



# Prospective timing in pigeons: Isolating temporal perception in the time-left procedure

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## ABSTRACT

In the time-left procedure, a task used to study prospective timing, animals choose between two stimuli that signal different delays to reinforcement. Trials begin with one stimulus signaling  $C$  seconds to reinforcement and, at different moments since its onset, another stimulus, signaling  $S$  seconds to reinforcement, with  $C > S$ , is introduced. Optimal performance consists in choosing the stimulus signaling the shorter time to reinforcement. Animals have been found to perform in this optimal way. However, this procedure is complex and variables other than time may be responsible for the results. In two experiments with pigeons we sought to improve the time-left procedure to better isolate the effect of time in the animals' behavior. We attempted to control for two confounding variables, the asymmetry in the time markers from training to testing and the cost of switching between the two response alternatives. We conclude that in the time-left task pigeons seem indeed to regulate their behavior based on time because, with our improved procedure, they still chose the stimulus associated with the shorter time to food. However, our version of the procedure created new interpretative difficulties, strengthening the idea that the time-left procedure may be too complex to study timing.

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## 1. Introduction

Our understanding of the temporal regulation of behavior in animals and humans has made substantial progress during the last decades. Researchers have developed a variety of procedures for studying timing and have obtained robust findings with them. A case in point is the time-left procedure, a prospective timing task developed by Gibbon and Church (1981).

In this procedure animals are required to judge, from moment to moment, which of two response options will yield food in the shorter amount of time. At the start of each trial, one option is likely to yield food sooner than the other, but as the trial continues, the time considerations shift in favor of the other option (see also Gallistel, 1990; Shettleworth, 1998).

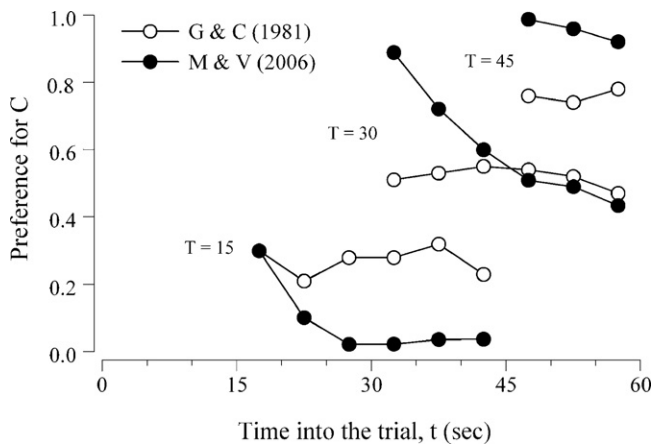
More specifically, animals choose between two stimuli that signal different delays to reinforcement, a *standard* ( $S$ ) stimulus associated with a fixed-interval (FI) schedule and a *comparison* stimulus ( $C$ ) associated with a longer FI schedule. A trial always starts with  $C$  and then, at a certain time  $T$  into the trial,  $S$  also is introduced. From then on, the animals can choose between the two alternatives. In the original procedure (Gibbon and Church, 1981; Experiment 1), rats chose between a FI 30 s ( $S$  = left lever) and a FI

60 s ( $C$  = right lever) and  $T$  could equal 15 s, 30 s or 45 s. The crucial question is how preference varies with  $T$ . If  $S$  is introduced at  $T$  seconds, then to minimize time to food the animal should choose  $C$  whenever  $C - T < S$ , i.e.,  $60 - T < 30$  or  $T > 30$ ; and it should choose  $S$  whenever  $C - T > S$ , i.e.,  $60 - T > 30$  or  $T < 30$ .

The aim of Gibbon and Church (1981) in developing the time-left procedure was to determine if the subjective time scale was linear or logarithmic. Consider the test when  $T = 30$  s. If the time scale is logarithmic, the subjective magnitude of the time-left to food signaled by  $C$  should be smaller than the subjective magnitude signaled by  $S$  (in a logarithmic scale, the subjective magnitude of the second 30-s interval, i.e., from 30 s to 60 s, is smaller than the subjective magnitude of the first 30-s interval, from 0 s to 30 s); therefore the animal should favor  $C$ . However, if the time scale is linear, the subjective magnitude of the time-left to food signaled by  $C$  should be equal to the subjective magnitude signaled by  $S$  and therefore the animal should be indifferent between the two levers. The results, displayed in Fig. 1, were consistent with a linear subjective time scale, for the rats were indifferent between the two levers at  $T = 30$  s and strongly preferred  $S$  at  $T = 15$  s but  $C$  at  $T = 45$  s.

Machado and Vasconcelos (2006) replicated with pigeons the foregoing experiment. As can be seen in Fig. 1, they obtained roughly the same results, with two differences. First, pigeons showed stronger preferences than rats, for  $S$  when  $T = 15$  s and for  $C$  when  $T = 45$  s. Second, the pigeons' preference curves decreased whereas the rats' preference curves remained relatively constant. Although the steady state results were mostly the same, Machado

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**Fig. 1.** Proportion of responses on the C stimulus as a function of time since the trial began. The parameter is the time of entry of the S stimulus. The empty circles show Gibbon and Church' (1981; Experiment 1) results and the filled circles Machado and Vasconcelos' (2006, Experiment 1) results.

and Vasconcelos (2006) found that the pigeons' performance changed during testing, evolving from the first to the last test sessions from non-optimal to optimal in terms of minimizing the time to reinforcement. In contrast with Gibbon and Church's account (1981), Machado and Vasconcelos (2006) showed that performance during testing is not due exclusively to the previous training with separate FIs, but requires the animals to experience the contingencies of the test trials.

The time-left procedure is complex and the relationships inherent in it are not yet fully understood (Preston, 1994; Cerutti and Staddon, 2004). Part of the complexity is methodological, for some variables may be confounded with temporal discrimination. First, the time marker for the S interval changes from training to testing. To see this consider that, during training, each FI trial starts with the illumination of the houselight and one of the two keylights, C or S, following a dark intertrial interval (ITI). Hence, the time marker for the two intervals is a salient event. In contrast, during testing, the time marker for the C interval remains the same, but the time marker for the S interval changes because, when the S key is introduced into the trial, the chamber is already illuminated by the houselight and the C key. Hence, the time marker for the S key is less salient during testing. If time markers inhibit responding, this asymmetry in salience may explain the fact that, in Machado and Vasconcelos' (2006) study, the preference for S was higher at the beginning than at the end of testing. The reduced salience of the time marker for S during testing may have disinhibited responding to this stimulus (Staddon and Innis, 1969); the pigeons would then relearn the time markers during testing.

Second, during test trials, behavioral momentum (Nevin, 2002) may reduce the likelihood that the animals will switch from one key to the other. In fact, Machado and Vasconcelos (2006) reported that on most test trials, with both keys available, the pigeons chose one key and stayed on that key till the trial ended. When the S key is introduced, the pigeon may be orienting, approaching or even pecking the C key. Because the pigeon may not be equidistant from the two keys and may actually already be pecking at the C key – conditions more likely to hold when  $T = 45$  s than when  $T = 15$  s – changing over to the S key may be more costly than staying at the C key; hence, the observed greater bias towards C at  $T = 45$  s than at  $T = 15$  s. In summary, differences in time markers and potential costs of switching may obscure the effects of temporal discrimination.

