

Short communication

Shifts in the psychophysical function in rats

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Abstract

The primary goal was to compare results from a free-operant procedure with pigeons [Machado, A., Guilhardi, P., 2000. Shifts in the psychometric function and their implications for models of timing. *J. Exp. Anal. Behav.* 74, 25–54, Experiment 2] with new results obtained with rats. The secondary goal was to compare the results of both experiments with dependent variables that were not used in the original publication. As in the original study with pigeons, rats were trained on a two-alternative free-operant psychophysical procedure in which left lever press responses were reinforced during the first and second quarters of a 60-s trial, and right lever press responses were reinforced during the third and fourth quarters of the trial. The quarters were reinforced according to four independent variable interval (VI) schedules of reinforcement. The VI duration was manipulated in each quarter, and shifts in the psychophysical functions that relate response rate with time since trial onset were measured. The results obtained with rats were consistent with those previously obtained with pigeons. In addition, results not originally reported were also consistent between rats and pigeons, and provided insights into the perception, memory, and decision processes in Scalar Expectancy Theory and Learning-to-Time Theory.

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1. Introduction

The results of an experiment can be replicated either directly, where the conditions are the same as the original experiment, or systematically, where the conditions differ from those of the original experiment (Sidman, 1966). If successful, systematic replications increase the reliability of the original findings and their generality with respect to the factors that differed from the original experiment. The goals of the present article were to systematically replicate the results described by Machado and Guilhardi (2000) introducing differences in the species, independent variables, operant response, and experimental apparatus.

Machado and Guilhardi (2000) used a free-operant psychophysical procedure (FOPP) to test predictions from two theories of timing, Scalar Expectancy Theory (SET; Church, 1984; Gibbon, 1977; Gibbon and Church, 1990), and Learning-to-Time (LeT; Machado, 1997). The procedure is shown in Fig. 1. Pigeons were exposed to a 60-s trial signaled by a stimulus (e.g., houselight) that was divided into four 15-s segments, referred to as Segments 1, 2, 3, and 4. Left responses (e.g., keypecks) were reinforced during the first two 15-s segments

(Segments 1 and 2) but not during the last two 15-s segments (Segments 3 and 4). Right responses were reinforced during the last two 15-s segments (Segments 3 and 4) but not during the first two 15-s segments (Segments 1 and 2). In each of the segments, reinforcers were scheduled according to one of two variable intervals, VI 40 s or VI 120 s.

The critical manipulation was whether the VI schedules during Segments 2 and 3 were equal (40–120|120–40 or 120–40|40–120, for Segments 1, 2, 3, and 4, respectively) or different (40–120|40–120 or 120–40|120–40). The overall reinforcement rate for each of the responses (left during Segments 1 and 2, and right during Segments 3 and 4) was kept constant. The pigeons were divided into two groups. Group EQU was exposed to equal VIs during Segments 2 and 3; that is, 120–40|40–120 in one condition, and 40–120|120–40 in another condition. Group DIF was exposed to different VIs during Segments 2 and 3; that is, 120–40|120–40 in one condition, and 40–120|40–120 in another condition. The groups were trained on the two conditions in separate blocks of sessions.

Two psychophysical functions relating the proportion of right responses to time since trial onset were obtained, one function per condition. Next, the magnitude of the (horizontal) shift between the two functions was calculated. The purpose of the original experiment (Machado and Guilhardi, 2000) was to determine whether the psychophysical function would shift

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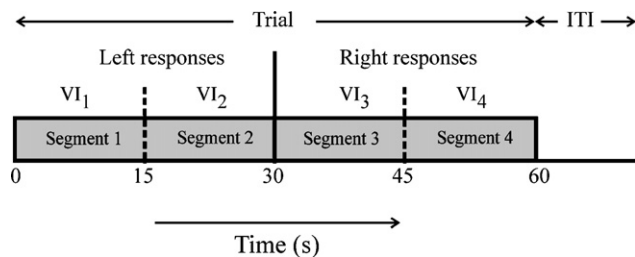


Fig. 1. Machado and Guilhardi (2000) free-operant psychophysical procedure.

when the reinforcement rates around the middle of the trial were the same (Group EQU) or different (Group DIF). More specifically, the purpose was to determine whether the magnitude of the shift would be greater for Group DIF than for Group EQU. The results showed a greater shift in the psychophysical function for Group DIF than for Group EQU.

Machado and Guilhardi's (2000) results extended the results described by Bizo and White (1995). These authors manipulated the overall reinforcement rate associated with the two responses. In one condition, they associated a VI 45-s schedule with the left response and a VI 90-s schedule with the right response (condition 45|90). In a second condition, the VI schedules were reversed (condition 90|45). In both conditions, left keypecks were reinforced during the first but not the last 25 s of a trial, whereas right keypecks were reinforced during the last but not the first 25 s of a trial. The pigeons switched from the left to the right key later during condition 45|90, and earlier during condition 90|45, producing a shift in the psychophysical functions between the two conditions. Similar results were observed in another experiment with the conditions 40|120 and 120|40. Machado and Guilhardi's (2000) results extended Bizo and White's (1995) results by showing that, in addition to differences in the overall reinforcement rate, differences in the reinforcement rate around the middle of the trial (i.e., at the time of switching from the first to the second response) determine the shifts in the psychophysical function.

