

Running head: INTERACTION OF TEMPORAL MEMORIES

Interaction of temporal memories in extinction

Carlos Pinto, Inês Fortes, Jeremie Jozefowicz & Armando Machado

University of Minho

Correspond with:

Dr. Armando Machado

Escola de Psicologia

Universidade do Minho

Campus de Gualtar

4710 - 057 Braga

Portugal

Email: armandom@psi.uminho.pt

Phone: +351-253-604-252

Fax: +351-253-604-224

Submitted March 2011

## Abstract

Two experiments tested how training in a fixed-interval (FI) 15-s schedule interfered with previous temporal learning. In both experiments, a control group was exposed to a FI 15-s schedule and then to a 500-s extinction trial. Its performance during extinction served as a baseline against which the performance of the experimental groups could be compared. The Experimental Group was initially exposed to either a FI 120-s schedule (Experiment 1) or a peak FI 120-s schedule (in Experiment 2); next it was exposed to the FI 15-s schedule and then to the extinction trial. In both experiments, the sole effect of the initial training was on the overall response rate of the Experimental Group, which was either higher (Experiment 1) or lower (Experiment 2) than the overall response rate of the Control Group. The data are not consistent with Machado's (1997) Learning-to-Time (LeT) model.

Keywords: Memory, Timing, Extinction, Reinforcement history, Fixed Interval, Peak Procedure, LeT, pigeon.

## Interaction of temporal memories in extinction

A common procedure to study the sense of time in animals is the Fixed Interval (FI) reinforcement schedule. In a FI schedule, a time marker (e.g., a light) signals the onset of an interval and the first response after a specified time has elapsed turns off the time marker and is reinforced. An animal well trained in this schedule shows a typical response pattern: After an initial pause, response rate increases and peaks around the time of reinforcement (e.g., Ferster & Skinner, 1957).

Previous studies have examined the effects of a particular reinforcement history on FI schedule performance. For example, rats and pigeons have been exposed to Fixed Ratio, Variable Ratio, or Differential Reinforcement of Low rates schedules to examine how such exposure affected response rate and response patterning on subsequent FI schedules (e.g., Freeman & Lattal, 1992; López & Menez, 2005). The rationale for these studies was the idea that the “subject’s history” includes a variety of sources of control of current performance and for that reason an Experimental Analysis of Behavior cannot ignore it.

One way to conceptualize history effects is in terms of memory formation and memory interaction with current context (see, for instance, Bouton, 2004 for a similar approach to the role of context and memory in Pavlovian conditioning). An experience at time  $t_1$  and in context  $c_1$  may leave an animal with memory  $m_1$ , and that memory may then influence the animal’s behavior at time  $t_2$  and in context  $c_2$ . In addition, the new experience may leave the animal with memory  $m_2$ , which may interact with  $m_1$ . If the experiences at times  $t_1$  and  $t_2$  involve temporal discriminations we refer to the memories as temporal memories. The main goal of the present study is to understand how the temporal memories  $m_1$  and  $m_2$  affect each other and relate to behavior.

To illustrate the approach, assume that a pigeon is exposed to a FI 120-s schedule for 30 sessions. At the end of training, it will have learned to suppress keypecking during the first half of the Inter Reinforcement Interval (IRI) such that, averaged across trials, its response rate curve shows the typical signature of temporal discrimination, the sigmoid curve. Most theories of timing (e.g., Gibbon, Church, & Meck, 1984; Jozefowicz, Staddon, & Cerutti, 2009; Killeen & Fetterman, 1988;

Machado, 1997; Staddon & Higa, 1999) assume that during training the pigeon forms a long lasting temporal memory. For example, Scalar Expectancy Theory (SET; Gibbon, Church, & Meck, 1984; see also Gibbon, 1977, 1991) assumes that the animal represents the IRI by a Gaussian random variable whose instances are stored in long-term memory; this memory is then used to decide when to start responding during a trial. Because the mean and standard deviation of the Gaussian variable are proportional to the IRI, different IRIs engender different temporal memories.

In the Behavioral Theory (BeT; Killeen & Fetterman, 1988), the Learning-to-Time (LeT; Machado, 1997; Machado, Malheiro, & Erlhagen, 2009) and the Behavioral Economic Model (BEM; Jozefowicz et al., 2009) family of models, the assumption related to temporal memory takes the form of associations or couplings between behavioral states and the operant response. During the IRI, the behavioral states are activated in series. In addition, the most active states during reinforcement become strongly coupled with the operant response, whereas earlier states in the series will become less strongly coupled because they are active mostly during extinction periods; the very first states in the series, active during the beginning of the IRI, will be either weakly coupled or even uncoupled with the operant response because they will rarely or never be active during reinforcement. Other things equal, given two distinct IRIs, 120 s and 15 s, for example, the states most strongly coupled with the operant response will be further down the series in the 120-s case than in the 15-s case. Hence, the vector of couplings between the states and the operant response is akin to a long-term memory of the IRI.

What happens to the temporal memory when the reinforcement conditions change? A few empirical studies have examined how a temporal memory acquired during periodic reinforcement (FI schedule) changes during extinction and reacquisition. Guilhardi and Church (2006; see also Guilhardi, Yi, & Church, 2006), exposed rats to three experimental phases. During the first phase, the rats were exposed to a three-component multiple schedule with discriminative stimuli A, B, and C: Mult.  $A \rightarrow FI\ 30\ s$ ,  $B \rightarrow FI\ 60\ s$ ,  $C \rightarrow FI\ 120\ s$ . During the second phase, the three component schedules changed to extinction and finally, during the third phase, the multiple schedule was

reinstated, either with the same stimulus mapping (i.e.,  $A \rightarrow \text{FI } 30 \text{ s}$ ,  $B \rightarrow \text{FI } 60 \text{ s}$ ,  $C \rightarrow \text{FI } 120 \text{ s}$ ; group consistent) or with a different mapping (e.g.,  $B \rightarrow \text{FI } 30 \text{ s}$ ,  $C \rightarrow \text{FI } 60 \text{ s}$ ,  $A \rightarrow \text{FI } 120 \text{ s}$ ; group inconsistent). They found that during extinction the overall response rate decreased significantly, but when the animals responded the response pattern was similar to the pattern displayed during acquisition (i.e., response rate increased throughout the interval, with greater slope in A, the stimulus associated with the FI 30 s, then in B, the stimulus associated with the FI 60 s, and then in C, the stimulus associated with the FI 120 s). This result suggests that the three temporal memories acquired during the first condition were preserved during extinction. Additional evidence for memory retention came from the first sessions of the reacquisition phase: For both groups of rats, consistent and inconsistent, responding increased rapidly and its gradient during the first 3 cycles of the multiple schedule was determined by the schedule associated originally with the discriminative stimulus. Whereas group consistent showed the final gradients since the first cycles of phase 3, group inconsistent needed a few sessions to learn the new stimulus mapping and display the appropriate gradients. These results show not only that the three temporal memories survived during the extinction phase, but also that they were accessed by the discriminative stimuli.

In Guilhardi and Church's (2006) study, the temporal memories were formed simultaneously during Phase 1 and they were always bound to particular exteroceptive stimuli such as a clicker (A), noise (B), or light (C). Hence, it is not clear whether their findings apply more generally, for example, to situations in which the temporal memories are formed successively and are not bound to distinct discriminative stimuli. Before we describe in greater detail the foregoing situation, consider a simpler, intermediate case. A pigeon is exposed to a mixed FI 15 s FI 120 s: On half of the trials, a FI 15-s schedule is in effect; on the other half, a FI 120-s schedule is in effect. The trials are intermixed randomly and only one response key is available. Results show that, at the steady state, the pigeon pauses for a few seconds, then it responds at a constant rate until either reinforcement occurs at 15 s and the trial ends or until a few seconds elapse after 15 s, in which case it pauses again and finally, closer to 120 s, it resumes pecking until it receives the reinforcer and the trial ends. Hence, on the

longer trials, performance consists of a break-run-break-run pattern (Leak & Gibbon, 1995; see also Ferster & Skinner, 1957, pp. 597–605; Catania & Reynolds, 1968). The initial break-run sub pattern is a function of the shorter FI duration; the final break-run sub pattern is a function of the longer FI duration. These sub patterns clearly express two temporal memories, one for the 15-s IRI and the other for the 120-s IRI. As in Guilhardi and Church's (2006) study, the two temporal memories were formed simultaneously<sup>1</sup>, but in contrast with their study, the memories are not bound to distinct stimuli. In fact, the only exteroceptive stimulus in the situation is the response key, turned on at trial onset<sup>2</sup>. Hence, the two memories seem to be accessed by a common stimulus or time marker, albeit at different times, one at trial onset (15-s IRI), and the other significantly later into the long trials (120-s IRI).