The goal of the present study was to better isolate the effect of temporal perception in the time-left procedure by controlling for some methodological variables that may be confounded with

this effect. To conclude that, in the time-left procedure, animals are regulating their behavior based on the signaled delays to food, we need to control for these non-temporal variables.

Although not a central question in the current study, we also return to the original goal of the time-left experiment and evaluate the nature of the subjective time scale, linear versus logarithmic.

## 2. Experiment 1

In the present experiment we attempted to overcome the two foregoing problems. First, we reduced the asymmetry in the salience of the time markers during training and testing. Specifically, during the ITI the houselight remained illuminated. This way, the time marker for the two FIs was the illumination of the corresponding keylight. Despite the fact that, on test trials, when the S key appeared, the C key was already illuminated, this difference seemed much weaker than the difference in the original time-left procedure.

Second, we attempted to reduce the cost of switching between keys during testing. To that end, the keys were alternately turned on and off during the trial (see also Dews, 1962, 1965a,b, 1966a,b). If the animals stop responding during the off-periods, then switching between keys may be less costly. At issue here is whether pigeons perform optimally in the time-left procedure when these non-temporal variables are controlled for.

### 2.1. Methods

#### 2.1.1. Subjects

Six experimentally naive pigeons (*Columba livia*) participated in the experiments: P170, P178, P841, P890, P948 and PG12. They were maintained at 80% of their free-feeding body weights and housed in individual home cages with water and grit continuously available. A 13:11 h light/dark cycle, beginning at 8:00 am, was in effect in the pigeon colony.

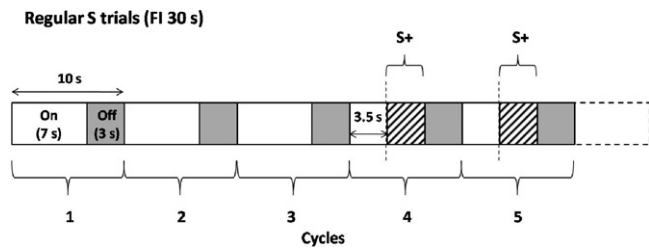
#### 2.1.2. Apparatus

Three standard experimental chambers for pigeons from Med Associates® were used. The front panel of each chamber contained three keys, 2.6 cm in diameter, centered on the wall 24 cm above the floor and 6 cm apart, center to center. The keys could be illuminated from behind with a red or green light. Directly below the center key and 6 cm above the floor was a hopper opening measuring 6 cm × 5 cm. The bird had access to mixed grain when the hopper was raised and illuminated with a white light. On the opposite wall of the chamber another white light provided general illumination. The box was also equipped with a 65-dB tone generator (Sonalert®). An outer box equipped with a ventilating fan enclosed the experimental chamber. A personal computer controlled all experimental events and recorded the data.

#### 2.1.3. Procedure

**Pretraining.** Two birds were randomly assigned to each of the three chambers. The six pigeons learned to peck the keys using an autoshaping procedure. On a given trial, the right or the left key was illuminated with a red or a green light. If 6 s had elapsed since trial onset or the pigeon had pecked the key, reinforcement was delivered for a period of 4 s. An ITI lasting 30 s followed. The houselight was always turned on except during feeding. Each session comprised 40 trials, 10 trials with the left key illuminated with green, 10 with the left key illuminated with red, 10 with the right key illuminated with green and 10 with the right key illuminated with red.

**FI training.** Next, all birds were trained on two modified FI schedules, FI 30 s and FI 60 s. The assignment of the FI schedules to the left and right keys and to the red or green colors was counterbalanced



**Fig. 2.** Structure of the regular S trials (FI 30 s). In each 10-s cycle, the keylight is on during the first 7 s and off during the last 3 s. S+ means that reinforcement is available.

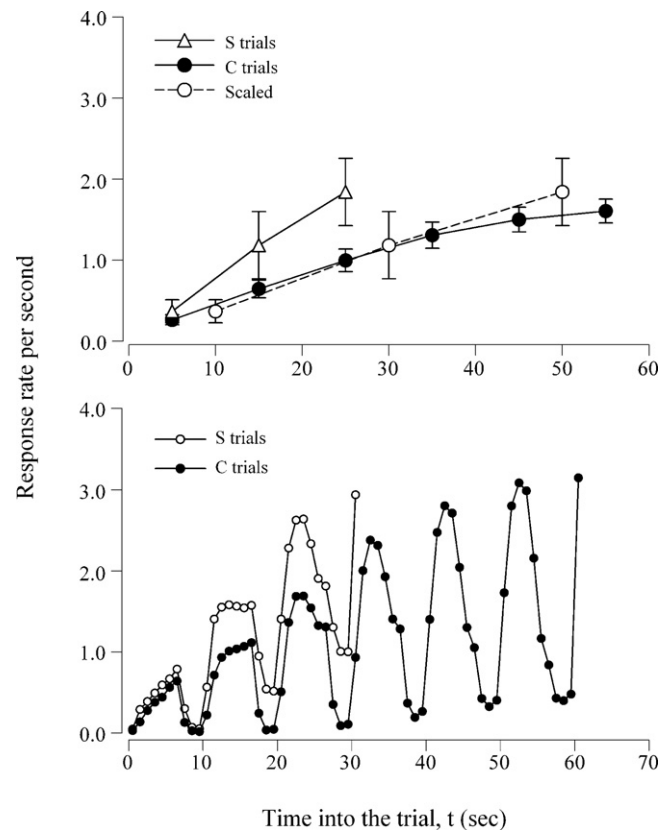
across birds. The assignment remained the same until the end of the experiment (e.g., for one bird the left key, illuminated with red light, was associated always with the FI 60 s schedule and the right key, illuminated with green light, was associated always with the FI 30 s schedule).

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 (*standard* trials – FI 30 s) and C trials (*comparison* trials – FI 60 s). Fig. 2 shows the typical structure of a training trial (in this case, a regular S trial). Each trial was divided into 10-s cycles and during each cycle the key was turned on for the first 7 s (the *on-period*) and turned off for the last 3 s (the *off-period*). The S trials lasted at least 3 cycles of 10 s each, and the C trials lasted at least 6 cycles of 10 s.

Each trial began with the illumination of one of the keys, with the appropriate light color, and a 500 ms tone. To prevent the birds from pecking the keys during the *off-periods*, reinforcement was made available only during the 3.5–7 s interval of the *on-period*. We called this interval the reinforcement period. For example, on the S trials (see Fig. 2), the first opportunity to get a reinforcer would be on the fourth cycle, but only after 3.5 s into its *on-period* (dashed area). We started the experiment (the first 12 sessions) with the reinforcement available during the entire *on-period*, but then we noticed that pigeons pecked at a high rate when the keys were turned off and suppressed responding when they were on. The unlit key had become a discriminative stimulus for pecking because pigeons were receiving reinforcement immediately after being exposed to it (food became available right after the key had been turned on). Once we restricted reinforcement to the last 3.5-s segment of the *on-period*, the pigeons pecked mostly when the keys were lit.