Similar results were also obtained by Stubbs (1980, Experiment 3). In that experiment, pigeons were trained on a 15-s trial during which left responses were reinforced during the first but not the last half of the trial, and right responses were reinforced during the last but not the first half of the trial. Although the overall reinforcement rate was kept constant for the left and right responses, in some conditions the local reinforcement rate during the last half of the trial was manipulated. Local changes in the reinforcement rate around the middle of the trial produced shifts in the psychophysical function. Machado and Guilhardi's (2000) results replicated Stubbs' (1980) results even though there were major procedural differences between the two experiments. For example, Stubbs used a changeover response key such that the pigeons could only switch between responses once per trial. In addition, in Stubbs' procedure, a trial terminated whenever reinforcement occurred, which exposed the pigeons to the early part of the trial more often than the later part of the trial. Nonetheless, the results were remarkably similar showing that differences in the local reinforcement rate around the middle of the trial are sufficient to produce shifts in the psy-

chophysical function, even when the overall reinforcement rates associated with the two responses remain equal.

The present article aimed to replicate the Machado and Guilhardi's (2000) results while introducing differences in the species (rats instead of pigeons), variable interval durations (VI 30 s instead of 40 s), operant response (lever press instead of keypeck), and apparatus. If successful, this systematic replication would increase our confidence in the claim that the shifts are caused by the manipulation of the reinforcement rate around the time of switching, which was preserved between replications, and not by other factors, which were not preserved between replications. Although Machado and Guilhardi (2000) has been cited 13 times (Science Citation Index search, August 18, 2006), it has not been replicated, or extended to other species. Most of these articles referred to the procedure and results obtained by Bizo and White (1995) and, although these experiments used different species, variable interval durations, response, and apparatus, they provided no further evidence to support the specific conclusion that reinforcement rate around the time of switching between the first and second responses, and not differences in overall reinforcement rate per se, determine shifts in the psychophysical function (e.g., Body et al., 2006; da Silva and Lattal, 2006). The remaining citations referred to the theoretical conclusions drawn by Machado and Guilhardi (2000) and, like the other articles, did not replicate the results described (e.g., Bizo et al., 2006; Machado and Pata, 2005; Whitaker et al., 2003).

Since the original data from Machado and Guilhardi's experiments were also available, secondary data analysis of the raw data (Church, 2002) could be based on new dependent variables. One such variable is the psychophysical function based on individual trials. The form of a psychophysical function for a single trial may consist of an abrupt change from one response to another, which can be characterized as a step function. Preliminary analysis showed that most of the single-trial response rate functions were step-like; that is, one function (responses reinforced in the first half of the trial) went down abruptly at time t_1 , and another function (responses reinforced in the second half of the trial) went up at time t_2 . Therefore, a transition point (tp) may be defined for each trial by the midpoint between t_1 and t_2 . This alternative, single-trial analysis is richer than analyses based on the mean psychophysical functions because it yields the entire distribution of the t_1 , t_2 , and transition points (not just their means). The familiar ogival psychophysical function may result from averaging such single-trial step functions (Church et al., 1994; Schneider, 1969). Hence, the question is whether or not the conclusions of Machado and Guilhardi (2000) hold with this new trial-based analysis. More specifically, will the mean transition points given by the psychophysical functions fitted to the averaged data match the mean transition points given by single-trial analysis? Will the two types of analysis yield shifts in the same direction and of similar magnitude? The new analysis will also reveal additional patterns in the data such as the potential correlations between t_1 and t_2 . The purpose of using this alternative measure of the shift, like the purpose of using different species, was to extend the generality of the conclusions of the original study. Such analyses have been reported for the fixed-interval (Schneider, 1969) and peak procedures (Church

et al., 1994), and provided insights into the perception, memory, and decision processes in SET.

2. Materials and methods

2.1. Subjects

Twelve male Sprague–Dawley rats (Taconic Laboratories, Germantown, NY) were housed individually in a colony room on a 12:12 light:dark cycle (lights off at 8:30 a.m.). Dim red lights provided illumination in the colony room and the testing room. The rats were fed a daily ration that consisted of 45-mg Noyes pellets (Improved Formula A) that were delivered during the experimental session, and an additional 15 g of FormuLab 5008 food given in the home cage after the daily sessions. Water was available ad libitum in both the home cages and experimental chambers. The rats arrived in the colony at 35 days of age and were handled daily until the onset of the experiment. Training began when they were 139 days old.

2.2. Apparatus

Twelve chambers (30.5 cm wide \times 24.1 cm deep \times 29.2 cm high) were located inside ventilated, noise-attenuating boxes (66 cm wide \times 55.9 cm deep \times 35.6 cm high). Each chamber was equipped with a food cup, a water bottle, and two levers. A stimulus, referred to as “houselight”, was a diffused houselight (Model ENV-227M, from Med Associates, St. Albans, VT) rated to illuminate the entire chamber over 200 lx at a distance of 3 in. A pellet dispenser (Model ENV-203) delivered 45 mg pellets into the food cup on the front wall. Each head entry into the food cup was detected by a LED-photocell (Model ENV-254). The food cup was centered between the two levers (Model ENV-112) that were 12 cm apart. The two levers were placed 7 cm above the grid, measured 4.5 cm wide, extended 2 cm into the box, and were 0.1 cm in height. The levers required a force of approximately 0.18 N to operate. The water bottle was mounted outside the chamber; water was available through a tube that protruded through a hole in the back wall of the chamber. Two Gateway Pentium® III/500 computers running the Med-PC for Windows Version 1.15 using Medstate Notation Version 2.0 (Tatham and Zurn, 1989) controlled experimental events and recorded the time at which events occurred with 2-ms resolution.

