix shows how the model fit the individual data.

Fig. 11 shows the corresponding results for Condition B (the parameter values for each bird during Condition B are not shown because they were similar to those for Condition A; the average VAC equaled 0.97 both in Phases 1 and 3). Again the model fitted the data well.

In summary, the model captured the major properties of the data: the elevated response rate on the *S* key during the combined trials of Phase 1, but its return to baseline during Phase 3; the overall preference for the *S* key during Phase 1, but its reduction during Phase 3; the within-trial decrease in preference for *C*; and the less extreme preferences in Condition B when compared with Condition A.

The model assumes that during a combined trial the pigeon chooses one key and then responds on that key until the end of the trial. Specifically, the animal stays on *C* with probability p and switches to *S* with probability $1 - p$. It follows that according

Table 3
Best-fitting parameters and variance accounted for by the model during Condition A

	A_S	λ_S	m_S	A_C	λ_C	m_C	p_1	p_2	p_3	s_1	s_2	s_3	VAC
Phase 1													
s14	152.7	0.19	21.7	100.0	0.11	38.0	0.35	0.45	0.35	6.6	20.4	32.0	0.995
s15	127.2	0.48	17.4	113.3	0.16	42.7	0.03	0.12	0.63	6.6	21.8	32.1	0.994
s19	104.4	0.19	23.5	105.6	0.13	36.4	0.37	0.27	0.64	3.0	11.9	27.3	0.973
s20	67.2	0.21	15.1	78.0	0.14	27.4	0.01	0.04	0.53	10.9	17.9	31.1	0.979
s23	97.2	0.24	20.8	82.8	0.12	39.1	0.15	0.25	0.39	4.5	17.0	27.3	0.981
s24	84.7	0.34	16.7	157.6	0.07	53.1	0.40	0.57	0.64	7.6	18.0	33.6	0.968
Avg	105.6	0.27	19.2	106.2	0.12	39.4	0.22	0.28	0.53	6.5	17.8	30.6	0.982
Phase 3													
s14	130.8	0.22	17.8	87.6	0.08	43.2	0.06	0.43	0.75	14.6	23.1	41.7	0.982
s15	223.2	0.23	21.9	97.2	0.14	48.6	0.00	0.73	0.81	15.6	30.1	40.7	0.969
s19	92.8	0.36	20.3	91.8	0.17	34.4	0.19	0.67	0.96	8.6	18.7	32.3	0.888
s20	86.4	0.29	17.0	87.6	0.20	29.8	0.00	0.50	1.00	11.1	21.9		0.986
s23	54.0	0.58	18.3	90.0	0.21	41.1	0.06	0.37	1.00	13.3	26.3		0.981
s24	91.2	0.28	20.4	114.0	0.11	48.0	0.01	0.38	1.00	12.4	27.4		0.987
Avg	113.1	0.33	19.3	94.7	0.15	40.9	0.05	0.51	0.92	12.6	24.6	38.2	0.965

Missing s_3 values in Phase 3 occur when the animal did not choose the *S* key when $T = 45$ s.