The first response emitted after the fixed-interval plus the left-over period of 3.5 s elapsed turned the keylight off and raised the food hopper. The hopper duration varied across birds from 2 s to 4.5 s. These durations were adjusted for each bird during the first sessions in order to maintain body weight with minimal extra session feeding. After feeding, a 15–45-s variable ITI (mean value = 30 s) began. The houselight was on during the entire session, except when food was delivered. Training with regular trials continued until the FI scallops were clearly established and did not change systematically by visual inspection. The number of training sessions ranged across birds from 58 to 61.

**Testing.** Test sessions included three types of trials: regular S trials, regular C trials and test C + S trials. Test trials started as if they were regular C trials (i.e., with the illumination of the C key) and, at  $T = 0$  s, 10 s, 20 s, 40 s, 50 s or 60 s, the S key also was illuminated and the 500 ms tone was presented (when  $T = 0$ , the trial started with both keys illuminated simultaneously). When food became available on one key, the first peck on that key during the reinforcement period turned both keylights off and raised the food hopper. After food delivery, the ITI began. As during regular trials, the houselight was on during the entire test session except during feeding.



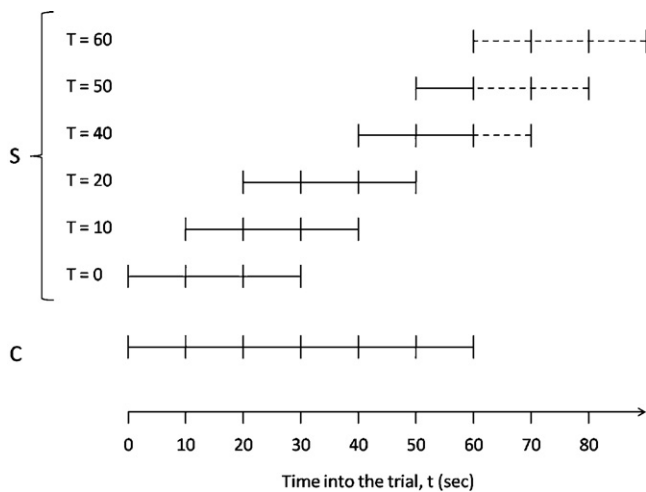
**Fig. 3.** Average performance during the last five training sessions in Experiment 1. The top panel shows the response rate curves, with corresponding standard errors, for the C trials (filled circles) and S trials (empty circles). The dotted curve represents the normalized S curve, i.e., the data for the S trials were transformed linearly by a factor of 2 in order to plot them in the same scale as the data from the C trials. The bottom panel shows the absolute number of responses to both keys as a function of the time into the trial.

Test sessions comprised 48 regular trials (24 of each FI schedule) and 12 test trials (so that each value of  $T$  was presented twice). All pigeons except P841 completed 35 test sessions. P841 completed 37 due to the accidental loss of two sessions.

## 2.2. Results and discussion

**FI training.** All pigeons learned the two temporal discriminations. As the top panel of Fig. 3 shows, average response rate increased as time elapsed in the intervals, reaching a maximum during the last cycle. These discriminations followed the scalar property (Gibbon, 1977): the curves for the C and S trials, when normalized, superimposed (compare the filled and empty circles). However, the curves did not have the standard sigmoid shape associated with FI schedules with an average response rate close to zero immediately after the time marker (e.g., Machado and Vasconcelos, 2006). In the present experiment the pause was significantly reduced and the functions, especially for the S trials, were almost linear.

The bottom panel of Fig. 3 shows average response rate per second. Two facts are noteworthy. First, animals reduced or even suppressed responding during the *off-periods* (i.e., 7–10 s, 17–20 s, etc.). And second, besides the FI discrimination (i.e., from 0 s to either 30 s or 60 s), there was evidence also of intra-cycle discrimination, for average response rate increased at the beginning of each cycle, peaked around 3.5 s, and then decreased. This finding can be seen most clearly during the third cycle of the S trials and after the third cycle of the C trials. The present trials' struc-



**Fig. 4.** Structure of the test trials. The C key was illuminated since trial onset ( $t=0$ ). The S key was illuminated at different times ( $T$ ) into the trial. Relative response rate was measured during the overlapping solid segments of the two keys.

ture is somewhat analogous to the peak procedure (Catania, 1970; Roberts, 1981), for the animals learn that if they do not receive reinforcement around 3.5 s in each cycle, then food will not be available on that cycle (resembling an empty trial of the peak procedure).

From this observed micro-timing, we may find an explanation for the fact that the post-time marker pauses were greatly reduced in the present experiment. The *off-periods* caused pigeons to develop small scallops within the first two cycles and this was probably responsible for the higher responses rates at the beginning of the time intervals. The linear instead of sigmoid-shaped curves seem to suggest that the temporal control exerted by the time markers (i.e., lighting of the key at the end of the illuminated ITI) was not very strong, at least when compared with the usual timer marker (i.e., the end of food delivery and the onset of the keylight and houselight).

**Testing.** All the analyses were restricted to the cycles during which both keys were available and neither could yield reinforcement. In Fig. 4 those cycles correspond to the overlapping segments of the C and S keys. When  $T=0$ , 10 or 20, the measures were taken for three cycles since S was introduced. Because on the fourth cycle the animals could already receive reinforcement on the S key, the cycle duration was not constant and therefore this cycle was not included in the analysis. When  $T=40$ , the test trial lasted at least two cycles. After these two cycles, the trial could end with reinforcement on the C key; therefore measures were taken only for the first two cycles. Similarly, when  $T=50$ , the test trial lasted at least one cycle; on the next cycle reinforcement was already available on the C key. Therefore, when  $T=50$ , measures were taken only for the first cycle. For the same reason, we did not include in the analysis test trials with  $T=60$ .

Preference for the C key was measured by relative response rate (i.e., the total number of pecks on the C key divided by the total number of pecks on both keys). The top left panel of Fig. 5 shows the preference functions for three different moments of the test phase. The average data were representative of the individual ones, therefore only the former are presented in the figure.<sup>1</sup> Data from the test sessions were grouped in 7 blocks of 5 sessions each and data from block 1 (first), 4 (middle) and 7 (last) are shown. Consider first the last block, the steady state. The mean curve shows that preference for the C key increased with  $T$ , the moment the

S key was inserted into the trial. When  $T=0$ , 10 and 20, pigeons preferred on average the S key and when  $T=40$  and 50 they preferred the C key. These results reproduce Gibbon and Church (1981) and Machado and Vasconcelos (2006). Individual preference curves revealed some variation across subjects mainly in the slope of the functions. However, it was the case that preference for C tended to increase with  $T$ . The point of subjective equality (PSE) averaged 22 s (range: 7–31 s), revealing a slight bias for C.

Most pigeons behaved differently during the first block. With the exception of P890, who presented from the beginning of testing a sigmoid-shaped function, the pigeons showed relatively flat functions, which revealed indifference (e.g., PG12), bias for C (e.g., P170 and P948), or bias for S (e.g., P178 and P841). For the latter four pigeons, and because of bias, the PSE could not be defined. For pigeons P890 and PG12 the PSE was 29 s and 13 s, respectively. From the first to middle to last blocks, the preference functions rotated and assumed steeper slopes. The PSE for the middle block averaged 25 s (range: 10–49 s). In summary, the PSE did not change systematically across testing: for some pigeons it decreased, for others it increased; in general, it was below 30 s.