2.3. Procedure

The sessions consisted of 75 trials that were signaled by the presentation of the houselight stimulus for 60 s followed by the termination of the houselight stimulus for 10 s. The left and right levers were inserted at the onset and retracted at the termination of the stimulus. Responses to one of the levers (e.g., left) were potentially reinforced only during the first 30 s of the stimulus. This response is referred to as the “early response”. Responses to the other lever (e.g., right) were potentially reinforced only during the last 30 s of the stimulus. This response is referred to as the “late response”. The stimulus period was divided into four segments of 15 s. During each 15-s segment, an independent

variable interval (VI) 30, 60, or 120-s schedule of reinforcement was in effect. During each second of the period, the reinforcer was primed with a constant probability $p = 1/\text{VI}$. The delivery of the reinforcer was contingent upon the early response during the first two segments and contingent upon the late response during the last two segments. A changeover delay (COD) of 2 s was introduced to prevent frequent switching between the early and late responses. There were three treatments:

- *Baseline 1*: All rats were exposed to VI 60 s during all four 15-s segments. This treatment is referred to as 60–60|60–60 and was in effect for 25 sessions.
- *Local reinforcement rate test*: During this treatment, the VI in each segment was either 30 or 120 s. Six rats were randomly assigned to Group EQU and the other six rats assigned to Group DIF. Three randomly assigned rats from Group EQU were exposed to 30–120|120–30 for 10 sessions followed by 120–30|30–120 for 12 sessions. The other three rats from Group EQU were exposed to the conditions in the reverse order, 120–30|30–120 for 10 sessions, and 30–120|120–30 for 12 sessions. Three randomly assigned rats from Group DIF were exposed to 30–120|30–120 for 10 sessions followed by 120–30|120–30 for 12 sessions. The other three rats from Group DIF were exposed to the conditions in the reverse order, 120–30|120–30 for 10 sessions, and 30–120|30–120 for 12 sessions.
- *Baseline 2*: All rats were exposed to 60–60|60–60 for 10 sessions.

2.3.1. Secondary data analysis

The primary data from the pigeons were provided by the authors and were used for secondary data analysis. These primary data consisted of the times of occurrences of procedural and response events with 1-s resolution. The procedure described in this article differed from the original procedure (Machado and Guilhardi, 2000, Experiment 2) in that: (a) rats were used instead of pigeons; (b) the response was lever press instead of keypeck; (c) VI 30 s was used instead of VI 40 s; (d) no preliminary training or response shaping was used; (e) the order of treatments (30–120|120–30 and 120–30|30–120 for Group EQU, and 30–120|30–120 and 120–30|120–30 for Group DIF) was counterbalanced across rats; and (f) the rats had fewer sessions during each treatment than the pigeons.

3. Results

The results are shown for the local reinforcement rate test trials. Data analysis was restricted to responses emitted prior to any reinforcement during the last five sessions of each condition. The left panels of Fig. 2 shows the relative response rate (response rate divided by the mean response rate) of the rats and pigeons as a function of time since stimulus onset for the EQU (top panels) and DIF (bottom panels) groups. Each of the left panels of Fig. 2 shows the response rate gradients for the early responses (generally decreasing functions) and late responses (generally increasing functions) for the two con-