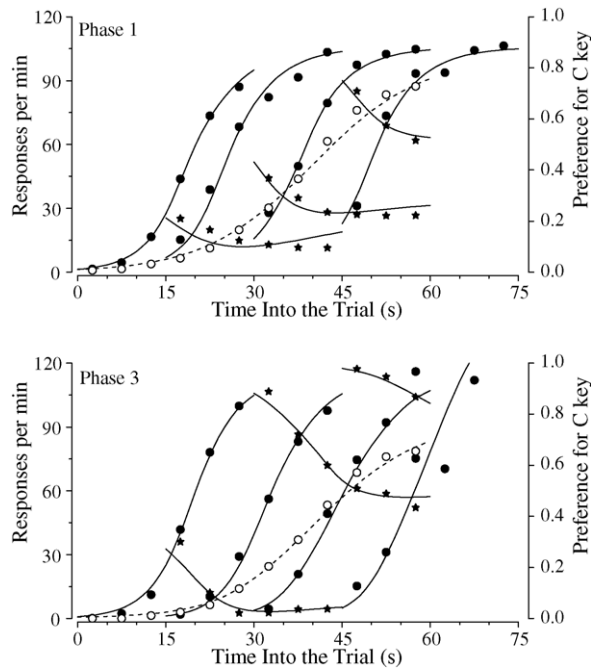


Fig. 10. Average data and model predictions for Condition A, Phase 1 (top) and Phase 3 (bottom). The response rate curves (left-hand Y axis) correspond to the average rate on the C key during regular trials (empty circles) and to the rate on the S key during (see filled circles from left to right) regular trials, combined trials with $T=15$ s, combined trials with $T=30$ s, and combined trials with $T=45$ s. The three preference curves (stars, right-hand Y axis) correspond to the three moments the S key was illuminated.

to the model each combined trial will be either a “Comparison” or a “Standard” trial and that the overall proportion of “Comparison” trials will equal p . This reasoning suggests that we use the observed proportion of “Comparison” trials to check the

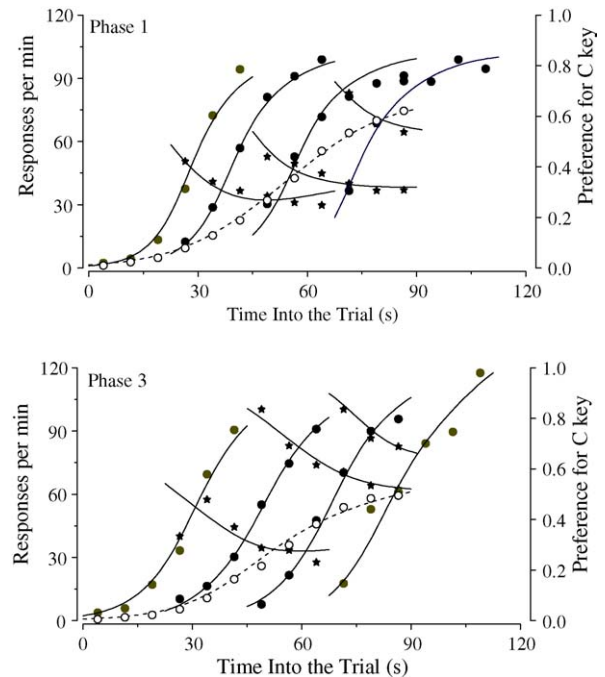


Fig. 11. Average data and model predictions for Condition B, Phase 1 (top) and Phase 3 (bottom). The response rate curves (left-hand Y axis) correspond to the average rate on the C key during regular trials (empty circles) and to the rate on the S key during (filled circles from left to right) regular trials and combined trials with $T=22.5$ s, combined trials with $T=45$ s, and combined trials with $T=67.5$ s. The three preference curves (stars, right-hand Y axis) correspond to the three moments the S key was illuminated.

probabilities estimated by fitting the preference functions. Ideally, these two sets of values should match. Fig. 12 plots the “observed p ” against the “estimated p ” for Conditions A and B, Phases 1 and 3.