To assess the statistical significance of the differences in preference for C across  $T$  and across blocks, we performed a two-way, repeated-measures ANOVA, with  $T$  and block as factors. The results revealed a significant effect of  $T$  [ $F(4,20)=26.06$ ,  $p<0.01$ ], but no effect of block [ $F(2,10)=0.16$ ,  $p=0.85$ ] or of their interaction [ $F(8,40)=1.96$ ,  $p=0.08$ ], although this last effect approached significance.

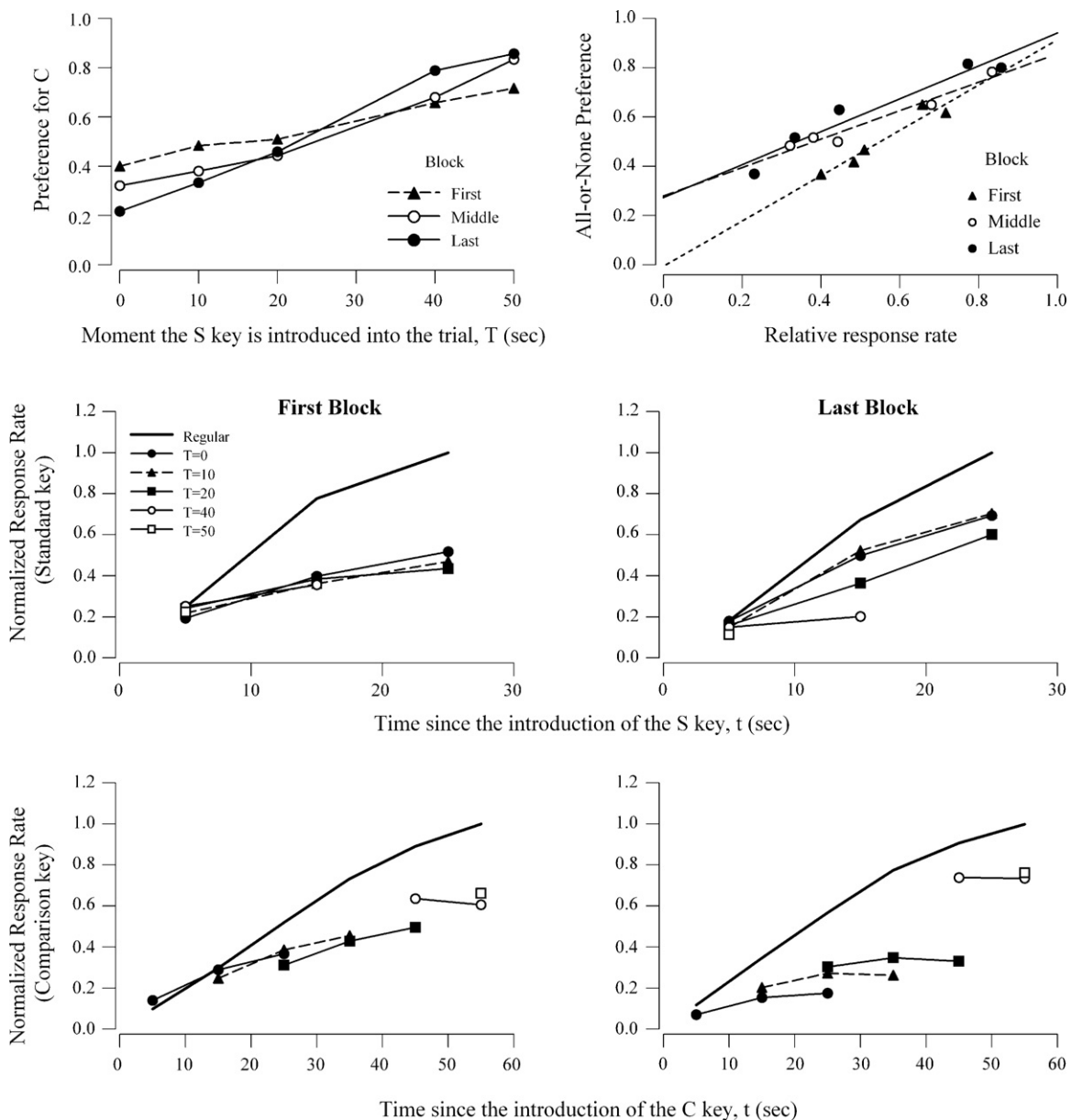
The foregoing results differ from those reported by Machado and Vasconcelos (2006). In their study, the pigeons started the test phase with a stronger bias for the S key and the preference curves for C at the end of testing assumed steeper slopes than in the present study. The fact that we found no systematic bias for S strengthens the idea that Machado and Vasconcelos' (2006) results could have been due to a disinhibition in responding to the S key as a consequence of the change in the salience of the time marker from the regular to the test trials. Relearning the time marker would account for the steeper functions at the end of testing.

The four lower panels of Fig. 5 show the average response rate curves on the S and C keys (regular and test trials), for the first and last blocks of testing. The curves for the regular trials (lines without symbols) were obtained as follows. First, for each bird, the response rate data from all S or C trials were averaged. Next, each point along the individual average curve was divided by the maximum response rate value of that curve. This transformation forced all curves to be between 0 and 1 and facilitated the comparison of curves with different terminal rates. In the end, the six individual curves were averaged to obtain the group curve. By comparing Fig. 3 and the four lower panels of Fig. 5 (lines without symbols), we found that performance on the regular trials did not differ appreciably from training to testing.

The remaining curves correspond to the group averages during the test trials. In Machado and Vasconcelos (2006), pigeons tended to choose one key and stay on that key until the end of the trial. Based on this fact, the authors defined two types of trials, those on which the animal preferred the S key and those on which the animal preferred the C key. From each trial type they obtained a response rate curve for the corresponding key. In our experiment, however, the animals switched frequently between the two keys and, consequently, all test trials were used to obtain the average response rate curves for both keys. For example, for the C key, the response rate data from all test trials of each pigeon were averaged into an individual average curve. Next, to make the comparisons across birds meaningful, each point of the individual average curve was divided by the maximum average response rate during that animal's regular C trials (i.e., the same value used to normalize the curve for the regular C trials). Finally, the curves were averaged across subjects.

<sup>1</sup> Figures with individual data were available from the authors.





**Fig. 5.** Pigeons' performance across the test phase in Experiment 1. Top left panel: average preference for the C key. Relative response rate to the C key is presented against the moment the S key was illuminated into the trial. The filled triangles show the data from the first block, the empty circles from the middle block and the filled circles from the last block. Top right panel: scatterplot showing the relationship between the two measures of preference for the first, middle and last blocks (average data). All-or-None preference is plotted against preference measured by the relative response rate. Middle and bottom panels: average response rate curves during the regular and test trials of the test phase. The graphs on the left show the data for the first five sessions (first block) and those on the right the data for the last five sessions (last block). The middle graphs show the response rate curves on the C key and the bottom ones on the S key.