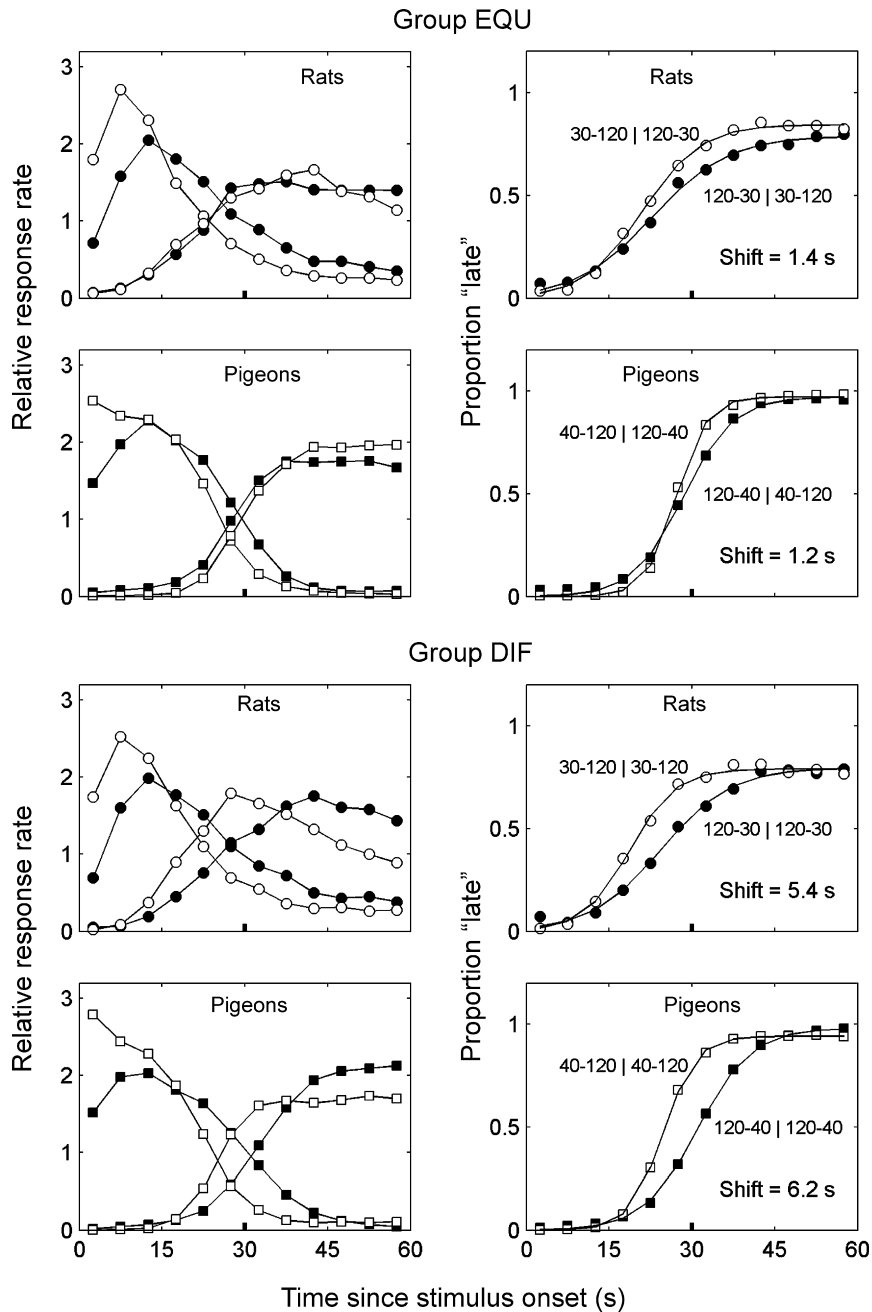


Fig. 2. Relative response rate (left panels) and proportion “late” (right panels) as a function of time since stimulus onset for Groups EQU (top panels) and DIF (bottom panels). The data are shown for rats (circles) and pigeons (squares). The proportion “late” panels show the functions for the conditions for Group EQU (30–120|120–30, and 120–30|30–120 for the rats, and 40–120|120–40, and 120–40|40–120 for the pigeons) and for Group DIF (30–120|30–120, and 120–30|120–30 for the rats, and 40–120|40–120, and 120–40|120–40 for the pigeons). The proportion of late responses in each 5-s bin is the number of late responses divided by the number of late and early responses. The open and filled symbols distinguished the two orders of the VIs, as labeled in the figure. The data are from the last five sessions of each condition.

ditions (empty and filled symbols) of Groups EQU and DIF. Specifically, the empty symbols show the response rate gradients during condition 30–120|120–30 for the rats and condition 40–120|120–40 for the pigeons in Group EQU, and during condition 30–120|30–120 for the rats and condition 40–120|40–120 for the pigeons in Group DIF. The filled symbols show the response rate gradients during condition 120–30|30–120 for the rats and condition 120–40|40–120 for the pigeons in Group

EQU, and during condition 120–30|120–30 for the rats and condition 120–40|120–40 for the pigeons in Group DIF.

During both conditions, and for both Groups EQU and DIF, the relative response rate of the early response increased to a peak shortly after stimulus onset and then slowly decreased, and the relative response rate of the late response started low and then slowly increased. The times at which the falling and rising response rate functions of the same condition crossed were the

times at which the subjects switched from the early to the late response.

The relationship between switching times across conditions is also shown when the proportion of late responses is plotted as a function of time since stimulus onset. The right panels of Fig. 2 shows these psychophysical functions for rats and pigeons during both conditions for Groups EQU and DIF. The functions for each rat and pigeon subject were fit by an ogive curve with scale (b), location (a), and terminal proportion (p) parameters. Eq. (1) describes the ogive curve:

$$f(t) = \frac{P}{1 + e^{-(t-a)/b}} \quad (1)$$

The location parameter (a) is the time from stimulus onset at which the smooth function reaches half of the way to its maximum p for $0 \leq t \leq 60$. The value of a measures the time of switching from the early to the late response. The mean switching times for the Group EQU rats were 21 s during condition 30–120|120–30 and 22 s during condition 120–30|30–120. For the pigeons they were 27 s during condition 40–120|120–40, and 28 s during condition 120–40|40–120. The mean switching times for the Group DIF rats were 19 s during condition 30–120|30–120, and 24 s during condition 120–30|120–30. For the pigeons they were 25 s during condition 40–120|40–120, and 31 s during condition 120–40|120–40.

The difference between the switching times for the two conditions of Group EQU and the two conditions of Group DIF were calculated for each rat and pigeon and used as a measure of the magnitude of the shift in the psychophysical functions. The mean shifts for Group EQU were 0.5 s for the rats and 1.1 s for the pigeons, and the mean shifts for Group DIF were 5.4 s for the rats and 6.4 s for the pigeons. Analysis of variance with groups (EQU and DIF), and species (rats and pigeons) as between-subjects factors revealed that the shift was greater for Group DIF than for Group EQU, $F(1,21) = 31.57$, $p < .001$. There was no effect of species, $F(1,21) = 0.83$, $p = \text{NS}$, and no group \times species interaction, $F(1,21) = 0.24$, $p = \text{NS}$.

