Stimulus control in multiple temporal discriminations

Marcelo S. Caetano · Paulo Guilhardi · Russell M. Church

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Abstract In multiple fixed interval (FI) schedules, rats are trained to discriminate different FIs that are signaled by different stimuli. After extensive training, the different stimuli often acquire control over performance, observed by an earlier increase in responding for stimuli that signal shorter FIs, as compared with stimuli that signal longer FIs. The order in which the different FIs are trained, either intermixed across cycles or in blocks of several cycles, may seem irrelevant given that average performance at asymptote may be similar. In this study, rats were trained in two procedures with multiple FIs presented intermixed within sessions or in blocks of one interval per session. Similar performance was observed at asymptote, but an inspection of early cycles in each session revealed that different stimuli acquired control over performance only when trained intermixed within each session. Although the stimuli reliably signaled the upcoming FI, when trained in successive blocks of 60 cycles, rats rapidly adjusted performance early in the sessions on the basis of the temporal aspects of the

M. S. Caetano · P. Guilhardi · R. M. Church Department of Psychology, Brown University, Providence, RI, USA

M. S. Caetano (☑)
The John B. Pierce Laboratory,
290 Congress Avenue,
New Haven, CT 06519, USA
e-mail: marceloscaetano@gmail.com

M. S. Caetano Department of Neurobiology, Yale University School of Medicine, New Haven, CT, USA

P. Guilhardi The New England Center for Children, Southborough, MA, USA

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task, and not on the basis of the stimulus presented in the current cycle. These results are discussed in terms of overshadowing of the stimuli by temporal cues and in terms of conditions under which a stimulus acquires control over performance.

Keywords Fixed interval · Overshadowing · Memory · Rat · Stimulus control · Temporal discrimination

In a fixed interval (FI) schedule, a common procedure used in timing studies, the first response after a fixed elapsed time from an event is reinforced. For example, in an FI-30 s schedule, a rat may get a food pellet upon the first lever press that occurs at least 30 s after the onset of a light stimulus. With repeated exposures to this contingency, rats learn the temporal relationship between the onset of the light and the time of food availability. They respond little or not at all early in the interval (what Pavlov termed *inhibition of delay* in fixed time schedules; Pavlov, 1927), and responding increases as the time to food availability approaches (Ferster & Skinner, 1957). This process is referred to as *temporal discrimination* and is often learned rapidly early in training (Balsam, Drew, & Yang, 2002).

Fast temporal discrimination learning is not restricted to single intervals. Rats can rapidly learn to time different FIs that are signaled by different stimuli (Guilhardi & Church, 2005). In this case, the different stimuli acquire temporal control over behavior, since response rates change in accord with the stimulus presented in a particular cycle or trial. It is assumed, therefore, that an association between the stimuli and their corresponding intervals is learned. However, depending on the conditions of training, performance at asymptote may only appear to be a result of such stimulus—interval associations. If different FIs are trained in a

blocked design, in which the same stimulus—interval pair is presented for several successive cycles before a new pair is introduced, rats can use the temporal aspects of the previous cycle (temporal cues) as a predictor of the FI in the current cycle without the need to associate it with any stimulus (Caetano, Guilhardi, & Church, 2007). Since transitions to new intervals have been shown to occur rapidly (Gallistel, Mark, King & Latham, 2001; Higa, 1996), performance at asymptote for the different stimuli would be a function of their intervals, but no association between stimuli and intervals would be needed to explain the results.

Guilhardi, Menez, Caetano, and Church (2010) extended these results to humans and showed that the discrimination difficulty of the stimuli that signaled different FIs is also involved in determining what factor acquires control over temporal performance (i.e., the stimulus or the temporal aspects of the previous cycles). In a modified version of the peak procedure (Catania, 1970; Roberts, 1981), participants had to shoot a moving target on a computer screen. Shots (presses on a keyboard) were always delivered at the center of the screen, through which the target always passed. The color of the background was consistent with the velocity at which the target moved (and, therefore, with the time it reached the center of the screen). On regular trials, participants could see the target moving along its trajectory. On test (peak) trials, the target and its trajectory were masked, so participants had to estimate when the target would reach the center of the screen to accurately hit it. Feedback on the accuracy of the shots was given after each trial. Three different background colors/target velocities were used. They were presented to participants either in blocks of 60 cycles each or intermixed across cycles, and the similarity between the different background colors (lightness) was manipulated. At the end of training, performance was similar between easy and hard discriminations, both trained in blocks and intermixed. In a subsequent transfer test (intermixed cycles for all participants), however, even though the participants could discriminate the different colors in the hard condition, performance was a function of the stimuli only when the different colors/intervals were trained intermixed. As was true for rats, when trained in blocks, participants rapidly adjusted their performance on the basis of the temporal aspects of the previous cycle, and not on the basis of the stimulus (background color) presented in the current cycle.