The same steps were followed to calculate the average response rate curve on the S key.

In Fig. 5, the middle and bottom panels show the response rates on the S and C keys, respectively. The corresponding left and right panels show the response rates during the first and last blocks.

Consider the left panels. They show that, during the first block, introducing the S key during a test trial caused response rate to decrease, both on the S (middle left panel) and C (bottom left panel) keys. This decrease varied with time since the introduction of the key (along  $t$ , the abscissa) but not with the moment the S key was introduced (with  $T$ , the parameter). Concerning the S key (middle left panel), the regular and test curves did not differ in the first data point. In contrast, in Machado and Vasconcelos' (2006) study, the first data points of the test curves were significantly above the first data point of the baseline (regular) curve, another expression of

the disinhibition of responding to the S key that resulted from the change in time markers from training to testing. Hence, our attempt to equate the time markers of training and testing seemed to have been effective.

The reduction with respect to baseline of response rate during test trials may be the result of distributing the responses by the two keys (response competition) or averaging all the test trials without classifying them (e.g., trials during which a pigeon pecked only the S key were included also in the curves for the C key). However, because the first data point of each test curve is close to baseline, we concluded that, at least for each key, there was no evidence of disinhibition of response rate immediately after the onset of the S key.

During the first block, the effect of  $T$  was either non-existent (S key, middle left panel) or small (C key, bottom left panel). Specif-

ically, for the same time into the trial,  $t$ , the response rates on the S key corresponding to different values of  $T$  were similar. On the C key there was a small effect of  $T$  in that, at  $t = 45$  s, the rate for  $T = 40$  was greater than for  $T = 20$ .

Comparing the left with the right panels, it can be seen that from the first to the last block response rate changed as follows. For the S key (middle), the amount of change in response rate with respect to baseline increased with  $T$  (i.e., for the same time into the trial,  $t$ , the points corresponding to the larger  $T$  values tended to be below the points corresponding to the shorter  $T$  values); for the C key (bottom), the opposite was the case, the amount of change in response rate decreased with  $T$  (i.e., for the same time into the trial,  $t$ , the points corresponding to larger  $T$  values tended to be above the points corresponding to shorter  $T$  values). These patterns are expected from the stronger preference for C with larger  $T$  values.

For the S key, optimal performance would be for the test curves with  $T \leq 20$  (empty symbols) to equal zero and those with  $T > 20$  (filled symbols) to overlap the regular curve. For the C key the opposite should be the case. During the last block our pigeons approached this optimal pattern.

We conclude that the schedule performance patterns and their changes during testing (middle and bottom panels of Fig. 5) were consistent with the analysis of preference (top left panel of Fig. 5). Together, they support the following description. During the first test trials, pigeons' behavior was not significantly affected by  $T$ . Most preference functions were either flat or increased slightly with  $T$ ; the response rate curves on the C and S keys were not significantly different for the different values of  $T$ . In the course of testing, performance changed. At the steady state, preference for the C key increased with  $T$ . Schedule performance analysis revealed that response rate on the S key decreased with  $T$ , whereas on the C key it increased with  $T$ .

**Switching.** When the two keys were present during testing, the pigeons switched frequently between keys. The total number of changeovers during the first block of sessions averaged 35 (range 12–66). As further evidence of learning during testing, three pigeons decreased significantly the number of changeovers from the first to the last block of sessions: from 12 to 1 for P170, from 62 to 39 for P890, and from 66 to 34 for PG12. However, because the other three pigeons did not change significantly the number of changeovers, a paired-samples  $t$ -test yielded no significant differences between the first and last blocks [ $t(5) = 1.28$ ,  $p = 0.26$ ; last block:  $M = 27$ , range: 1–39].

High switching rates may obscure or even exclude temporal regulation. In fact, by switching frequently, a pigeon would eat as soon as possible without paying the costs of comparing the delays to food associated with the two keys. This hypothesis could explain the fact that the preference functions were not steep: except for pigeon P170, preference for the S key when  $T$  was small, and for the C key when  $T$  was large, was only halfway between indifference and exclusive preference. In fact, the pigeon that switched the least between the two keys displayed the most extreme performance at the steady state (P170). The other pigeons switched more frequently (from 26 to 39 switches per session) and had less extreme preference functions at the steady state.

**All-or-None preference.** Measuring preference using the relative rate of responding may be hard to interpret if the animal pecks the two keys at different rates. In our experiment we observed that, on regular trials, all pigeons pecked the S key with higher rates than the C key (see Fig. 3 for the average). This fact suggested a second way to measure preference. On a test trial, the first response made by the animal after the S key was illuminated determined which key was considered the preferred key on that trial. If the first peck was on the C key, that trial received a score of 1. If the first peck was on the S key, it received a score of 0. Preference was then measured

by averaging the scores for each value of  $T$ . We called this measure 'All-or-None preference'.

When a two-way, repeated-measures ANOVA was run with the All-or-None preference measure, it revealed a significant effect of  $T$  [ $F(4,20) = 8.11$ ,  $p < 0.01$ ], but no effect of block [ $F(2,10) = 0.77$ ,  $p = 0.49$ ] or of their interaction [ $F(8,40) = 0.56$ ,  $p = 0.81$ ]. These results were consistent with those obtained from relative response rate.

To analyze the relationship between the two measures of preference, the top right panel of Fig. 5 displays the scatterplot for the average data, with fitted linear regression equations. The individual data (not presented in the figure) showed some variability, both between subjects and between blocks for the same subject. We found strong positive correlations (e.g., P170 and P948 for all blocks), almost zero correlations (P178 and P890 during the last block) and even negative correlations (P841 in the first and PG12 in the middle blocks). Despite this variability, on average, the two measures of preference were strongly positively correlated (top right panel of Fig. 5;  $r^2 = 0.93$  for the first and last blocks, 0.96 for the middle block). These findings seem to suggest that, with a few exceptions, the two measures of preference were consistent and, therefore, that relative rate of responding may be a reliable measure of preference in this task.

### 2.3. Conclusions

The present findings globally replicated Gibbon and Church (1981) and Machado and Vasconcelos (2006). At the steady state, pigeons chose the key associated with the least time to reinforcement. The specific values of our subjects' steady state preference functions were more similar to those obtained by Gibbon and Church (1981) with rats, but they were achieved only after learning took place during testing, bringing support to the idea first stated by Machado and Vasconcelos (2006), that in the time-left task performance changes with testing.

Our goals in this experiment were partially achieved. First we reduced the asymmetry in time markers as evidenced by the absence of disinhibition in responding to the S key during test trials. Second, we reduced pecking during the *off-periods*. However, these procedural changes seem to have triggered new interpretative difficulties. Pigeons switched frequently between keys during test trials and this fact yielded preference functions that were shallower than in Machado and Vasconcelos' (2006) study. The second experiment attempted to reduce switching and better reveal how preference varies with the signaled delays to food.

### 3. Experiment 2

In Experiment 2, we attempted to prevent the pigeons from switching frequently between the two keys during the test trials, thereby making it more likely that they would regulate their choices on the basis of the delays to food. To that end, we restricted the time of choice to the first 3.5 s from the moment the S key was illuminated. Only during this period could the animals switch freely between keys; the first peck after this period eliminated the non-chosen alternative.