An alternative measure (adapted from Church et al., 1994; also Guilhardi and Church, 2004, 2005) based on individual trials was obtained for the early and late responses independently. This adapted measure, described in Fig. 3, determined the time at which the animal changed from either a high to a low state of responding (top panel) or from a low to a high state of responding (bottom panel) on a trial. Specifically, the time of transition was determined as the time of the response within the trial that maximized the area, A , given by the following equation:

$$A = t_1|r_1 - r| + (t_2 - t_1)|r_2 - r| \quad (2)$$

where t_1 is the time of a response on the trial, t_2 the time at which the trial ended (in this procedure, it was always 60 s), r the overall response rate, r_1 the response rate up to time t_1 , and r_2 is the rate between t_1 and the end of the trial. The time of transition measure was calculated only for trials on which at least one response occurred. For each trial, a value of A was calculated for each response emitted on that trial (using the time of occurrence of the response as the value of t_1 in Eq. (2)). The value of t_1 that maximized A was defined as the time of

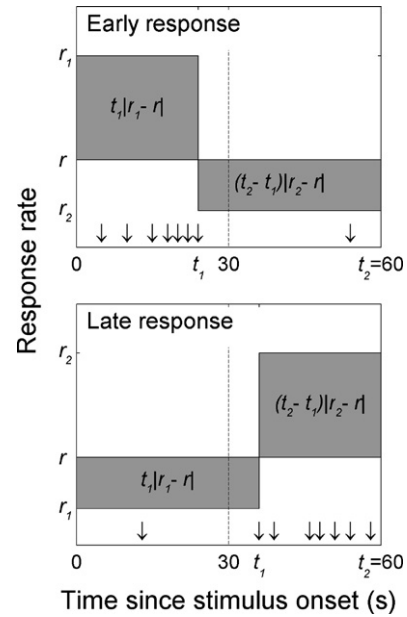


Fig. 3. An alternative dependent measure based on performance on individual cycles for the early and late responses (adapted from Church et al., 1994). The algorithm described in Eq. (2) was used to determine the time at which the animal changed from a high to a low state of responding (top panel) or from a low to a high state of responding (bottom panel). See text for details.

transition on that trial. For trials with only one response, the time of transition was the time of the response. Fig. 3 shows the geometric equivalents of the two terms on the right hand side of Eq. (2). In the figure, time t_1 maximizes the sum of these two terms (i.e., area A).

A comparison of the rates r_1 and r_2 for both levers determined whether the transition was from a low-to-high ($r_1 < r_2$) or a high-to-low ($r_1 > r_2$) response state. As expected, most of the early response transitions were from a high-to-low response state (88% for the rats and 98% for the pigeons in Group EQU, and 87% for the rats and 94% for the pigeons in Group DIF). These results make sense because reinforcement for the early response was delivered only during the first 30 s of the trial. Most of the late response transitions were from a low-to-high response state (90% for the rats and 98% for the pigeons in Group EQU, and 89% for the rats and 95% for the pigeons in Group DIF). Again, the results make sense because reinforcement for the late response was delivered only during the last 30 s of the trial. To reduce variability, the analyses of the times of transitions for the early and late responses were restricted to the transitions that occurred in the expected direction. Therefore, transition times for the early response are referred to as the “stop early-response times” and transition times for the late response are referred to as “start late-response times”. Although not examined here, note that the times of transition in the unexpected direction may provide information about response discrimination errors or uncharacteristic variability in time perception.

The stop early-response and start late-response times for Groups EQU and DIF were highly correlated for every condition, for both rats and pigeons. The mean correlation coefficients (r) for the Group EQU rats was 0.45 during con-