Consider now the case in which the two memories, accessible by a single stimulus, are formed sequentially. To be concrete suppose that a pigeon is exposed to a FI 120-s schedule for 30 sessions (Phase 1) and then to a FI 15 s for an additional 15 sessions (Phase 2). Throughout, the discriminative stimulus remains the same – the keylight is turned on at trial onset. At the end of Phase 2, will there be two memories, one for the 120-s IRI and another for the 15-s IRI, or will the memory for the 15-s IRI replace the memory for the 120-s IRI? If the older memory is retained, will it be changed by the new memory, a form of retroactive interference, or will the new memory be affected by the older memory, a form of proactive interference? More generally, how do the two memories affect each other? In addition, if two distinct temporal memories are formed sequentially, can they still be accessed by the same discriminative stimulus? In Guilhardi and Church's (2006), three distinct stimuli accessed three distinct temporal memories (see left panel of Figure 1). In the example with the mixed FI 15-s FI 120-s schedule, the same discriminative stimulus, S, accessed two temporal memories but these memories were formed simultaneously (see middle panel of Figure 1).

---

<sup>1</sup> It remains to be seen whether the two temporal memories acquired during a mixed FI FI schedule and expressed in the break-run-break-run pattern are preserved under extinction and revealed under reacquisition, as in Guilhardi & Church's (2006) study.

<sup>2</sup> The discriminative stimulus may be more complex and comprise, in addition to the keylight illumination, the reinforcer delivery that ends the previous trial and the changes in the houselight that follow the reinforcement period. But the point of the argument is that regardless of the precise nature of the discriminative stimulus, it remains the same for the two temporal memories.

In the current example, the discriminative stimulus is bound during Phase 1 to the temporal memory for the 120-s IRI (M1 in the right panel of Figure 1) and then the same stimulus is bound during Phase 2 to the temporal memory for the 15-s IRI (M2 in the right panel of Figure 1). Hence, it is unclear whether S can still access the original memory for the 120-s IRI.

Of the timing models considered above, only LeT makes specific predictions concerning the foregoing situation. With respect to SET, BeT, and BEM, neither model is sufficiently explicit about how temporal memories are formed or changed with experience and, for that reason, neither model can answer questions related to the potential interactions of sequentially formed temporal memories or their accessibility by a single stimulus (see also Machado & Silva, 2007; Gallistel, 2007, for the difficulties of SET with mixed FI schedules). With respect to LeT, under reasonable assumptions, it predicts that the vector of couplings (the temporal memory) learned during the FI 120-s schedule will change during the FI 15-s schedule such that, at the end of training, there will be two sets of states strongly coupled with the operant response, the set active around 15 s and the set active around 120 s. The states that are active well before 15 s ( $t < 15$  s) and the states that are active well after 15 s but well before 120 s ( $15 < t < 120$  s) will be poorly coupled with the operant response because these two intervals are extinction periods. In fact, when the two IRIs are significantly apart, as in the current example with 120 s and 15 s, LeT predicts that the vector of couplings will be similar to that engendered by a mixed schedule. That is, exposing the animals to a FI 120 s and then to a FI 15 s (right panel of Figure 1) should engender approximately the same vector of couplings (temporal memories) as exposing the animals to a random mixture of a FI 15-s and a FI 120-s schedules (middle panel of Figure 1). In terms of measurable behavior, LeT predicts that if the experimenter extends the trial significantly beyond 15 s, then the states that are active around 120 s will reveal their couplings with the operant response. That is, on such trial, response rate will be low during the

first seconds of the trial, attain a peak during 15 s (revealing M2), decrease thereafter and then increase again until a new peak is reached around 120 s (revealing M1) (Figure 2)<sup>3</sup>.

The present study attempted to answer the foregoing questions and predictions by means of the following experimental design. Pigeons were first exposed to a 120-s IRI such that temporal memory M1 would be formed and accessed by the single key, S, present in the situation. Next, the IRI changed to 15 s so that temporal memory M2 would be formed and accessed by the same stimulus, S. Finally, two long periods of extinction were included in each session to determine whether memory M1 could still be accessed by S. A control group was exposed only to the 15-s IRI and therefore only memory M2 was formed. Any difference between the two groups during the extinction period, in particular any difference in response rate or response patterning around 120 s, would reveal the presence of M1 and its accessibility by S.

## Experiment 1

### *Method*

#### *Subjects*

The subjects of Experiment 1 were twelve adult pigeons (*Columba livia*). Four of the animals were experimentally naïve while the remaining birds had participated in a time-left experiment or a categorical discrimination experiment. The birds were divided in two groups, and care was taken to distribute the birds with different experimental histories equally between the two groups. Throughout the experiment, the animals were maintained at 80% of their free-feeding body weight. Water and grit were always freely available in their living cages. The pigeon colony room was maintained in a 13h:11h light/dark cycle, with the lights on at 08:00, and its temperature was kept between 20 and 22°C.

#### *Apparatus*

---

<sup>3</sup> What happens after 120s depends on the assumption concerning the initial couplings of the states. The original LeT model (Machado, 1997) predicts that response rate will decrease after 120 s (i.e., response rate will show a generalization gradient around 120 s; see Machado & Cevik, 1998). The new LeT model (Machado, Malheiro, & Erlhagen, 2009) predicts that response rate will remain high for a long while because it assumes that all states are initially sufficiently coupled to sustain the operant response. That is, the animal learns when not to respond.



Six operant chambers were used in Experiment 1, three Lehigh Valley pigeon chambers and three Med Associates test chambers. The two types of chambers differed slightly only in their dimensions. The Med Associates chambers (31.8-cm long, 25.4-cm wide and 34.3-cm high) were enclosed in a PVC Sound Attenuating Cubicle equipped with a ventilation fan. The response panel was equipped with three circular response keys distributed in a horizontal line, 8 cm apart, center to center. The diameter of each key was 2.5 cm and they were located 20.5 cm above the floor grid. Below the response keys, a grain feeder (with a 6 x 6.5 cm opening) allowed access to food. A houselight, centered horizontally on the wall opposite to the response panel and 22 cm above the floor, provided illumination to the chamber.

The dimensions of the Lehigh Valley chambers were 34 cm (height) x 35 cm (length) x 31 cm (width). Each chamber was enclosed in an outer box, equipped with a ventilation fan. Three response keys, 2.5 cm in diameter, were arranged in a horizontal row, 9 cm apart center to center. The bottom edge of each key was 22.5 cm above the wire mesh floor. The hopper opening (6 x 5 cm) was centered horizontally on the response panel, 8.5cm from the floor. When activated, the food hopper was illuminated with a 7.5-W light. On the wall opposite the response panel, a houselight was centered horizontally, 30cm above the floor. In all chambers, the response keys could be illuminated with colored hues. The ventilation fans circulated air inside the boxes and masked outside noises. The experimental events were controlled through Lafayette Instrument's "Animal Behavior Environment Test System" (ABET II) software program, which also recorded the session data.

### *Procedure*

The pigeons were divided into an Experimental and a Control Group (see Table 1). The Control Group was trained only with a FI 15-s schedule, but the Experimental Group received FI 120-s training before the FI 15-s training.