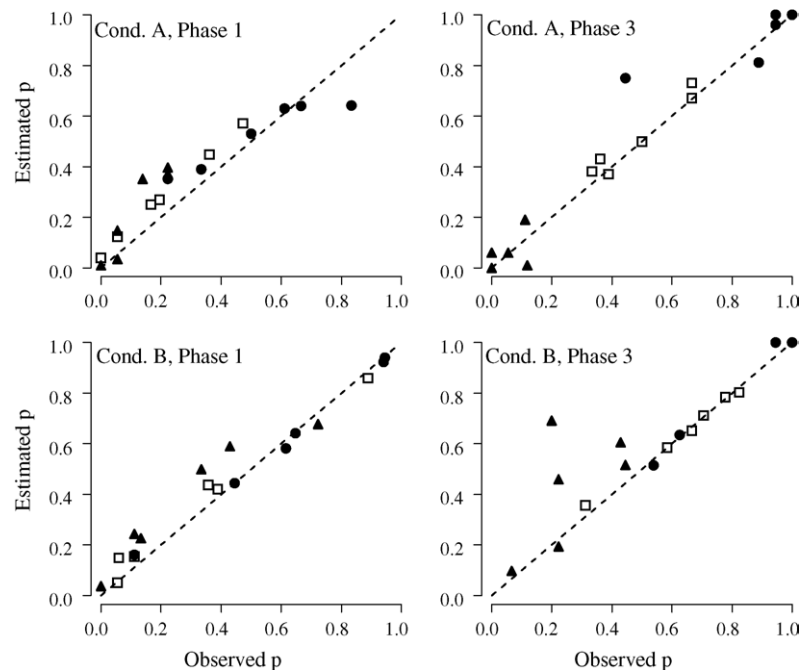


Fig. 12. The graphs plot the estimated individual p values against the obtained individual p values in Phases 1 and 3 of Conditions A and B. The obtained p values correspond to the proportion of trials classified as “Comparison”. The three symbols correspond to the three moments the S key was introduced into the combined trials (triangles: early; squares: middle; and circles: late).

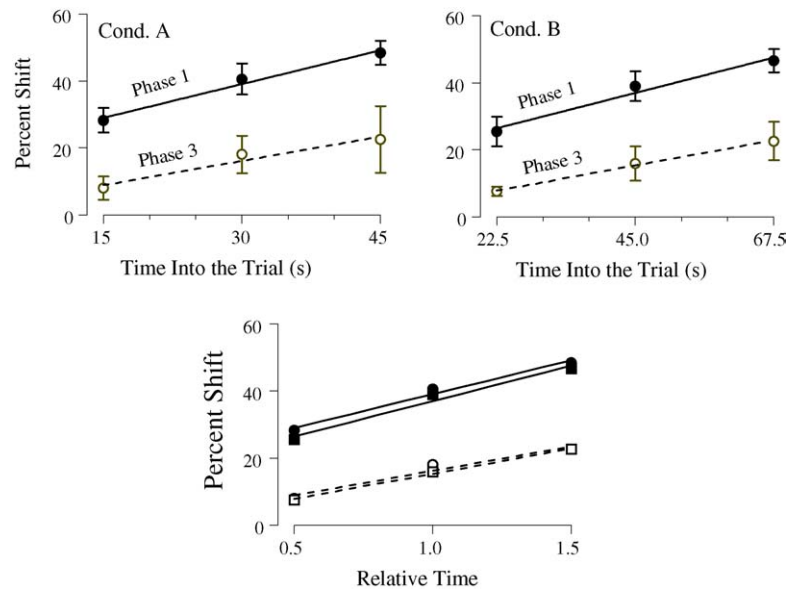


Fig. 13. Top panels: Average horizontal shift of the response rate functions for the *S* key (parameter *s*) plotted against the moment the *S* key was illuminated during combined trials, *T*. The shift is expressed as a percentage of the standard FI schedule (30 s in Condition A, 45 s in Condition B). The bars show the standard error of the mean. The lines are best-fitting regression lines. The bottom panel plots the same data against the time the *S* key was illuminated relative to the Standard FI schedule.

In Phase 3, the data sets match reasonably well. With one exception, the deviations were relatively small and unsystematic. In Phase 1 there is some indication of systematic deviations, particularly in Condition A (top left panel) because the observed p_1 values, and to a less extent the observed p_2 values, tended to be smaller than their estimated counterparts. In any event, this consistency check with parameter *p* shows that the model captured the main features of the birds' performance.