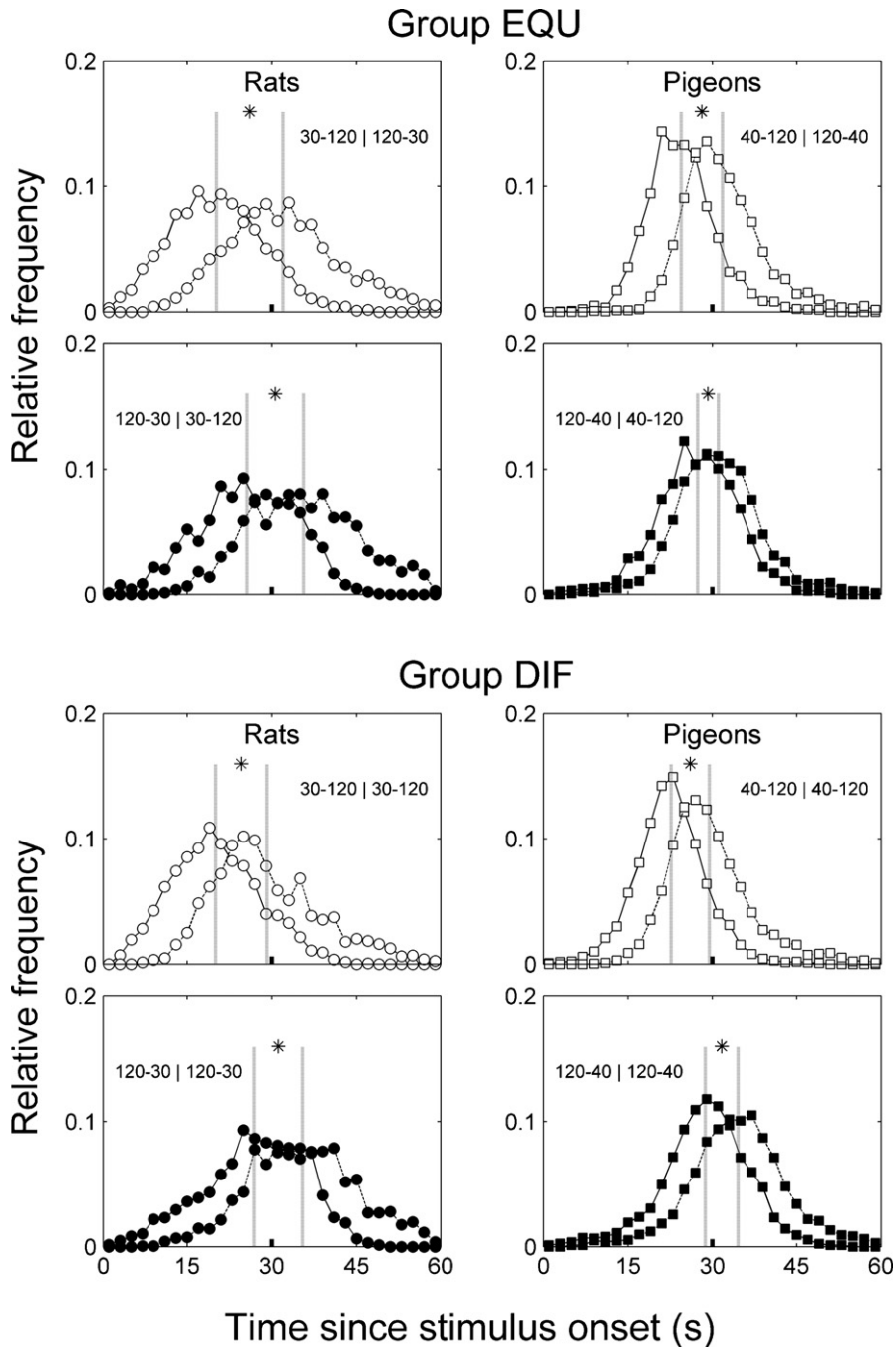


Fig. 4. Frequency distributions of the stop early-response times (solid lines) and start late-response times (dashed lines) for the conditions of Group EQU (top panels, empty symbols) and Group DIF (bottom panels, filled symbols). The data for rats (circles) are shown in the left panels, and the data for pigeons (squares) are shown in the right panels. The vertical dotted lines are the mean start and stop times and the asterisks are the times of transitions between the early and late responses based on a measure from individual trials.

ditions 30–120|120–30 and 120–30|30–120; for the Group EQU pigeons they were 0.58 and 0.82 during conditions 40–120|120–40 and 120–40|40–120, respectively. The mean correlation coefficients for the Group DIF rats were 0.53 and 0.59 (conditions 30–120|30–120 and 120–30|120–30) and for the Group DIF pigeons they were 0.64 and 0.73 (conditions 40–120|40–120 and 120–40|120–40).

Because the correlation coefficients were high, shifts between conditions in the time at which the subjects switched from the

early to the late responses were due to both a shift in the time at which the subjects stopped the early response and a shift in the time at which the subjects started the late response. Fig. 4 shows the distributions of the stop early-response times (solid lines, left curve in each panel) and start late-response times (dashed lines, right curve in each panel) for both the conditions of Groups EQU (top four panels) and DIF (bottom four panels) for rats (left panels) and for pigeons (right panels). The two vertical lines show the mean stop early-response time (left line) and the mean

start late-response time (right line). The time of transition from the early to the late response was determined for each trial by the midpoint between the stop early-response time and the start late-response time. The mean across trials of these transition times is shown as an asterisk in Fig. 4—it is halfway between the two vertical lines.

Within each group and species, the difference between the transition times in the two reinforcement conditions is a measure of the shift in the point of subjective equality based on the behavior during individual trials. For example, for pigeons in Group DIF (two bottom-right panels of Fig. 4) the asterisk for condition 40–120|40–120 is to the left of the asterisk for condition 120–40|120–40. This shift is greater than the corresponding shift for the pigeons in Group EQU (two top-right panels of Fig. 4). The same pattern holds for the rats. The mean shifts were 4.6 s for the Group EQU rats, 1.1 s for the Group EQU pigeons, 6.6 s for the Group DIF rats, and 5.6 s for the Group DIF pigeons. The shifts were greater for Groups DIF than for Groups EQU, $F(1,21) = 31.31$, $p < .001$. There was an effect of species, $F(1,21) = 15.70$, $p < .001$, and a group \times species interaction, $F(1,21) = 4.34$, $p < 0.05$.

4. Discussion

The transition time from the early to the late response has been shown to be a function of the discrepancy between the overall reinforcement rate for the early and late responses. As described by Bizo and White (1995) and replicated by others, the center of the psychophysical function relating the relative response rate for the late response to time into the trial varied inversely with the relative reinforcement rate of the late response. This bias indicates that pigeons shifted earlier to the late response if the late response was reinforced at a higher rate. This bias has also been obtained in a procedure in which the overall reinforcement rates for the early and late responses were the same but the local rate of reinforcement near the transition point was different (Machado and Guilhardi, 2000). Those authors found a bias that indicated that the pigeons shifted earlier to the late response if the late response was reinforced at a higher rate near the point of transition. The results of the present experiment obtained with rats were consistent with those reported by Machado and Guilhardi (2000, Experiment 2) and obtained with pigeons. As in the original article, when the psychophysical functions were based on average response rate functions, the magnitude of the shift of the psychophysical functions was greater in Group DIF than in Group EQU.

An alternative measure based on the performance during individual trials dissociated the time at which rats and pigeons stopped the early response, from the time at which they started the late response. This measure provided additional information: the stop time of the early response was correlated with the start time of the late response. Moreover, the point of transition from the early to the late response (i.e., the midpoint between the stop and start times) shifted across conditions in the same direction and with the same magnitude as described by the averaged psychophysical functions. This alternative analysis was reported using newly collected data from the rats and previously collected

data from the pigeons. The results from the pigeons and the rats were consistent.