*FI 120-s training:* Only the pigeons from the Experimental Group went through this phase. A trial started with the illumination of the center key with a red hue. The first peck on the key after an interval of 120 s had elapsed operated the feeder for 4 s. Reinforcement was followed by a 10-s inter-

trial interval (ITI), spent in darkness. Each daily session comprised 40 trials. After a minimum of 15 sessions, the pigeons moved to the next phase of the experiment if the average response rate functions for the last three consecutive sessions superimposed, as determined by visual inspection. If this stability criterion had not been met even after 30 sessions, the pigeon moved to the next phase.

*FI 15-s training:* All pigeons went through this phase. The procedure was identical to that for the FI 120-s phase except that a) the FI was 15-s long, b) if no peck occurred between 15 and 20 s into the trial, the trial was cancelled (this limited hold ensured that no reinforcement occurred between 20 and 120 s); c) to keep body weight constant, the reinforcement duration varied across pigeons from 2.5 to 3 s; and d) sessions ended after 60 trials. The learning criterion was the same as in the previous phase. If it was not met after 25 sessions, the pigeon moved to the next phase.

*Test:* All pigeons went through this phase. Sessions remained as in the previous phase, except that they included two more trials, each lasting 500 s and ending without reinforcement. Specifically, each session comprised 60 trials divided into 5 blocks. The first, third, and fifth blocks comprised 10 FI 15-s trials. The second and forth blocks comprised one 500-s extinction trial and 14 FI 15-s trials, with the location of the extinction trial determined randomly. Therefore, there were two 500-s extinction trials in each daily session. Reinforcement duration on the FI 15-s trials varied across birds from 2 to 4 s. The test phase ran for 5 sessions.

### *Results and Discussion*

Pigeons in the Control Group took an average of 20 sessions to meet the stability criteria (range: 15 to 25 sessions); pigeons in the Experimental Group took on average 24 sessions (range: 17 to 30) to meet the criterion in the FI 120-s phase and 24 sessions (range: 23 to 25 sessions) to meet it in the FI 15-s phase.

Figure 3 shows the temporal pattern of response rate for both groups during each FI phase. The right panel of Figure 3 shows the response rate pattern during the FI 120-s phase for the Experimental Group, as well as the response pattern for both groups during the FI 15-s phase. Average response rate increased steadily during both the 120-s interval and the 15-s interval, which

reveals good temporal control. Moreover, overall response rate was much lower during the FI 120-s phase than the FI 15-s phase. This result is consistent with data on the effect of reinforcement rate on response rate (Killeen, 1998; Shull, 2005).

The left panel of Figure 3 suggests by visual inspection that both groups exhibited temporal control during the FI 15-s stage, somewhat better in the Control than the Experimental Group. However, because of substantial variability in absolute response rates across birds, only when the response rate functions were normalized the differences between the two groups were statistically significant (i.e., a between-within ANOVA on relative response rate yielded a significant Group x Time-into-the-trial interaction,  $F(14,140)=5.13, p<.001$ ). We conclude that the groups differed in response patterning, with the Control Group showing better temporal control than the Experimental Group.

The cause for the difference in response patterning is unclear. Because the reinforcement rate was much lower in the FI 120-s schedule than in the FI 15-s schedule, the transition from the former to the latter might have inflated the subjective value of the reinforcer for the Experimental Group relative to the Control Group. If subjective value is functionally similar to reinforcement magnitude, then greater subjective value could have engendered higher response rates (see Shull, 2005) and shorter wait times (see Galtress & Kirkpatrick, 2009; Ludvig, Conover, & Shizgal, 2007). Yet another possibility to explain the difference in response rate is the number of sessions. Because the FI 15-s and the FI 120-s phases had an equivalent number of sessions, the Experimental Group, by virtue of its two training phases, completed a larger number of sessions than the Control Group. Be that as it may be, appropriate memories for the FI 15 s and FI 120 s have been induced by training.

Overall, 10 extinction trials were run, but because the first trial was the most informative, only data for the first extinction trial will be presented and analyzed. Figure 4 shows the response rate pattern during that trial for the individual pigeons from the Control (left column) and Experimental (right column) groups, and Figure 5 shows two average functions, the absolute

response rate function (left panel) and the relative response rate function (right panel). Both figures tell the same story: A decrease in response rate follows an initial increase in both groups. In the Control Group, despite decreasing, responding continues at least until 150 to 200 s had elapsed. This is consistent with previous data which have shown that, on the first peak trial, animals keep on responding past the time of reinforcement for about 10 times the duration of the FI previously trained (Machado & Cevik, 1998). The pattern is identical in the Experimental Group except that the response rate never falls as low as in the Control Group (Figure 5, left panel) and the decrease is slightly slower (Figure 5, right panel). Although the first effect is not confirmed by the statistical analysis, which fails to find any significant difference between the groups, a between-within ANOVA on the relative response rate using time in a trial and group as factors found a significant interaction between the two factors,  $F(31,310)=2.15$ ;  $p=.001$ .

Overall, there is no indication that the memory for the FI 120 s has been reactivated in the Experimental Group, as predicted by LeT. In this case, based on the performance in the FI 120 s (Figure 3, right panel), we should have observed an increase in responding between 45 s and 120 s into the trial; we did not. In fact, the temporal pattern of responding in the Experimental Group during the test trial was roughly identical to the one in the Control Group. The only clear difference was the higher response rate observed in the Experimental Group at the end of the test trial and the slower decrease in responding. Although the differences could be due to a reactivation of the FI 120-s memory, it seems more parsimonious to explain them as carry-over effects of the differences observed during the FI 15-s phase (Figure 3, left panel).

In conclusion, the prediction of LeT was not verified. The memory for the FI 120-s was not re-accessed, and either it was erased by the FI 15-s training or it could not be retrieved because of interference from the FI 15-s memory. A difficulty with this interpretation is the difference in average response rate between the two groups (Figure 3, left panel). During the test trial, the average response rate curves decreased for both groups and, around 200 s, they reached the terminal rate observed during the FI 120-s schedule. It is possible that any effect of the reactivation of the FI 120-s

memory was masked by the higher response rate activated by the FI 15-s memory. If that was the case, then any effect of the reactivation of the FI 120-s memory could be detected only after about 200 s into the extinction trial. Alas, past this point, LeT predicts that, under reasonable conditions, the animal will continue to respond at a constant rate. Hence, under these assumptions, LeT could accommodate the present data. On the other hand, if the pigeons had been trained in a peak FI 120 s instead of a FI 120 s, the model would predict that response rate past approximately 120 s in extinction should decrease. In this case, the reactivation shortly after 120 s into extinction of the 120-s memory would lead to a faster decrease in responding in the Experimental Group than in the Control Group. We tested this prediction in Experiment 2.

## Experiment 2

### *Method*

#### *Subjects and Apparatus*

Twelve adult pigeons (*Columba livia*) participated in Experiment 2. As in Experiment 1, four of the animals were experimentally naïve whereas the remaining birds had previous experience with categorical discrimination, time-left procedure or temporal bisection tasks. Housing conditions and the apparatus were the same as in Experiment 1.

#### *Procedure*

The pigeons were divided into two groups, Experimental and Control (Table 2). The Control Group was trained with a FI 15-s schedule and then exposed to extinction test trials. The Experimental Group was trained with a peak FI 120-s schedule, followed by the FI 15-s schedule and then the extinction test trials.

*FI 120-s training:* Only the pigeons in the Experimental Group went through this phase, which was identical to the corresponding phase in Experiment 1.

*Peak FI 120-s training:* Only the pigeons in the Experimental Group went through this phase, which was identical to the previous phase, except that 10 of the 40 FI 120-s trials were replaced by 10 unreinforced peak trials lasting 500 s (empty trials). A session began with five FI 120-s trials, and

was followed by two blocks of 15 trials each. In each block there were 10 FI 120-s trials and 5 500-s empty trials, presented in random order. The session ended with 5 FI 120-s trials.