The procedure from Experiment 1 was designed to reduce the potential cost of switching between the two keys. In Experiment 2 we added another improvement. As in Experiment 1, we maintained a reduced cost of switching for the first changeover because, immediately before the S key was introduced, both keys were turned off (*off-period*). However, once the pigeon made its choice (during the first 3.5 s of the *on-period*), only the chosen key remained available, therefore preventing the large amount of switching observed in Experiment 1.

### 3.1. Methods

#### 3.1.1. Subjects and apparatus

The same six pigeons that participated in Experiment 1 were used. Housing conditions remained the same. The chambers were the same as in Experiment 1, except that the keys could be illuminated from behind with a yellow light or a white triangle in a dark background.

#### 3.1.2. Procedure

**FI training.** In Experiment 2 the two FI schedules remained the same, FI 30 s and FI 60 s. To reduce potential carryover effects from the previous experiment, the keys were now illuminated with either a yellow light or a white triangle and the left–right assignment of the two schedules was reversed.

The structure of training sessions and trials reproduced Experiment 1. 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 30 to 45.

**Testing.** The structure of test sessions and trials reproduced Experiment 1 except that, during test trials, the pigeon had only a period of 3.5 s after the illumination of both keys to choose; the first peck after this period elapsed turned the non-chosen key off until the end of the trial. If a response was not emitted during the first cycle when both keys were illuminated simultaneously, in the following cycle the 3.5 s period rule operated again. Pigeons P170, P890, P948 and PG12 completed 35 sessions of testing. Pigeon P178 completed 45 and pigeon P841 completed 50 sessions.

### 3.2. Results and discussion

**FI training.** Stable performances were similar to those observed in Experiment 1 in that response rate increased monotonically with time, reaching a maximum during the last cycle of the interval. In addition, the pigeons showed also an intra-cycle discrimination similar to that illustrated in Fig. 3.

**Testing.** As in Experiment 1, preference for the C key was measured by the relative rate of responding to that key, but because the first peck after 3.5 s turned off the non-chosen key, we restricted the measure of preference to the period when both keys were illuminated, i.e., until one peck turned the non-chosen key off.

The top left panel of Fig. 6 shows how preference for the C key evolved across the test phase (average data).<sup>1</sup> Consider first steady state performance. As found in Experiment 1, preference for the C key increased with  $T$ . The sigmoid-shaped average curve reproduced well the data of four pigeons. The exceptions were pigeons P841 and P948 who showed stronger bias for C when  $T$  was small. For five pigeons, the PSE averaged 19 s (range: 7–19 s); for pigeon P841 the PSE could not be defined.

During the first and middle blocks, sigmoid-shaped functions were already well defined and very similar to the function obtained for the last block. Concerning the PSE, it averaged 21 s in the first block (range: 6–32 s) and 16 s in the middle block (range: 8–26 s). It was not possible to define the PSE for P178 in the first block and for P841 in the middle block. In summary, the PSE tended to be below 30 s and practically did not change with testing.

A two-way, repeated-measures ANOVA, with  $T$  and block as factors yielded a significant effect of  $T$  [ $F(4,20) = 42.30, p < 0.01$ ], but no effect of block [ $F(2,10) = 1.32, p = 0.31$ ] or of  $T \times$  block [ $F(8,40) = 0.94, p = 0.50$ ].

In summary, the preference functions in Experiment 2 did not change appreciably across testing. At the steady state, they were steeper than in Experiment 1 (compare top left panels from Figs. 5 and 6), which means that by reducing switching during test trials the pigeons' performance approached optimal perfor-

mance. The performances displayed by the pigeons in Experiment 2 at steady state were more similar to those obtained in Machado and Vasconcelos (2006) than in Gibbon and Church's (1981) study.

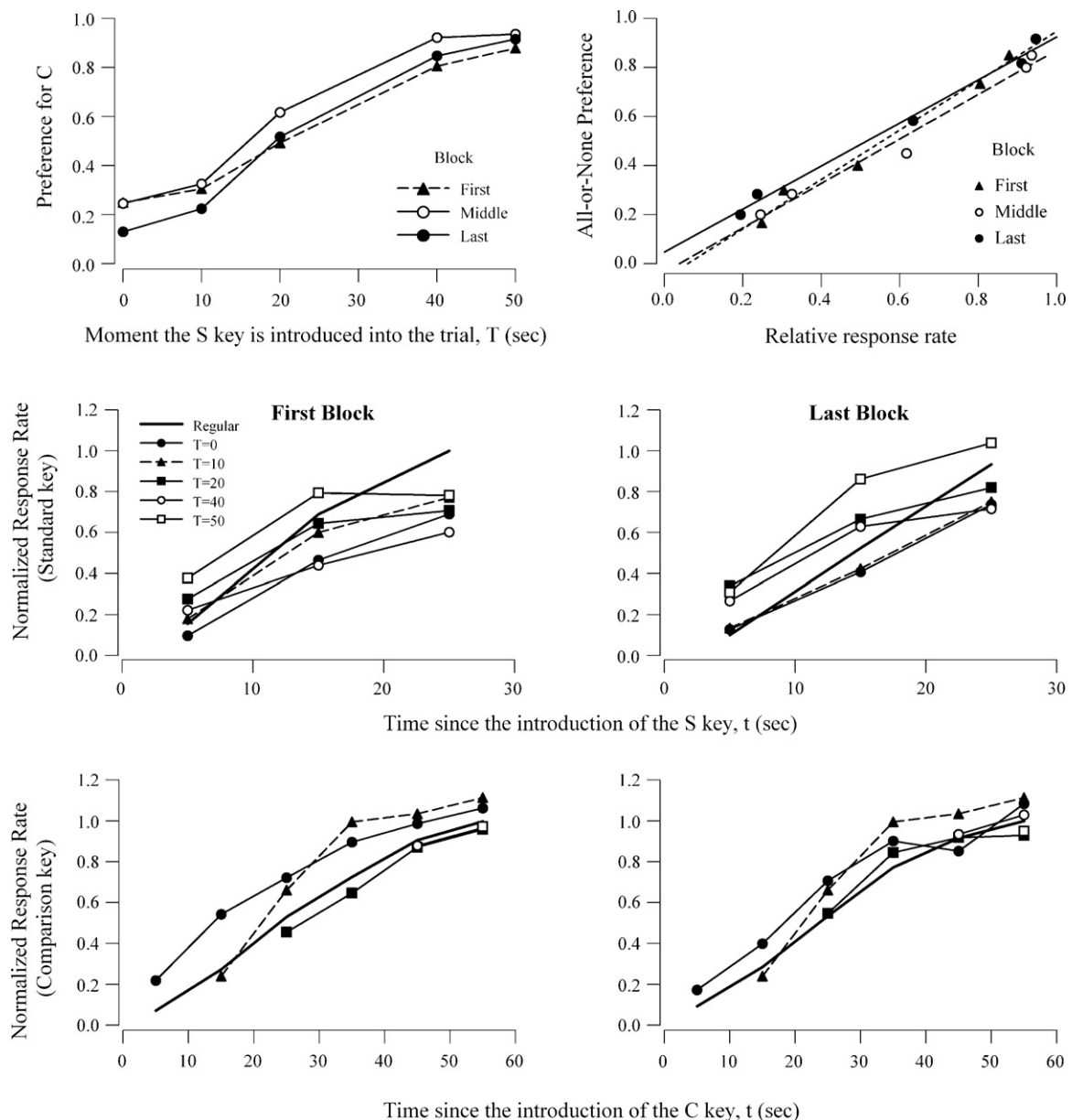
The four bottom panels in Fig. 6 show the average response rate curves on the S and C keys (regular and test trials), for the first and last five sessions of testing. The curves for the regular trials (lines without symbols) were obtained as in Experiment 1, but the curves for the test trials were not. Because one key was eventually turned off, we could define whether a bird preferred the C or S keys on any given test trial. Having classified each test trial as a C or S trial, the curves were obtained as follows. First we averaged the response rate data from all the test trials on which the birds chose the S key. Next, we divided each individual average curve by the value used to normalize the curve for the regular S trials. Finally, we averaged across birds. The same steps were carried out for the trials on which the pigeon preferred the C key.