One way of describing such results is to consider the possibility that the temporal characteristics of the previous cycle overshadowed the information provided by the stimulus currently presented. Initially discussed by Pavlov (1927), overshadowing is a phenomenon observed when two or more cues presented simultaneously predict the same outcome. Presumably due to differences in salience between the cues, associations formed between the outcome and the

different cues are not equal. The more salient cue overshadows the less salient ones, eliciting more (or less, depending on the procedure) responding. There is an extensive literature on overshadowing in classical and operant conditioning procedures. In the timing domain, however, few studies have examined overshadowing effects, mostly dealing with discrete stimuli, and not time intervals, as the competing cues (e.g., Jennings, Bonardi, & Kirkpatrick, 2007; McMillan & Roberts, 2010).

In the present study, the goal was to demonstrate that temporal performance can be a function of discrete stimuli or a function of temporal aspects of the task, depending on the training arrangements. We show that adequate temporal performance can be observed when rats cannot rely on the discriminative stimulus to predict the FI on the current cycle (Experiment 1) and that, depending on the training conditions, even a reliable stimulus may fail to gain control over temporal performance (Experiment 2).

Experiment 1

In Experiment 1, rats were trained with different fixed intervals that were signaled by the same stimulus or by different stimuli over sessions. Performance between the two types of stimuli was compared, and we tested the hypothesis that, by relying on temporal aspects of previous cycles of training, adequate temporal performance can be observed even when the discriminative stimulus is an unreliable cue to the interval presented in the current cycle.

Method

Animals Twelve male Sprague Dawley rats (Taconic Laboratories, Germantown, NY) were housed individually in a colony room on a 12:12-h light:dark cycle (lights off at 8:00 a.m.). Illumination in the colony and testing rooms was provided by dim red lights. The daily ration consisted of 45-mg Noyes pellets (Improved Formula A) delivered during the experimental sessions and of an additional 15 g of FormuLab 5008 delivered in the home cages after the daily sessions. Water was available ad lib in both home cages and experimental chambers. The rats arrived in the colony at about 34 days of age and were handled daily until the onset of the experiment. Training began when they were about 54 days old.

Apparatus Twelve chambers ($25 \times 30 \times 30$ cm) were located inside of ventilated, noise-attenuating boxes ($74 \times 38 \times 60$ cm). A magazine pellet dispenser (Model ENV-203) delivered 45-mg Noyes pellets into a food cup mounted on the front wall. Each head entry into the food cup was detected by an LED photocell. A water bottle was mounted



outside the chamber, with a tube that protruded through a hole in the back wall of the chamber. Three stimuli, referred to as noise, light, and clicker, were generated by modules from Med Associates, St. Albans, VT. The noise was a 70dB white noise with an onset rise time and termination fall time of 10 ms, which was generated by an audio amplifier (Model ANL-926). The light was a diffused houselight (Model ENV-227 M) rated to illuminate the entire chamber over 200 Lux at a distance of 3 in. The clicker (Model ENV-135 M) consisted of a relay mounted outside of the chamber and was used to produce an auditory click at a rate of 2/s. Two Gateway Pentium® III/500 computers running the Med-PC for Windows Version 1.15 using Medstate Notation Version 2.0 (Tatham & Zurn, 1989) controlled experimental events and recorded the time at which events occurred with 2-ms resolution.

Procedure Rats were trained on three different fixed intervals (30, 60, and 120 s) that were signaled by three different stimuli (S_1 , S_2 , and S_3). S_1 always signaled the 30-s interval, and S_3 always signaled the 120-s interval (fixed stimulus—interval pairs), while S_2 signaled a different interval on each training session (varied pairs; see Fig. 1). The assignment of light, noise, and clicker to S_1 , S_2 , and S_3 was counterbalanced across rats.