After an average of 27 sessions (range: 24 to 33 sessions), we still did not observe a reliable decrease in responding after 120 s. Hence, the following procedural modifications were introduced sequentially:

- a) The number of empty trials increased from 10 to 18. A session now began with 4 FI 120-s trials followed by a block of 36 trials (18 FI 120-s trials and 18 500-s empty trials, presented in random order), for a total of 40 trials per session. This was done for an average of 16 sessions (range: 16 to 17 sessions).
- b) The duration of the empty trial was doubled. As a consequence, the number of trials decreased from 40 to 30. After an initial block of 5 FI 120-s trials, a block of 25 trials followed (20 FI 120-s trials and 5 1000-s empty trials, presented in a random order). Because performance still did not improve (after 12 sessions for all birds), we reasoned that the absence of a clear break after 120 s was less a matter of the proportion of FI to extinction trials, or of the duration of the empty trials, than the salience of the time marker.
- c) To increase the salience of the time marker, the houselight was turned on at trial onset, so that each trial was now signaled by the illumination of both the houselight and the (red) center keylight. This modification improved the temporal discrimination slightly.

At this point the experiment was restarted from the FI 120-s phase. The procedure was exactly the same with the difference in the time marker. Under these conditions, in the peak FI120-s phase, each session lasted for 30 trials, 25 reinforced trials and 5 empty trials. A session began with five FI 120-s trials and was followed by a block of 25 trials, 20 FI 120-s trials and 5 empty trials, presented in random order. The pigeons were trained for a minimum of 15 and a maximum of 30

sessions, and until the response rate pattern of the last three sessions superimposed by visual inspection.

*FI 15-s training and testing:* All pigeons went through these phases. Except for the change in the time marker (i.e., houselight on, together with response key, during the trial but off during ITI), they were identical to the corresponding phase in Experiment 1.

### *Results and Discussion*

The birds from the Control Group needed 20 sessions on average (range: 15 to 25 sessions) to reach the stability criterion; birds in the Experimental Group needed 20 sessions in the FI 120-s phase, 30 sessions in the peak FI 120-s phase, and an average of 20 sessions (range: 18 to 21 sessions) in the FI 15-s phase.

The right panel of Figure 6 shows responding during the peak FI 120-s for the Experimental Group and during the FI 15-s for both the Control and Experimental groups. Performance during the peak trials reveals good temporal discrimination, with a clear peak in responding, even though response rate after the peak never falls down to zero. Also, although the peak usually occurs at the time of reinforcement (120 s in this case), the peak in Figure 6 is clearly shifted to the right (180 s). The shift may have been due to the more salient time-marker. In fact, Staddon and Higa's (1999) Multiple Time Scale (MTS) model predicts a shift in both wait time and peak time when the salience of the time marker increases, although the shift should have been transient and disappeared with prolonged exposure. Similar to Experiment 1, the overall response rate in the peak FI 120-s schedule is much lower than in the FI 15-s schedule.

The left panel of Figure 6 shows responding in the FI 15-s for the Experimental and Control groups. As in Experiment 1, there are differences between the two groups, although they are not in the same direction. In Experiment 1, the Experimental Group had a higher response rate and a shorter pause than the Control Group. In Experiment 2, the curves for both groups are similar during the early part of the trial but the difference increases as a function of time. Indeed, a between-within ANOVA on the absolute response rate using time in the trial and group as factors found a significant

interaction between the two factors,  $F(14,112)=3.46$ ,  $p<.001$ . According to Cheng and Westwood (1993), performance on individual FI trials consists of an initial period of low responding followed by a period of high responding. One way to interpret the curves shown in the left panel of Figure 6 is to say that the two groups did not differ much in response rate during the low-response period nor in the point where they switch from the low- to the high-response period, but they differ in response rate during the high-response period, with the Experimental Group showing a lower rate than the Control Group. The rate of the Experimental Group may have been lower because of the extended exposure to the FI 120-s and peak FI 120-s phases, where response rate tends to be lower.

Figure 7 shows the temporal pattern of responding during the first test trial for the individual birds in the Control (left column) and Experimental (right column) groups, and Figure 8 shows the average data, absolute response rate on the left panel, and relative response rate on the right panel. Both figures tell the same story. There is no difference in the temporal pattern of responding between the Control and Experimental groups, as indicated by the fact that the relative response rate curves for both groups superimpose (Figure 8, right panel). A between-within ANOVA on the relative response rate using time in the trial and group as factors failed to find any significant effect besides the one of time,  $F(31,248)=4.11$ ,  $p<.001$ . The only clear difference between the groups is a lower response rate in the Experimental Group, clearly illustrated in the left panel of Figure 8. A between-within ANOVA on the absolute response rate using time in a trial and group as factors, found a significant effect of time,  $F(31,248)=4.95$ ,  $p<.001$  and of group  $F(1,8)=7.44$ ;  $p=.026$ , but no interaction. This difference is clearly a consequence of the discrepancy in response rate between the two groups already observed in the FI 15-s phase (Figure 6, left panel).

Hence, overall, the predictions of LeT were not verified. There is no indication that the peak FI 120-s memory has been reactivated during the test trial: There is no increase in responding around 180 s (where the peak was observed in the peak FI 120-s performance) and the decrease in responding past that point is not faster than in the Control Group.





### General Discussion

In two experiments, performance in extinction of pigeons trained on a FI 15-s schedule was compared with the performance of pigeons trained also on a FI 15-s schedule but who had previously been trained in a FI 120 s (Experiment 1) or a peak FI 120 s (Experiment 2) schedule. The goal was to test the predictions of LeT regarding the way long-term temporal memories are formed and retained. According to this model, states activated late in a trial would have shown their coupling with responding changed during the FI 120 s or the peak FI 120-s training. Because those states are not accessed again during the FI 15-s training, their coupling with responding should have been left intact. Hence, compared to the control groups, we should have observed a resurgence of responding around 120 s in both experimental groups, followed by a further decrease in responding only in the peak FI 120-s group.

These predictions were not confirmed by the data. As far as the temporal pattern of responding during the test trials is concerned, we found no evidence that the experimental groups differ from the control groups. Contrary to what LeT predicted, the memory for the FI 120 s or the peak FI 120 s was never reactivated during the test trials, either because it was erased by the FI 15-s memory or because that memory interfered with its retrieval. Anyway, the temporal pattern of responding during the test trial seems to have been controlled only by the FI 15-s memory. This is an outcome incompatible with LeT, but also with other associative model of timing (i.e. Jozefowicz et al., 2009; Killeen & Fetterman, 1988). Its implications for cognitive models like SET are not clear, as those models have no framework describing the way temporal memories interfere with each other.

The only long-term impact of the (peak) FI 120-s training on performance was not on the response pattern but on the response rate, even though this effect was not consistent between Experiment 1 and Experiment 2. In Experiment 1, the Experimental Group had a higher response rate and a shorter pause than the Control Group. In Experiment 2, there was no clear difference in the pause between the two groups and the overall response rate was lower in the Experimental Group. This inconsistency may reflect simply the difference in training between the experimental groups (FI

120-s vs. peak FI 120-s) as well as the larger number of sessions of the Experimental Group in Experiment 2. Anyway, the results suggest a clear dissociation between response rate, which shows an effect of previous training, and the temporal pattern of responding, which shows none. This dissociation is consistent with the proposal made by several independent researchers (i.e. Guilhardi, Yi, & Church, 2007; Jozefowicz, Cerutti, & Staddon, 2005) that response rate and the temporal pattern of responding are controlled by two independent processes, one sensitive to the overall reinforcement rate, the other to the time-of-reinforcement distribution.

In summary, the current data do not support LeT's conception of how long-term temporal memories are stored and accessed. They also call for further research into the way new temporal memories interfere with older ones, how old temporal memories are retrieved, and how they are expressed in measureable behavior. Only then will our understanding of temporal learning improve significantly.