The middle panels display the response rate data for the S key during the first (left) and last (right) blocks. There was substantial variability among the test curves, caused mainly by the different number of trials contributing to each curve. Specifically, the curves for  $T = 40$  and 50 in the left panel and for  $T = 20, 40, 50$  in the right panel were based on less than 20 trials (out of 60 possible trials) – on most of those trials the pigeons preferred the other key. No strong or systematic effect of  $T$  was found. During the first block (left panel) and immediately after the S key was introduced (see first data point of each curve) there was some increase in response rate in relation to baseline for  $T \geq 20$ . During this first cycle (still concerning the first data points) response rate increased roughly directly with  $T$  (the exception was for  $T = 40$ ). However, the inversion was due to the fact that one pigeon contributed to the  $T = 40$  curve with just one trial, and on that trial it started to respond only during the third cycle. Without the data from this pigeon, the first data point of the  $T = 40$  curve superimposed that from the  $T = 20$  curve. During the last cycle (see last data point of each curve), there was a general suppression of responding for all values of  $T$ .

During the last block (right panel), the first data point of the test curves was close to baseline for  $T = 0$  and 10, but it was above baseline for the other  $T$  values. The response rate curve for  $T = 50$  was above baseline across the entire interval, while for the other values of  $T$  the terminal rates were below baseline.

The bottom left panel shows that, during the first block, response rate on the C key on test trials was greater than the baseline when  $T = 0$  and 10, but not when  $T \geq 20$ . From the first to the last block (compare bottom left and right panels), performance did not change appreciably. For this key, the number of trials contributing to the curves when  $T = 0, 10$  and 20 in the left panel and to the curves when  $T = 0$  and 10 in the right panel was very small (between 11 and 25 trials, out of 60 possible).

The procedural differences introduced in Experiment 2 brought that experiment closer, from a functional viewpoint, to Machado and Vasconcelos' (2006) study. In the latter, on most trials the pigeons chose one key and then stayed on that key until the end of the trial, behaving as if the other key had been turned off. The similarities between Machado and Vasconcelos' (2006) results and the results from Experiment 2 extend somewhat to the response rate changes on the S key. In Machado and Vasconcelos (2006), responding to the S key immediately after its onset was disinhibited and the amount of disinhibition varied with  $T$ . In the present experiment, during the first cycle (immediately after the onset of the S key), there was disinhibition in responding to the S key for some values of  $T$  (namely  $T \geq 20$ ) and there was an increase in response rate varying roughly directly with  $T$ . The results for the C key differed between the two cases because in Experiment 2, but not in Machado and Vasconcelos's (2006) study, response rate increased



**Fig. 6.** Pigeons' performance across the test phase in Experiment 2. Top left panel: average preference for the C key. Relative response rate to the C key is presented against the moment the S key was illuminated into the trial. The filled triangles show the data from the first block, the empty circles from the middle block and the filled circles from the last block. Top right panel: scatterplot showing the relationship between the two measures of preference for the first, middle and last blocks (average data). All-or-None preference is plotted against preference measured by the relative response rate. Middle and bottom panels: average response rate curves during the regular and test trials of the test phase. The graphs on the left show the data for the first five sessions (first block) and those on the right the data for the last five sessions (last block). The middle graphs show the response rate curves on the C key and the bottom ones on the S key.

when  $T=0$  and 10. However, given the small number of trials on which some of these curves are based, the differences may not be reliable.

**All-or-None preference.** When preference was measured by the first choice made by the animal (All-or-None preference) the patterns observed were roughly the same. The statistical tests revealed the same effects found with the relative rate of responding as a measure of preference: a significant effect of  $T$  [ $F(4,20)=34.14$ ,  $p<0.01$ ], but no effect of block [ $F(2,10)=1.46$ ,  $p=0.28$ ] or  $T \times$  block [ $F(8,40)=0.46$ ,  $p=0.88$ ].

As the top right panel of Fig. 6 shows, the two measures of preference were strong positively correlated ( $r^2$  values near 1–0.98 for the first and middle block and 0.99 for the last block). The fact that this correlation was better in Experiment 2 is probably related to the decrease in the amount of switching, which allowed the relative

rate of responding to better reflect the animals' preferences based on the signaled delays to reinforcement.

In summary, preference measured in two different ways (relative response rate and All-or-None preference) revealed the same effect: the later the S key was inserted into the trial, the more the birds preferred the C key, and this performance was shown since the first test sessions. Similarly, schedule performance analysis revealed only small changes in performance across testing.

### 3.3. Conclusions

The present results, as well as those from Experiment 1, generally reproduced Gibbon and Church (1981) and Machado and Vasconcelos (2006). At the steady state, pigeons' preference for the C key increased directly with  $T$ , the moment the S key was inserted



into the trial. However, contrary to what was found in Experiment 1, the animals' performance practically did not change with testing.

The main goal of the present experiment was to reduce switching during test trials. By successfully achieving this objective, pigeons displayed steeper preference functions at steady state, resembling more Machado and Vasconcelos' (2006) results, and meaning that their performance approached optimal performance.

#### 4. General discussion

Some authors have argued that the time-left procedure is not adequate to study timing because variables other than temporal intervals may be masking the results (Preston, 1994; Cerutti and Staddon, 2004). The goal of the present study was to control for two of these variables, differences in the salience of time markers and the cost of switching. To that end, we introduced two main procedural changes. The first was to make the onset of the two keylights the time markers for the two time intervals in an attempt to reduce the asymmetry in the salience of the time markers for the S key from training to testing. The second was to turn on and off the keys signaling the delays to food and thereby attempt to reduce the cost of switching between keys (particularly once pecking at the C key has started).

These two changes increased the complexity of the original time-left procedure and naturally raise the question of whether control by the time left to food was still present. The answer is affirmative because, at the steady state, preference for the C key increased directly with  $T$ . The data from the two experiments replicate the steady state findings reported by Gibbon and Church (1981) with rats and by Machado and Vasconcelos (2006) with pigeons.

In what follows we summarize the effects of the new procedural changes on the preference functions and response rate curves and discuss the evidence for learning during the test sessions in the two experiments.