The correlation between the stop time of the early response and the start time of the late response was consistent with the start–stop responding correlation pattern reported on the peak procedure (Cheng and Westwood, 1993; Cheng et al., 1993; Church et al., 1994; Gibbon and Church, 1990). The peak procedure (Catania, 1970; Roberts, 1981) is a modified fixed-interval procedure in which food is not presented on some trials and the stimulus remains on for much longer than the FI duration. Responding during the peak procedure is characterized by a low–high–low rate of responding. The observed positive correlation in the peak procedure is between the time at which subjects change from a low to a high rate of responding (start), and the time at which subjects change from a high to a low rate of responding (stop). The correlation observed in the present study was between the stop of the early response and the start of the late response. Although the correlations in the two procedures involve the judgment of different times of events (time of reinforcement in the peak procedure and time of transition between the early and late responses in this procedure), and different responses (a single response for the peak procedure and two responses for the present procedure), both procedures involve subjective judgments of the arrival to and departure from, a target duration.

An interesting feature of the results from the studies using the FOPP procedure is that they provided empirical evidence that was used to evaluate perception, memory, and decision learning processes from two theories of timing: Scalar Expectancy Theory (SET, Church, 1984; Gibbon, 1977; Gibbon and Church, 1990) and Learning-to-Time Theory (LeT, Machado, 1997).

4.1. Predictions from Scalar Expectancy Theory (SET)

In one of the simplest versions of SET, a pacemaker generates pulses at a high rate; the pulses are added in an accumulator; and, at the end of the interval to be timed, the number of pulses in the accumulator is stored in memory. Therefore, memory consists of exemplars of the values from the accumulator that were stored at the time of reinforcement. At the beginning of a trial, a number is sampled from memory and, if the ratio between the sampled number and the current value in the accumulator is below a threshold, instrumental responses are emitted.

Although SET has not been formally applied to the FOPP, an adaptation of SET's account of the temporal bisection procedure (e.g., Gibbon, 1981, 1991; also Church and Deluty, 1977; Stubbs, 1968) may be a reasonable way to do so. First, consider the example of Bizo and White (1995) procedure (e.g., 45|90 or 90|45 conditions). With training, two memory stores are formed, one containing the times of the reinforcers received from pecking the left key, and the other containing the times of the reinforcers received from pecking the right key. At the beginning of each trial, a number from each memory store is sampled and the decision to respond is based on the similarity between each sample and the current value in the accumulator. Because the two memories store the times of reinforcement (via the number in the accumulator), and the left response is reinforced only during the

first half and the right response is reinforced only during the second half of the trial, SET predicts that the switching time between the left and right responses will occur approximately at the middle of the trial. The reason is that the distributions of the times of reinforcement in the two memories are not influenced by differences in overall reinforcement rates between the two keys (see Machado and Guilhardi, 2000, for further details). SET can only account for the shift observed in Bizo and White (1995) results with the assumption of a threshold bias due to the differential reinforcement rate of the two responses. According to this account, the animal has a tendency to remain at or change to the condition that provides greater overall reinforcement rate.

This additional assumption in SET, however, cannot account for the pattern of shifts in the psychophysical functions reported here and by Machado and Guilhardi (2000) because the overall reinforcement rate was constant across the early and late responses. It is possible that SET can account for these results if the differences in the distributions of exemplars in each of the two memories, produced by the local rates of reinforcement, are sufficient to produce a shift. For example, consider condition 120–30|120–30 from the present experiment. Although the two memories store the times of reinforcement, the left response is reinforced only during the first half, and the right response is reinforced only during the second half of the trial. Therefore, there are more exemplars from 16 to 30 s than from 0 to 15 s in the left response memory, and there are more exemplars from 46 to 60 s than there are from 31 to 45 s in the right response memory. Considering that on each trial only one exemplar is sampled from each memory, exemplars from 16 to 30 s from the left memory will be sampled more often than exemplars from 31 to 45 s from the right memory. It is possible that this sampling difference would be sufficient to produce shifts in the psychophysical function. It remains to be seen whether the pattern of findings obtained with the FOPP could be accounted for by a quantitative application of SET that incorporates a decision threshold biased by differences in reinforcement rate and takes into account the local frequency of reinforcement for both responses.

4.2. Predictions from Learning-to-Time (LeT)

The LeT model, an offspring of the behavioral theory of timing (e.g., Killeen and Fetterman, 1988), postulates three elements: a serial organization of behavioral states, a vector of associative links coupling the behavioral states to one or more operant responses, and the operant responses themselves. At the onset of the interval to be timed only the first state is active, but as time elapses the activation of each state flows to the next state in the series. Each behavioral state is coupled with the operant responses. The degree of the coupling decreases during extinction and increases during reinforcement. Specifically, states that are strongly active when a response is extinguished lose their coupling with that response and eventually may not support it, whereas states strongly active when a response is reinforced increase their coupling with that response and may therefore sustain it. The strength of an operant response at time t depends on the degree of the coupling between the states most active at time t and that response.

To apply the model to the FOPP, consider three states: the first maximally active early into the trial, the second maximally active during the middle of the trial, and the third maximally active late into the trial. These states control (via their couplings) the operant responses during the beginning, middle, and end of the trial, respectively. In the FOPP, the first state will always become coupled more with the left than the right responses because while that state is active, left keypecks are reinforced and right keypecks are extinguished. Similarly, the third state will always become coupled more with the right than the left responses because while that state is active, right keypecks are reinforced and left keypecks are extinguished. According to LeT, whether or not the psychophysical functions shift will depend on the couplings of the second state, the state most active during the middle of the trial. For example, when the reinforcement rates around the middle of the trial differ, and the schedule associated with the left key is richer (e.g., 120–40|120–40), the second state becomes coupled more with the left than the right key. Therefore, around the middle of the trial, the animal continues to prefer the left key and the psychophysical function shifts to the right. When the VI for the right key is richer (40–120|40–120), the second state becomes coupled more with the right than the left key and the psychophysical function will shift to the left. In summary, LeT provides a straightforward account of the shifts in the psychophysical function: these shifts are caused by differences in reinforcement rate between the two keys, provided these differences surround the middle of the trial as in the conditions for Group DIF but not for Group EQU. Machado and Guilhardi's (2000) results supported the prediction.