## References

- Bouton, M. E. (2004). Context and behavioral processes in extinction. *Learning and Memory*, 11, 485-494.
- Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, 11, 327–383.
- Cheng, K., & Westwood, R. (1993). Analysis of single trials in pigeons' timing performance. *Journal of Experimental Psychology: Animal Behavior Processes*, 3, 216-228.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. New York: Appleton-Century-Crofts.
- Freeman, T. J., & Lattal, K. A. (1992). Stimulus control of behavioral history. *Journal of the Experimental Analysis of Behavior*, 57 (1), 5-15.
- Gallistel, C. R. (2007). Flawed foundations of associationism? Comments on Machado and Silva (2007). *The American psychologist*, 62, 682–685.
- Galtress, T., & Kirkpatrick, K. (2009). Reward value effects on timing in the peak procedure. *Learning and Motivation*, 40, 109-131.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, 84, 279–325.
- Gibbon, J. (1991). Origins of scalar timing theory. *Learning and Motivation*, 22, 3–38.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In L. Allan & J. Gibbon (Eds.), *Timing and time perception* (pp. 52–77). New York: Annals of the New York Academy of Sciences.
- Guilhardi, P., & Church, R. M. (2006). The pattern of responding after extensive extinction. *Learning & Behavior*, 34(3), 269-284.

- Guilhardi, P., Yi, L., & Church, R. M. (2006). Effects of Repeated Acquisitions and Extinctions on Response Rate and Pattern. *Journal of Experimental Psychology: Animal Behavior Processes*, 32(3), 322-328.
- Guilhardi, P., Yi, L., & Church, R. M. (2007). A modular theory of learning and performance. *Psychonomic Bulletin & Review*, 14, 543-559.
- Jozefowicz, J., Cerutti, D. T., & Staddon, J. E. R. (2005). Timing in choice experiments. *Journal of Experimental Psychology: Animal Behavior Processes*, 31, 213-225.
- Jozefowicz, J., Staddon, J. E. R., & Cerutti, D. T. (2009). The behavioral economics of choice and interval timing. *Psychological Review*, 116, 519-539.
- Killeen, P. R. (1998). The first principle of reinforcement. In C. D. L. Wynne & J. E. R. Staddon (Eds), *Models of action: Mechanisms for adaptive behavior* (pp. 127-156). Mahwah, NJ: Lawrence Erlbaum Associates.
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review*, 95, 274-285.
- Leak, T., & Gibbon, J. (1995). Simultaneous timing of multiple intervals: Implications of the scalar property. *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 3-19.
- López, F. & Menez, M. (2005). Effects of reinforcement history on response rate and response pattern in periodic reinforcement. *Journal of the Experimental Analysis of Behavior*, 83 (3), 221-241.
- Ludvig, E. A., Conover, K., & Shizgal, P. (2007). The effects of reinforcer magnitude on timing in rats. *Journal of the Experimental Analysis of Behavior*, 87, 201-218.
- Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological Review*, 104, 241-265.
- Machado, A., & Cevik, M. (1998). Acquisition and extinction under periodic reinforcement. *Behavioural Processes*, 44, 237-262.

- Machado, A., Malheiro, M. T., & Ernhagen, W. (2009). Learning to Time: A Perspective. *Journal of the Experimental Analysis of Behavior*, 92(3), 423-458.
- Machado, A., & Silva, F. J. (2007). Toward a richer view of the scientific method: The role of conceptual analysis. *The American Psychologist*, 62, 671–681.
- Shull, R. L. (2005). The sensitivity of response rate to the rate of variable-interval reinforcement for pigeons and rats: A review. *Journal of the Experimental Analysis of Behavior*, 84, 99-110.
- Staddon, J. E. R., & Higa, J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior*, 71, 215–251.

## Author Note

Carlos Pinto, Inês Fortes, Jeremie Jozefowicz and Armando Machado, Escola de Psicologia, Universidade do Minho, Braga, Portugal. Armando Machado and Jeremie Jozefowicz are supported by the Fundação para a Ciência e a Tecnologia. Correspondence should be addressed to Armando Machado, Escola de Psicologia, Universidade do Minho, Campus de Gualtar, 4710-057 Braga, Portugal. Email: arandom@psi.uminho.pt.

Table 1. Training and testing conditions in Experiment 1.

Group	Training		Testing
Control	---	FI 15 s	FI 15 s + 500-s Extinction
Experimental	FI 120 s	FI 15 s	FI 15 s + 500-s Extinction



Table 2. Training and testing conditions in Experiment 2.

Group	Training		Testing	
Control	---	---	FI 15 s	FI 15 s + 500-s Extinction
Experimental	FI 120 s	peak FI 120 s	FI 15 s	FI 15 s + 500-s Extinction

## Figure Captions

*Figure 1.* Diagram of stimulus-memory associations in different training situations. M1 and M2 and M3 refer to distinct temporal memories. In the Multiple Schedule, the three memories are formed simultaneously and are accessed by three distinct stimuli. In the Mixed FI FI schedule, the two memories are formed simultaneously but are accessed by the same stimulus. In the Sequential task, the two memories are formed sequentially (M1 at time t1, M2 at time t2) and are accessed by the same stimulus.

*Figure 2.* Predictions of Machado's (1997) LeT model for extinction following training in two FI schedules, FI 15 s and FI 120 s.

*Figure 3.* Average response rate as a function of time in a trial in the FI 15-s phase (left and right panels) and the FI 120-s phase (right panel) in Experiment 1.

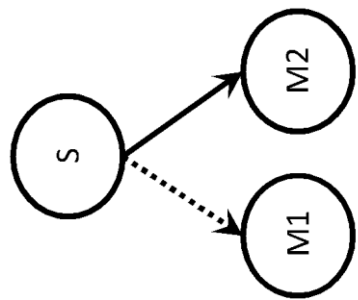
*Figure 4.* Response rate as a function of time in a trial for each individual pigeon during the first test trial of Experiment 1. The left and right columns show the data from the Control and Experimental groups, respectively.

*Figure 5.* Average absolute (left panel) and relative (right panel) response rate curves during the first test trial of Experiment 1. The arrow shows the 120 s reinforcement time.

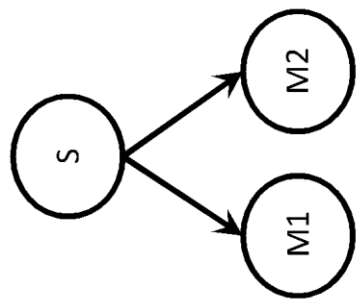
*Figure 6.* Average response rate as a function of time in a trial in the FI 15-s phase (left and right panels) and the FI 120-s phase (right panel) in Experiment 2. The arrow shows the 120 s reinforcement time.

*Figure 7.* Response rate as a function of time in a trial for each individual pigeon during the first test trial of Experiment 2. The left and right columns show the data from the Control and Experimental groups, respectively.

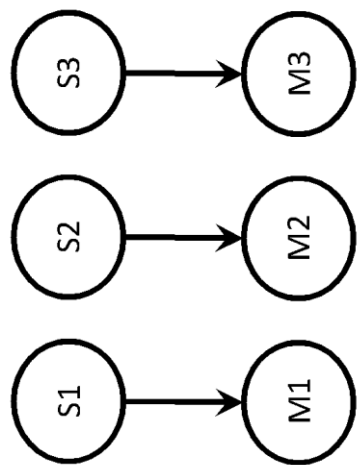
*Figure 8.* Average absolute (left panel) and relative (right panel) response rate curves during the first test trial of Experiment 2. The arrow shows the 120 s reinforcement time.