Each session consisted of 60 cycles. Each cycle started with a 20-s period with no stimuli (intertrial interval, ITI), followed by the onset of one of the three stimuli. Food was primed after an FI from the onset of the stimulus, and the first head entry (measured as the time of breaking a photo beam inside the food cup) after the time of food prime delivered a food pellet, terminated the stimulus, and restarted the cycle (Fig. 1). Head entries made during the

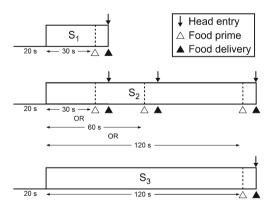


Fig. 1 Basic training procedure. Each cycle is initiated by a 20-s period with no stimuli, followed by the onset of a light, clicker, or noise $(S_1, S_2, \text{ or } S_3)$. Food is primed (open triangles) after a fixed interval from stimulus onset (30, 60, or 120 s). The first head entry after food prime (black arrows) terminates the stimulus, delivers a food pellet, and restarts the cycle. S_1 and S_3 always signaled the 30- and 120-s intervals, respectively (fixed pairs), while S_2 signaled a different interval in each session (varied pairs)

fixed interval (before the time of food prime) and during the ITI were recorded but had no effect.

There was a probability of 1/3 of presenting each of the three stimulus—interval pairs (S_1 -30 s, S_2 -varied, and S_3 -120 s) on each cycle. The interval signaled by S_2 was consistent within sessions but changed between sessions in the following manner: Each block of three sessions consisted of a random permutation of the three possible intervals paired with S_2 , with the restriction that the same interval was never paired with S_2 on two successive sessions. The rats were trained for 102 morning sessions (5 sessions/week and 90 min/session, on average).

Data analysis Mean responses per minute as a function of time since stimulus onset, used to describe the rats' performance, were calculated with MATLAB® v.7.12.0 (R2011a). For statistical comparisons, the temporal gradients on the last five sessions were averaged (asymptotic performance). Then the averaged gradient for each rat was fitted with the best linear function (least squares criterion) for the first 30 s following stimulus onset, and the slopes of these linear functions were compared. Data from five sessions (94, 97, 98, 101, and 102) were excluded from the analyses due to technical problems with recording the data.

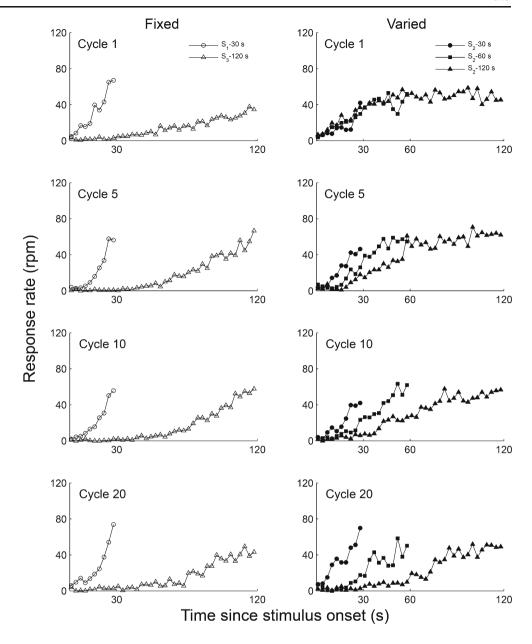
Results

Responses per minute as a function of time from the beginning of the cycle, averaged across the last five sessions of training and across rats, are shown for cycles 1, 5, 10, and 20 (top to bottom panels) in Fig. 2. Fixed stimulus—interval pairs $(S_1 \text{ and } S_3)$ are shown in the left panels, and varied pairs (S_2) are shown in the right panels. Response gradients were a function of the intervals for the fixed pairs from the first cycle (nonoverlapping gradients in the upper-left panel), while for the varied pairs, the rats adjusted their performance within each session: The different gradients gradually moved from a low temporal discrimination at the beginning of the session (cycle 1, overlapping gradients) to a higher temporal discrimination at the end of the session (cycle 20, differentiated gradients).

To quantify this within-session change in temporal discrimination, the first 30 s of both 30- and 120-s interval gradients were individually fitted with the best linear function in each panel, and the slopes were used for comparison (Table 1). The gradual adjustment in performance observed only in varied pairs was expressed by a significant three-way interaction in a repeated measures analysis of variance (ANOVA) with interval (30 and 120 s), type of pair (fixed and varied), and cycle (1, 5, 10, and 20) as within-subjects factors, F(3, 33) = 4.66, p = .008. The other significant terms in the analysis were interval, F(1, 11) = 52.53, p < .001, the interval × type of pair interaction, F(1, 11) = 11.1,



Fig. 2 Asymptotic performance, Experiment 1. Responses per minute as a function of time since stimulus onset for the fixed (open symbols, left panels) and varied pairs (filled symbols, right panels) in cycles 1, 5, 10, and 20. Response rate gradients were averaged across the last five sessions of training and across all rats



p = .001, and the interval × cycle interaction, F(3, 33) = 2.94, p = .048. The three-way interaction, in particular, suggests that performance in the two extreme intervals was different as a function of cycles only for the varied pairs, as shown in Fig. 2. This difference in performance between fixed and varied pairs observed after extensive training was also seen during the initial sessions of training (data not shown).