3.3. What needs to be explained?

A good descriptive model identifies the features of the data that need explaining. In the present case these features are (a) the variation of parameters *s* and *p* with the moment the *S* key is illuminated, *T*, and (b) the changes in these parameters from Phase 1 to Phase 3. Consider the shift parameter first. Fig. 13 (top) shows the estimated parameters in Conditions A and B as a function of *T*. The shifts are expressed as a percentage of the FI schedule associated with the *S* key. Clearly, the later the *S* key was illuminated the greater the mean shift of the rate curve. In addition, the magnitude of the shift was considerably reduced from Phase 1 to Phase 3, an effect obtained for *all* birds.

Two other features of the shift data are noteworthy. First, the average data from Conditions A and B superpose when the shifts are plotted against the time the *S* key was illuminated, but with both variables expressed as a percentage of the Standard FI schedule (see bottom panel). Second, at least within the examined range, the average shifts increase linearly with the time the *S* key was illuminated.

What explains the variations in the shift parameter? As suggested above, the decrease in the shifts from Phase 1 to Phase 3 may be due largely to the learning of the new time marker, for whereas during the regular trials the *S* key was illuminated at

the end of the ITI, during combined trials the *S* key was illuminated when both the houselight and the *C* keylight were turned on. To put it differently, the rate curve shifts in Phase 1 because of generalization decrement, but the shift is reduced with testing because the pigeon learns the new time marker. However,

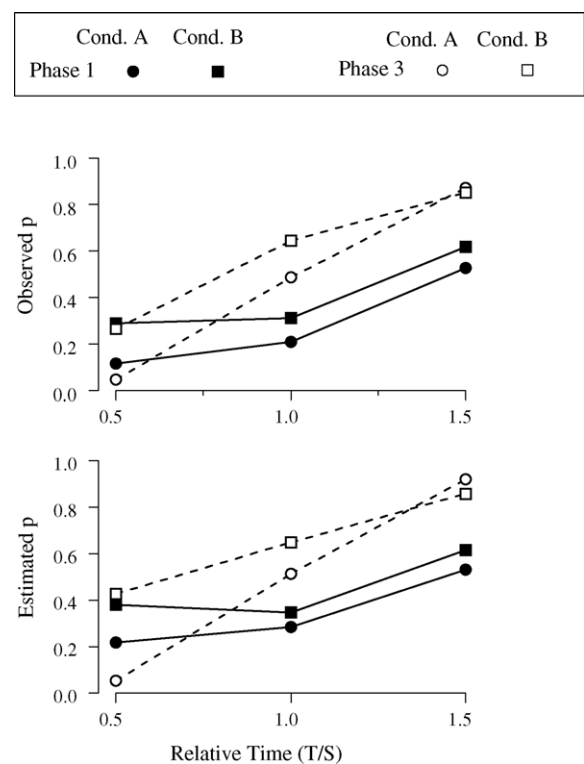


Fig. 14. Average of the observed (top) and estimated (bottom) *p* values as a function of relative time the *S* key was illuminated during combined trials. The parameters are Condition A or B and Phase 1 or 3.

something else must influence the shift because the shift varied also with the moment the *S* key was illuminated, *T*. We hypothesize that the animal, metaphorically speaking, carries over to the *S* key a fraction of its ongoing timing of the *C* key. In other words, the internal clock may be incompletely reset when the animal switches to key *S*. This confusion-like effect could explain why the shift varies with *T*.

Consider now the other parameter, *p*, the probability of staying on key *C*. As Fig. 14 shows, *p* also changed across phases and with *T*. The top and bottom panels plot, respectively, the observed and the estimated *p* against the relative time the *S* key was illuminated. The two conditions yielded the same general trend: *p* increased with relative time in both phases (effect of *T/S*), apparently in a nonlinear way during Phase 1 and in a linear way during Phase 3.