Sequential

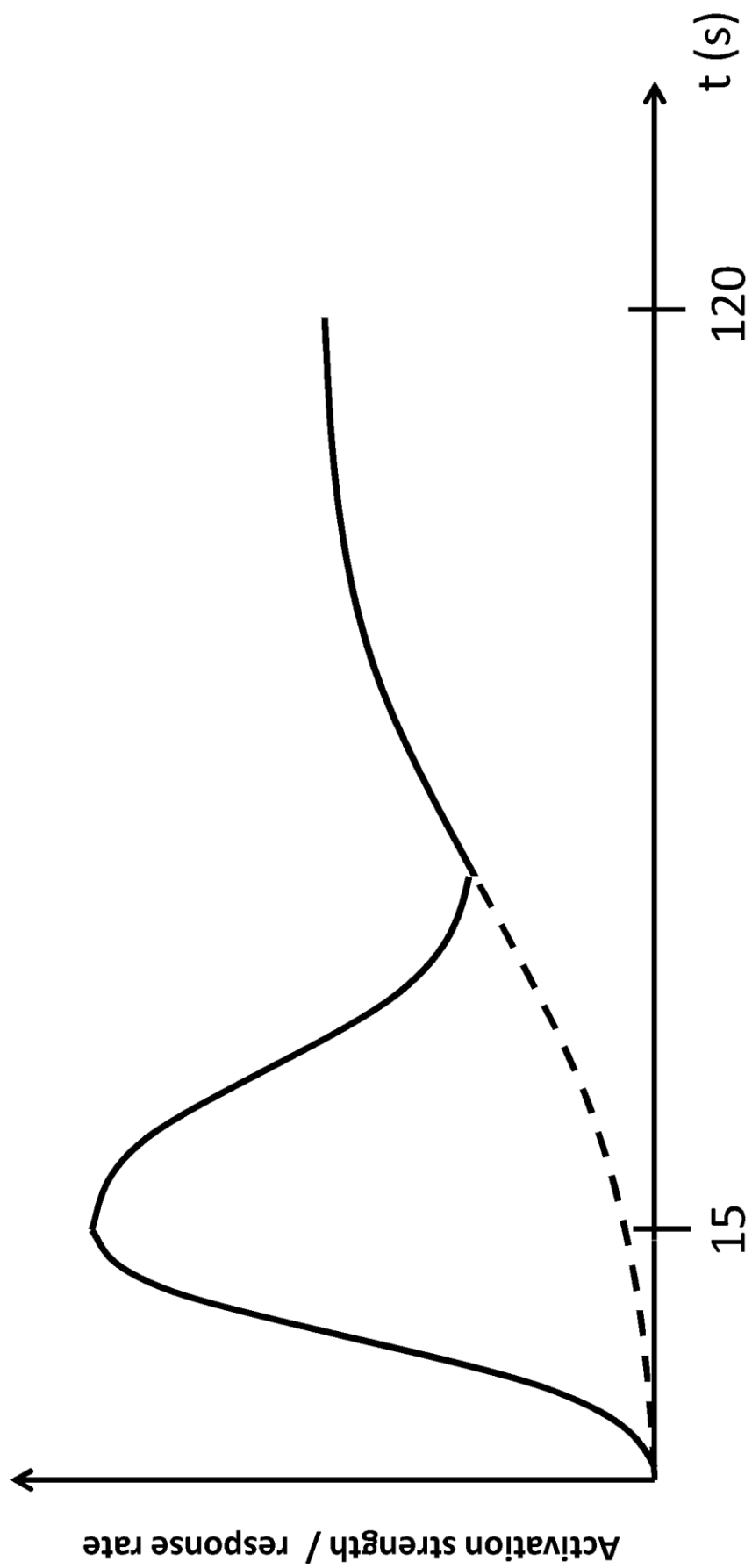


Mixed FI FI

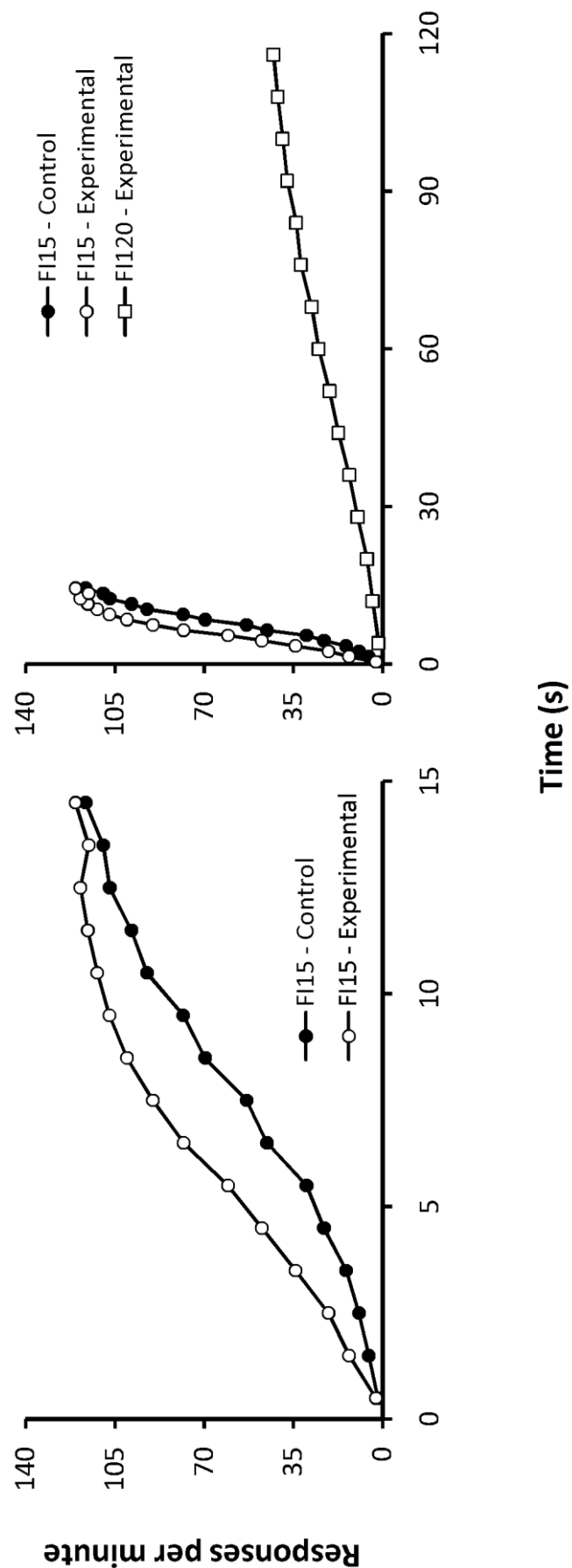


Multiple FI FI FI

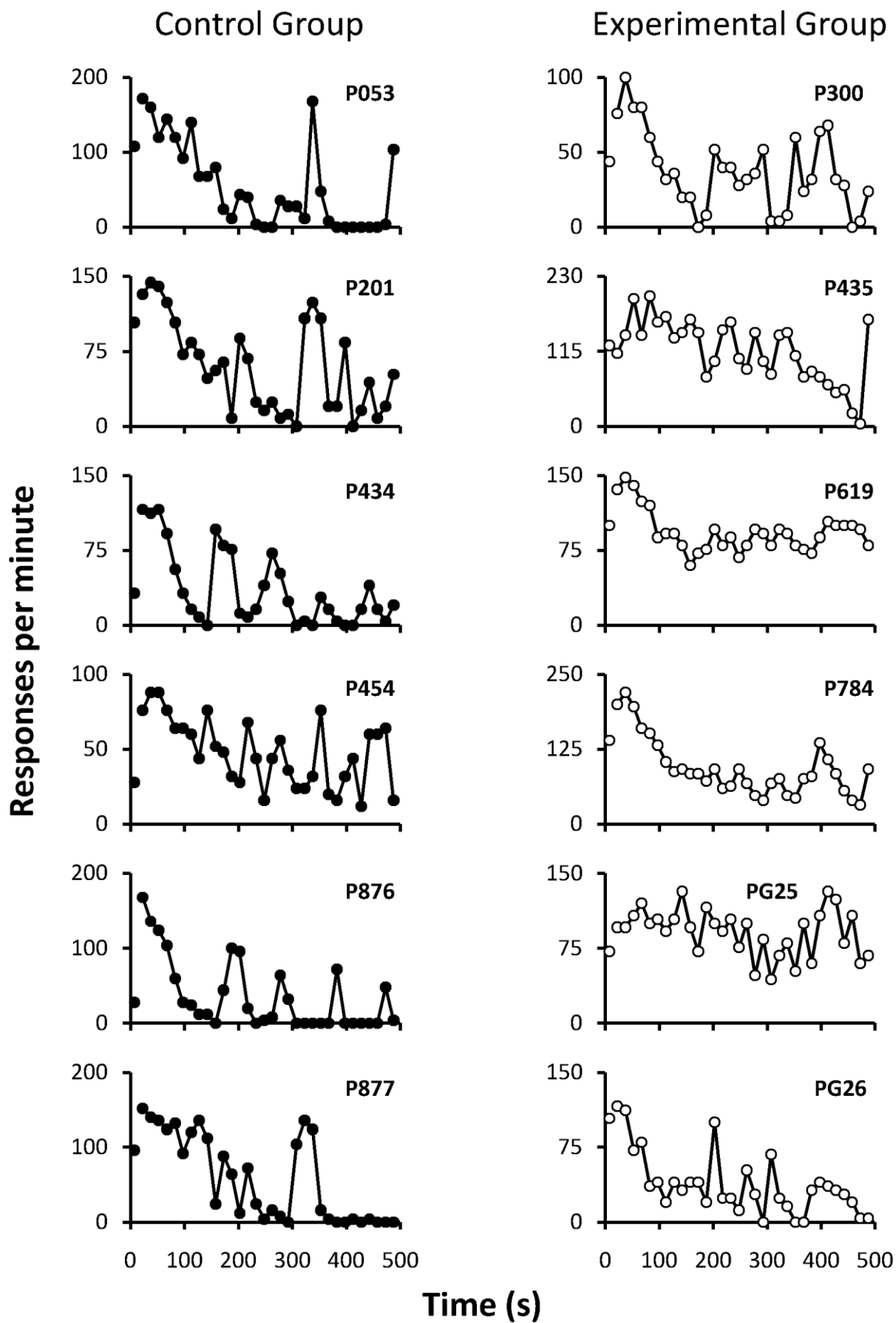
Pinto, Fortes, Jozefowicz, & Machado - Figure 1