Source of adjustment of performance for the varied pairs Since the association of S_2 to one of the three fixed intervals changed daily and could not be predicted in the first cycle of each session, it is possible that the rats simply averaged the past intervals associated with S_2 to perform reasonably well at the beginning of each session. This would lead to a

temporal gradient early in the sessions that was an average of the asymptotic gradients of all intervals associated with S_2 . To test this hypothesis, performance in the first cycle of

Table 1 Means (and standard errors) of the slopes for the individual linear fits performed on the first 30 s of each response gradient shown in Fig. 2

	Fixed pairs		Varied pairs	
	30 s	120 s	30 s	120 s
Cycle 1	2.35 (0.30)	0.02 (0.03)	1.06 (0.19)	1.06 (0.24)
Cycle 5	2.17 (0.38)	0.00 (0.02)	1.77 (0.33)	0.45 (0.24)
Cycle 10	2.00 (0.45)	0.00 (0.02)	1.60 (0.43)	0.20 (0.06)
Cycle 20	2.20 (0.52)	0.06 (0.09)	2.09 (0.45)	0.01 (0.03)



the last five asymptotic sessions was replotted in the upper panel of Fig. 3 (same gradients shown in the upper-right panel of Fig. 2). Individual averages of the temporal gradients for S₂-30 s, S₂-60 s, and S₂-120 s in cycle 20 were computed, and the average across rats is shown in gray (asymptotic average). The asymptotic average gradient roughly superposed with the gradients for each interval only during the first 30 sec of the sessions, suggesting that a simple averaging rule cannot account for performance in the varied pairs early in each session.

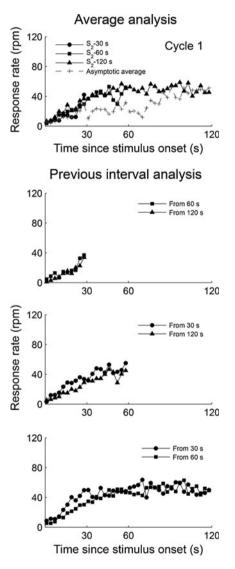
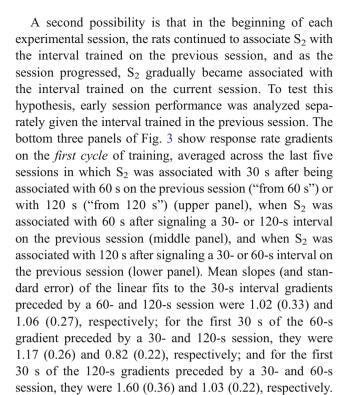


Fig. 3 Source of adjustment for the varied pairs. Top panel: Responses per minute as a function of time since stimulus onset for the varied pairs in the first cycle of the asymptotic sessions (solid lines, gradients reproduced from Fig. 2, top-right panel) and for the average gradients in cycle 20 across all three intervals (dashed line). Bottom three panels: Responses per minute as a function of time since stimulus onset for sessions in which S_2 was associated with 30-, 60-, or 120-s intervals (top to bottom), taking into account the intervals trained on the previous session



The difference between the slopes of the fitted lines for the two gradients in each of the three panels was calculated individually. A repeated measures ANOVA on the individual differences, with one within-subjects factor, interval (30, 60, or 120 s; upper, middle, and lower panels, respectively), did not reveal a significant effect of interval, F(2, 22) = 0.62, p = .549. Since slopes were similar across panels, overall differences between gradients (differences averaged across panels) were computed. They were not statistically different than zero (one-sample *t*-test, t(11) = 1.67, p = .124), which further suggests that performance early in a session was not related to the interval trained on the previous session.

Discussion

Rats learned the association between the different stimuli and intervals when the stimulus was a reliable cue for the time of food availability in each cycle throughout training (fixed pairs). When the stimulus was not a reliable cue (varied pairs), rats rapidly adjusted performance in each session. The fast adjustment of performance in the varied pairs was possible because, within each session, S₂ was associated with the same interval, so the time to reinforcement in the next cycle signaled by S₂ could be predicted from the time to food prime in the last cycle signaled by S₂. The adjustment of performance was not only fast, but also complete: By the end of each experimental session, performance on a given interval signaled by the varied stimulus was indistinguishable from performance on the same interval signaled by a fixed stimulus.