In Experiment 1, the pigeons began the test phase displaying several different but generally far from optimal performances (see Fig. 5, top left panel). The average preference for C ranged from 0.40 at  $T=0$  to 0.70 at  $T=50$ . In the course of testing, their choices became more extreme (preference for C ranged from 0.20 at  $T=0$  to 0.85 at  $T=50$ ), which means that they learned to minimize the delay to food. However, the rotation of the preference curves during testing was not sufficiently consistent across the six pigeons to reach statistical significance.

The analyses of the response rate curves revealed no disinhibition in responding to the S key during the first cycle of the test trials (Fig. 5, middle panels), which suggests that our manipulation concerning the time markers was effective. Moreover, on the first test trials, response rate curves to the C and S keys were not significantly affected by  $T$ . Afterwards, for the S key, the curves for  $T \leq 20$  increased with testing and those for  $T \geq 40$  decreased, whereas for the C key the opposite pattern was observed. These changes are expected when preference for C increases with  $T$  or, equivalently, when the pigeons' performance approaches optimal performance.

In general, the results from Experiment 1 are consistent with Machado and Vasconcelos' (2006) results and suggest that, in the time-left procedure, behavior during the test trials does not depend exclusively on the previous training with the regular trials. The optimal, or close to optimal, behavior observed at the steady state depends on learning that takes place during testing. This finding has important theoretical consequences, namely, it casts doubts on Gibbon and Church's (1981) account of the time-left procedure based on Scalar Expectancy Theory (SET; Gibbon, 1977, 1991; Gibbon et al., 1984). According to this account, performance during testing results from the learning that takes place during training

trials, in particular, the two delays to food signaled by the S and C keys. Whether SET, or a modified version of SET, can accommodate the presence of learning during the test phase remains to be ascertained.

However, the procedural changes introduced new difficulties. On one hand, because the houselight was turned on during the ITI, the salience of the time markers may have been reduced. As evidence, note that during regular trials the response rate curves were almost linear (see Fig. 3), in contrast with sigmoid response rate functions usually obtained with standard FI schedules (e.g., Machado and Vasconcelos, 2006).

On the other hand, the *on-* and *off-periods* may have been too effective in promoting switching. In Experiment 1, the pigeons switched frequently between the two keys during the test trials, perhaps because switching is an effective, easy-to-learn strategy that insures the shortest delay to food and circumvents the costs of choosing based on the delays to reinforcement. Frequent switching was associated with relatively shallow preference functions and, during the first test trials, the absence of a strong effect of  $T$  (see Fig. 5). More generally, switching may have masked the effect of  $T$  in the animals' preferences.

In Experiment 2 we attempted to reduce switching by turning off the light of the non-chosen key. Results showed that, in general, preference functions were steeper than in Experiment 1 (compare the top left panels of Figs. 5 and 6) – as expected, preference for the C key increased with  $T$ . In contrast to Experiment 1, in Experiment 2 pigeons' performances were similar during the first and last sessions of testing. However we must be careful in interpreting these findings as the exclusive outcome of reduced switching, because the pigeons were already familiar with the procedure. Previous experience may explain both the steeper preference functions and the fact that they were exhibited from the beginning of testing.

Response rate data from Experiment 2 are difficult to interpret. It seems that some disinhibition in responding to the S key at the beginning of the intervals occurred, especially for larger values of  $T$  (Fig. 6, middle panels). In addition, there was some evidence of suppression of responding at the end of the intervals. The response disinhibition with respect to the S key reproduced to some extent Machado and Vasconcelos' (2006) findings and suggested that our manipulation may not have eliminated completely the differences in the salience of the time markers. There is a difference in stimulus conditions from regular to test trials that is impossible to eliminate: during regular trials there is only one key lit and during test trials there are two. In some instances, this difference may be sufficient for the animals to respond at distinct rates during the two types of trials. If our interpretation is correct, we are still left with the problem of explaining why the same manipulation of the time markers yielded different results in Experiment 1 (no evidence of disinhibition) and Experiment 2 (some evidence of disinhibition) immediately after the onset of the S key.

In summary, our version of the time-left procedure still suffers from interpretation difficulties. In an attempt to eliminate some problems, the methodological changes we introduced gave rise to new issues. A subsequent study using the same procedure of Experiment 2 and naïve animals should be conducted to verify if the same steep functions obtained at the steady state occur immediately at the onset of testing. Until there, we have to agree with Preston (1994) and Cerutti and Staddon (2004) in that the current versions of the time-left procedure are not well suited for studying prospective timing. The variables influencing the animals' behavior in this task are still not completely understood and of great importance is the difficulty of integrating timing and choice data.

We return to the original goal of the time-left procedure (Gibbon and Church, 1981), to determine whether the subjective time scale is linear or logarithmic. In the present study, the analysis of the PSEs does not allow any strong conclusions about the nature of the sub-

jective time scale. First, we found substantial variability between subjects. Second, in some conditions, the PSE was not defined. And third, and more important, PSEs below 30 s may be consistent with the two scales. The reason follows.

Gibbon and Church' (1981) account assumed a decision rule based on the difference between the subjective time to food on the two response alternatives. Consider  $X_C$  as the subjective time left to food on the C alternative and  $X_S$  as the subjective time left to food on the S alternative. The difference  $X_C - X_S$  determines the animal's choice at a given time,  $t$ , into the trial. When  $X_C - X_S > 0$ , then  $X_C > X_S$  and the animal favors S. When  $X_C - X_S < 0$ , then  $X_C < X_S$  and the animal favors C. Finally, when  $X_C - X_S = 0$ ,  $X_C = X_S$  and the animal is indifferent between the two options (PSE). If the subjective time scale is logarithmic, the PSE should be significantly below 30 s. On the other hand, if the subjective time scale is linear, the PSE should be approximately at 30 s.

At first sight, the results from the present study seem more consistent with a logarithmic scale, because the average of the PSEs (see Figs. 5 and 6, top left panels) equaled 22 s in Experiment 1 and 19 s in Experiment 2. However, if we consider a linear time scale but add a bias factor,  $b$ , to the decision rule (as suggested by Gibbon and Church, 1981), the animal's preference is now computed as  $bX_C - X_S$ . If  $b > 1$  the subjective time left to food on C is magnified and therefore the PSE will be  $>30$  s; for similar reasons, if  $b < 1$ , the PSE will be  $<30$  s, as in the present study (see also Cerutti and Staddon, 2004). To summarize, our results may be explained by a logarithmic scale or by a linear scale with bias.

Although not a central question in the present study, we call attention to the very interesting behavior shown by our pigeons during training trials. As Fig. 3 shows, during these trials, pigeons timed two events simultaneously. They discriminated the whole intervals (response rate increased while the two intervals elapsed) and, at the same time, they also discriminated each cycle (response rate increased during the first 3.5 s and decreased thereafter). The delivery of reinforcement after 3.5 s within a cycle, as well as the presence of cycles without reinforcement, made the procedure equivalent to a short peak procedure, with food trials 3.5-s long, and empty trials 10-s long. This result extends to pigeons Meck and Church's (1984) findings that rats are able to process information from two temporal events simultaneously.

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