Although it is possible that Scalar Expectancy Theory as applied to the bisection procedure with additional assumptions may account for the pattern of results obtained with the FOPP, a quantitative account of the data has not been developed. In contrast, the Learning-to-Time Theory has been used to fit these results quantitatively with a simple set of assumptions (Machado and Guilhardi, 2000). Nonetheless, both accounts provide insights into the perception, memory, and decision learning processes involved in performance on the FOPP task.

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References

- Bizo, L.A., Chu, J.Y., Sanabria, F., Killeen, P.R., 2006. The failure of Weber's law in time perception and production. *Behav. Process.* 71, 201–210.
- Bizo, L.A., White, K.G., 1995. Biasing the pacemaker in the behavioral theory of timing. *J. Exp. Anal. Behav.* 64, 225–235.
- Body, S., Asgari, K., Cheung, T.H., Bezzina, G., Fone, K.F., Glennon, J.C., Bradshaw, C.M., Szabadi, E., 2006. Evidence that the effect of 5-HT2 receptor

- stimulation on temporal differentiation is not mediated by receptors in the dorsal striatum. *Behav. Process.* 71, 258–267.
- Catania, C.A., 1970. Reinforcement schedules and psychophysical judgments: a study of some temporal properties of behavior. In: Schoenfeld, W.N. (Ed.), *The Theory of Reinforcement Schedules*. Appleton-Century-Crofts, New York, pp. 1–42.
- Cheng, K., Westwood, R., 1993. Analysis of single trials in pigeons' timing performance. *J. Exp. Psychol.: Anim. Behav. Process.* 19, 56–67.
- Cheng, K., Westwood, R., Crystal, J.D., 1993. Memory variance in the peak procedure of timing in pigeons. *J. Exp. Psychol.: Anim. Behav. Process.* 19, 68–70.
- Church, R.M., 1984. Properties of the internal clock. *Ann. N. Y. Acad. Sci.* 423, 566–582.
- Church, R.M., 2002. The effective use of secondary data. *Learn. Motiv.* 33, 32–45.
- Church, R.M., Deluty, M.Z., 1977. Bisection of temporal intervals. *J. Exp. Psychol.: Anim. Behav. Process.* 3, 216–228.
- Church, R.M., Meck, W.H., Gibbon, J., 1994. Application of scalar timing theory to individual trials. *J. Exp. Psychol.: Anim. Behav. Process.* 20, 135–155.
- da Silva, S.P., Lattal, K.A., 2006. Contextual determinants of temporal control: behavioral contrast in a free-operant psychophysical procedure. *Behav. Process.* 71, 157–163.
- Gibbon, J., 1977. Scalar Expectancy Theory and Weber's law in animal timing. *Psychol. Rev.* 84, 279–325.
- Gibbon, J., 1981. On the form and location of the psychometric bisection function for time. *J. Math. Psychol.* 24, 58–87.
- Gibbon, J., 1991. Origins of scalar timing. *Learn. Motiv.* 22, 3–38.
- Gibbon, J., Church, R.M., 1990. Representation of time. *Cognition* 37, 23–54.
- Guilhardi, P., Church, R.M., 2004. Measures of temporal discrimination in fixed-interval performance: a case study in archiving data. *Behav. Res. Meth. Instrum. Comput.* 36, 661–669.
- Guilhardi, P., Church, R.M., 2005. Dynamics of temporal discrimination. *Learn. Behav.* 33, 399–416.
- Killeen, P.R., Fetterman, J.G., 1988. A behavioral theory of timing. *Psychol. Rev.* 95, 274–295.
- Machado, A., 1997. Learning the temporal dynamics of behavior. *Psychol. Rev.* 104, 241–265.
- Machado, A., Guilhardi, P., 2000. Shifts in the psychometric function and their implications for models of timing. *J. Exp. Anal. Behav.* 74, 25–54.
- Machado, A., Pata, P., 2005. Testing the Scalar Expectancy Theory (SET) and the Learning-to-Time model (LeT) in a double bisection task. *Learn. Behav.* 33, 111–122.
- Roberts, S., 1981. Isolation of an internal clock. *J. Exp. Psychol.: Anim. Behav. Process.* 7, 242–268.
- Schneider, B.A., 1969. A two-state analysis of fixed-interval responding in the pigeon. *J. Exp. Anal. Behav.* 12, 677–687.
- Sidman, M., 1966. *Tactics of Scientific Research: Evaluating Experimental Data in Psychology*. Authors Cooperative, Boston, MA.
- Stubbs, A., 1968. The discrimination of stimulus duration by pigeons. *J. Exp. Anal. Behav.* 11, 223–238.
- Stubbs, D.A., 1980. Temporal discrimination and a free-operant psychophysical procedure. *J. Exp. Anal. Behav.* 33, 167–185.
- Tatham, T.A., Zurn, K.R., 1989. The MED-PC experimental apparatus programming system. *Behav. Res. Meth. Instrum. Comput.* 21, 294–302.
- Whitaker, S., Lowe, C.F., Wearden, J.H., 2003. Multiple-interval timing in rats: performance on two-valued mixed fixed-interval schedules. *J. Exp. Psychol.: Anim. Behav. Process.* 29, 277–291.