The changes in *p* from Phase 1 to Phase 3, namely, an increment when *T/S* = 1.0 and 1.5 and either no change or a decrement when *T/S* = 0.5, suggest a learning effect. Perhaps the learning of the new time markers not only reduces the shifts in the rate curves mentioned above, but also changes the *p* values. Consider the case *T/S* = 1.5 (rightmost data point of each curve). Initially, the birds are approximately indifferent between the two keys, which means that on half of the trials they choose *C* and obtain a reward 15 s after the *new* time marker, whereas on the other half of the trials they choose *S* and obtain a reward 30 s after the *new* time marker. As the pigeons experience the test trials, they

learn about the new time marker and change their choice from indifference to a strong preference for *C*. A similar reasoning applied to the case *T/S* = 0.5 predicts that, at the steady state, the birds will prefer the *S* key strongly. Perhaps due to generalization from both sides of the Relative Time dimension, the preference at *T/S* = 1.0 approaches 0.5. Hence, the increasing line relating *p* to *T/S* at the steady state.

The foregoing qualitative account of the effects of testing may explain why *p* changes with Phase and why it varies linearly with *T/S* at the steady state, but it does not explain why *p* varies (nonlinearly) with *T/S* during Phase 1. Why, in other words, do birds prefer *S* when *T/S* = 0.5 and 1.0 but are indifferent when *T/S* = 1.5 during Phase 1? We have no principled answer, only a partial hypothesis. Perhaps, as Staddon and Higa (1999, p. 221) suggested, the initial *p* depends on the relative value of the two stimuli, with value given by the reciprocal of the delay to food, $1/(60 - T)$ for *C* and $1/30$ for *S*. This hypothesis predicts a hyperbolic relation between *p* and *T*, which is qualitatively, but not quantitatively, consistent with our findings. It remains to be seen whether a more complex hyperbolic-like function of value explains how and why *p* varies with *T* during Phase 1. In any event, one would still be lacking an account of how that hyperbolic-like function changes with testing into a linear function.

In conclusion, the present empirical findings and theoretical analyses suggest that in the time-left procedure one must