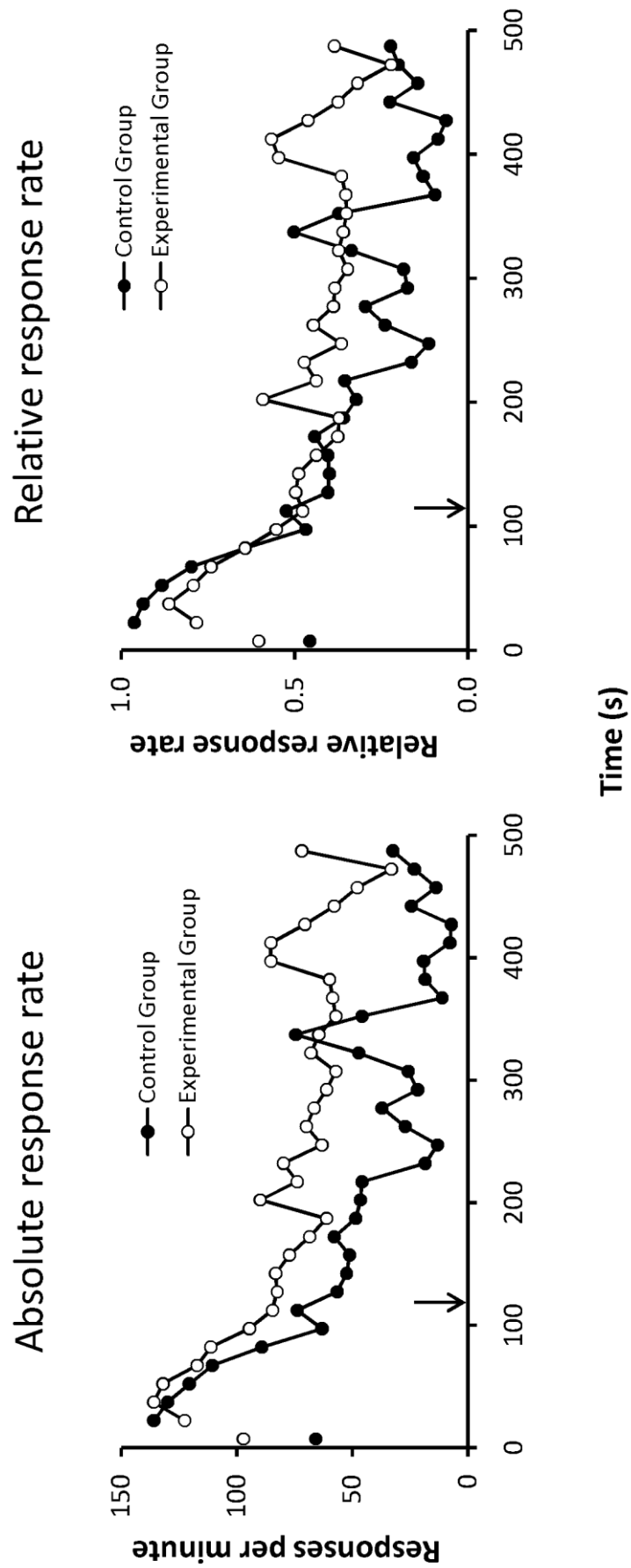


Pinto, Fortes, Jozefowicz, & Machado - Figure 2



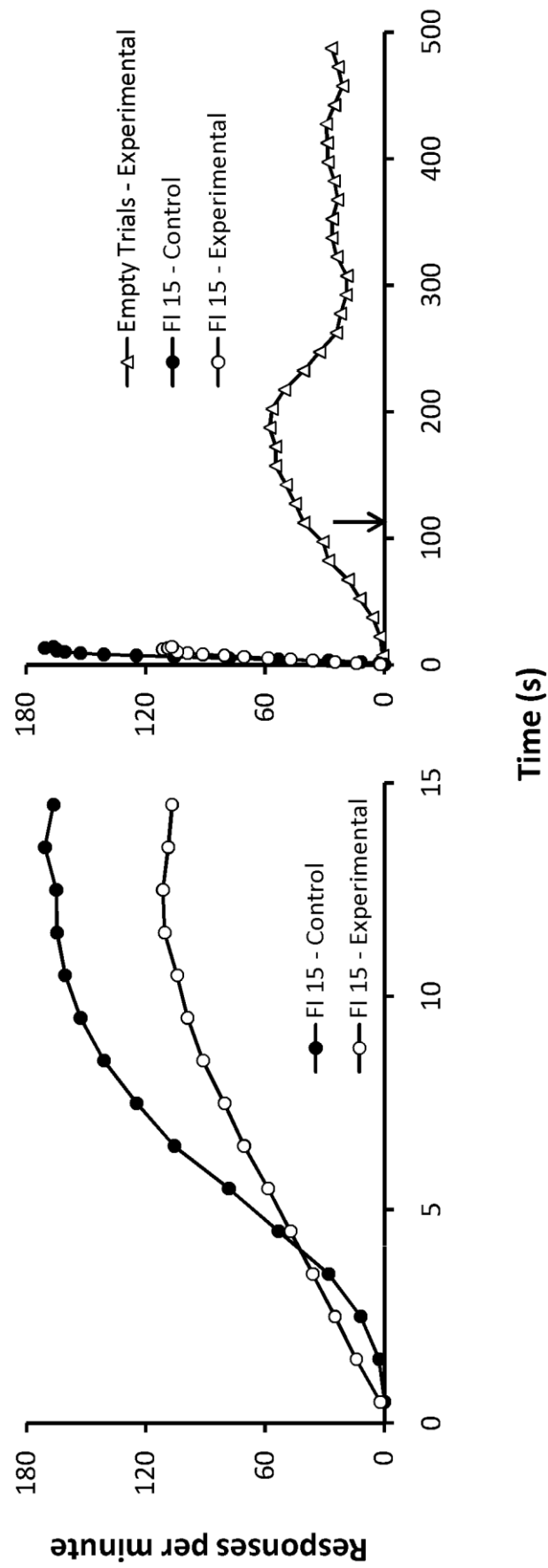
Pinto, Fortes, Jozefowicz, & Machado - Figure 3



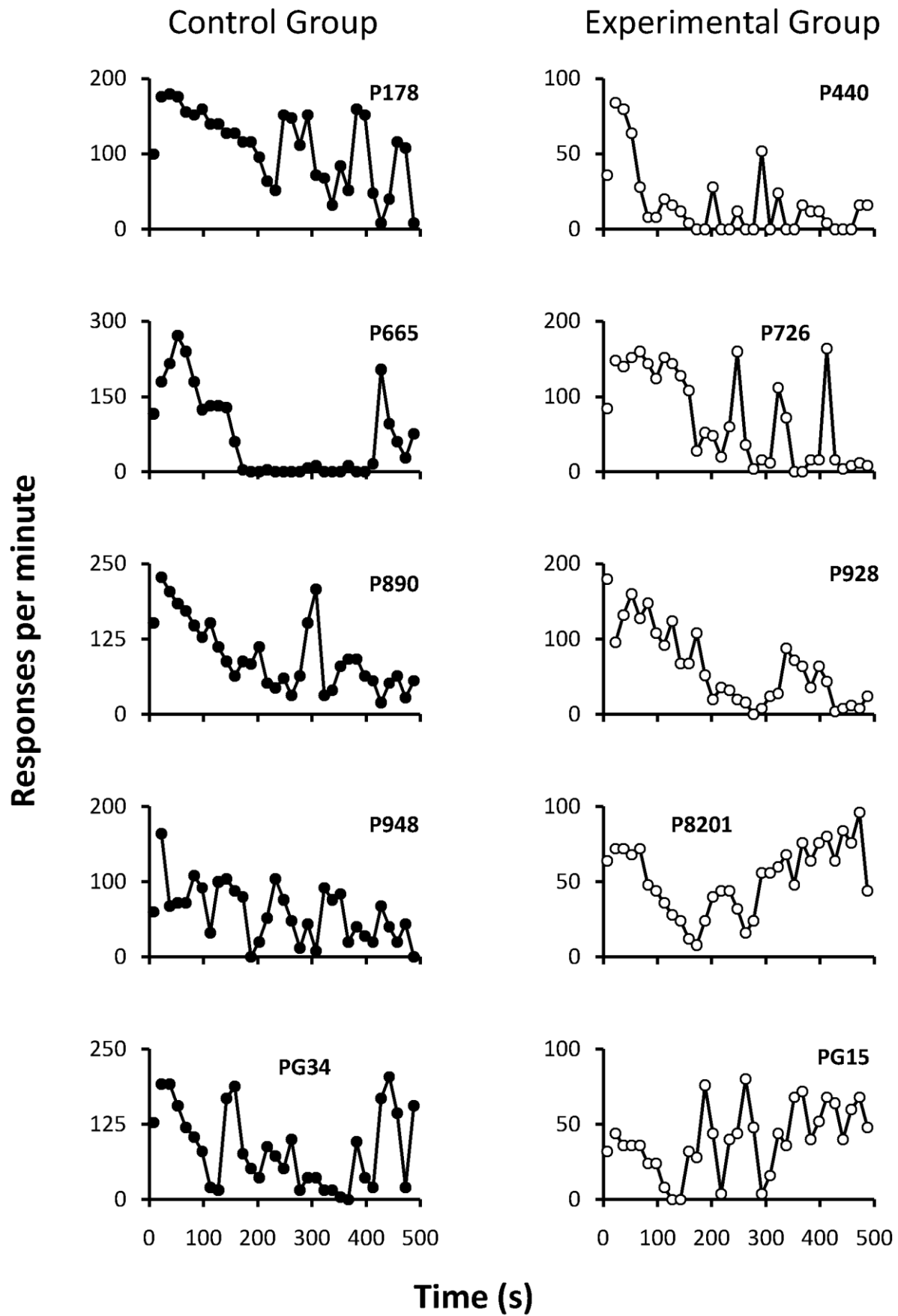


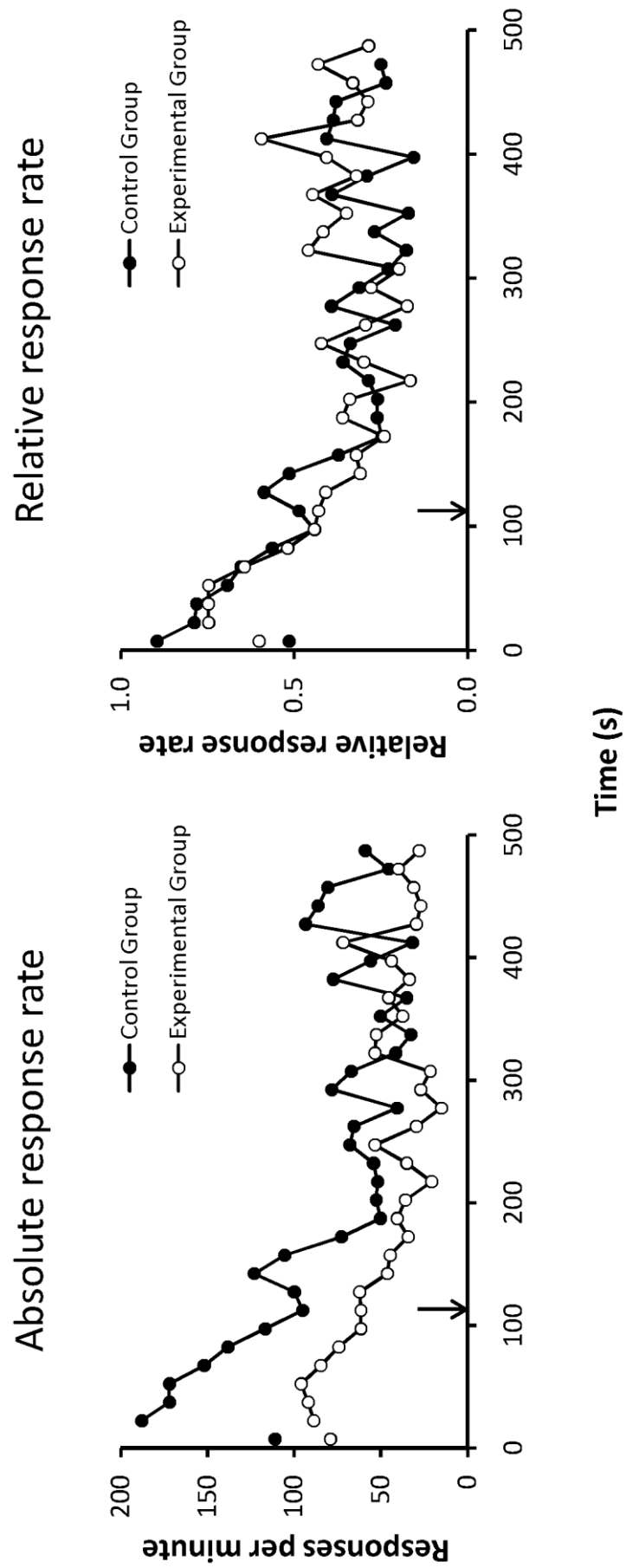
Pinto, Fortes, Jozefowicz, & Machado - Figure 5





Pinto, Fortes, Jozefowicz, & Machado - Figure 6





Pinto, Fortes, Jozefowicz, & Machado - Figure 8