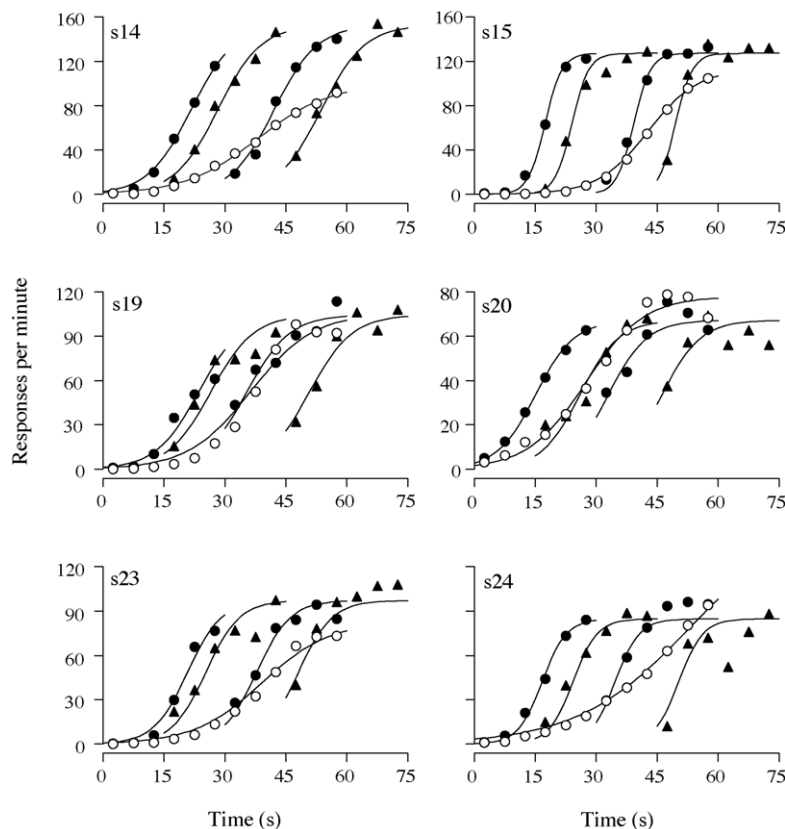


Fig. 15. Individual response rate data from Condition A, Phase 1 and the model's best-fitting curves. The filled symbols represent response rate on the *S* key; from left to right they correspond to the regular *S* trials and the *T* = 15, 30 and 45 s "Standard" trials. The empty circles show the rate on the *C* key. The lines show the model fits.

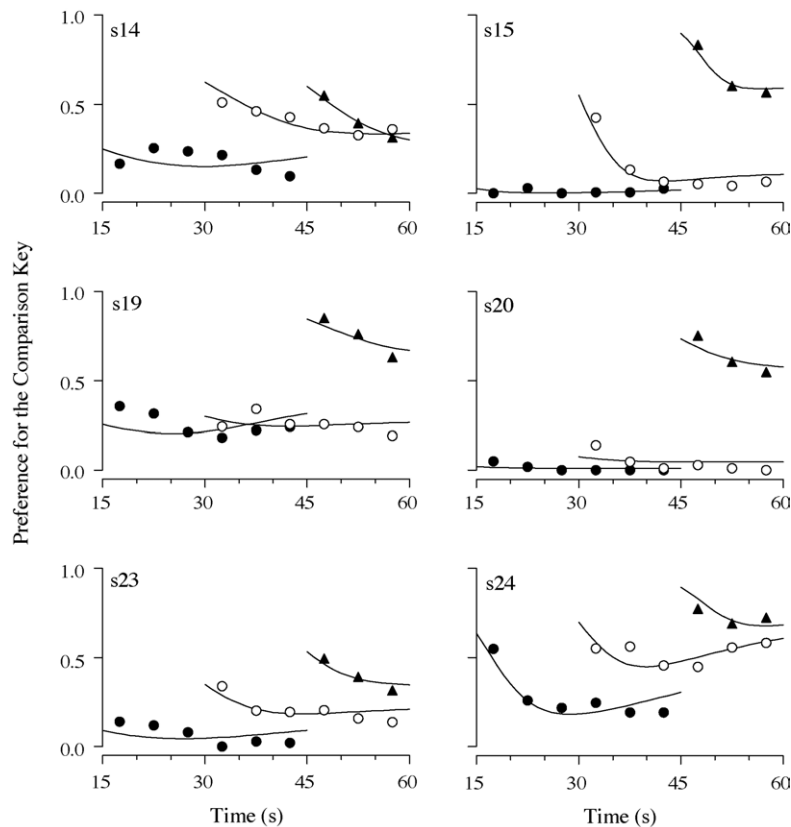


Fig. 16. Individual preference data from Condition A, Phase 1 and the model's best-fitting curves. The parameter is the time the *S* key was illuminated during combined trials (filled circles: $T = 15$ s; empty circles: $T = 30$ s; and triangles: $T = 45$ s). The symbols show the average data and the lines show the best-fitting curves.

distinguish choice processes, which yield preference for *C* or *S*, from response rate processes, which yield schedule performance on *C* or *S*. Having distinguished these processes, one must then explain how they are affected by the *separate* FI training (to account for Phase 1 data) and how they change with *combined* FI testing (to account for the trajectory from Phase 1 to Phase 3). The descriptive model presented above may help us reach these goals.

Acknowledgements

Research supported by a grant from the Portuguese Foundation for Science and Technology to the first author. Please address correspondence to Armando Machado, Instituto de Educação e Psicologia, Universidade do Minho, 4710 Braga, Portugal. E-mail: armandom@iep.uminho.pt. The second author is now at Purdue University

Appendix A

See Figs. 15 and 16.

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