These results represent an instance in which different learning histories (fixed vs. varied pairings of stimuli and intervals) can produce similar asymptotic performance. The different methods of training (fixed vs. varied pairings) presumably led to different strategies adopted by the rats to perform the task (learning of the association between stimuli and intervals vs. rapid adjustment of performance, respectively). Therefore, the procedure used in Experiment 1 allows for the study of different underlying mechanisms, either cognitive or neuronal, that lead to similar performance.

Experiment 2 further investigated the conditions under which rats learn the different stimulus—interval associations, or rapidly adjust performance on the basis of the previous interval, by training rats on a procedure in which both the stimuli and the previous cycle were reliable cues to the time to food prime in the current cycle.

Experiment 2

In Experiment 1, temporal performance was a function of the different stimuli when they were reliable cues to the upcoming FI, and rats rapidly adjusted performance when the stimulus was an unreliable source of information about the FI. In Experiment 2, we tested the hypothesis that even when the discriminative stimuli are reliable cues to the different FIs, performance may not be a function of the stimulus but, instead, may be controlled by temporal aspects of the task.

Method

Animals Twelve male Sprague Dawley rats (Taconic Laboratories, Germantown, NY) were trained in Experiment 2. Details on housing, daily ration, and water availability were identical to those described in Experiment 1. The rats weighed between 75 and 100 g at the time of arrival in the laboratory and were handled daily until the onset of the experiment. Training began 36 days after their arrival. The same apparatus as that used in Experiment 1 was used in Experiment 2.

Procedure The procedure in Experiment 2 was similar to that described in Experiment 1, except for two important differences: (1) S_2 was always the cue for the 60-s fixed interval, and (2) only one stimulus—interval pair was trained on each session. Rats were trained for 35 sessions (5 sessions/week).

On each session, all rats had 60 cycles on S_1 -30 s, S_2 -60 s, or S_3 -120 s (i.e., only one stimulus—interval pair per session). The choice of the pair trained on each session was determined by a random permutation of the three possible

pairs without replacement, with the only restriction that the same stimulus-interval pair was never presented in two consecutive sessions.

Results

Figure 4 shows mean response rate gradients in cycles 1, 5, 10, and 60 (top to bottom panels) averaged across the last five sessions of training of each stimulus—interval pair. Even though the stimulus—interval pairs were fixed (i.e., the same stimuli consistently signaled the same intervals), performance of rats in Experiment 2 was similar to that observed for the varied pairs in Experiment 1: All gradients moved from a lower to a higher temporal discrimination as the session progressed (i.e., the gradients gradually spaced out as a function of cycles within the sessions).

Importantly, there were individual differences in the degree to which the three gradients superposed in the first

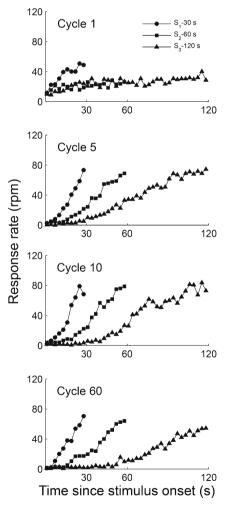


Fig. 4 Asymptotic performance, Experiment 2. Responses per minute as a function of time since stimulus onset in cycles 1, 5, 10, and 60, averaged across the last five sessions of training of each stimulus—interval pair and across all rats



cycle. Individual response rate gradients in the first and in the last cycles of the session, averaged across the last five sessions of training, are shown in Figs. 5 and 6, respectively. The different panels in each figure show performance for individual rats. Two rats in particular (rats 1 and 3) seemed to anticipate the 30-s interval from the first cycle (Fig. 5), which explains the slight separation of the 30-sec interval gradient from the other gradients shown in cycle 1 in Fig. 4. However, the magnitude of this difference was very low, as compared with the difference observed in cycle 60 (Fig. 6) or with the difference observed in the first cycle for the fixed pairs in Experiment 1 (Fig. 2). Moreover, apart from those 2 rats, the three gradients for the remaining rats roughly superposed in the first cycle (Fig. 5) and were distinct from each other in the last cycle of the asymptotic sessions (Fig. 6).

As in Experiment 1, the first 30 s from the 30-, 60-, and 120-s interval gradients were fitted individually with the best linear function (Table 2), and the slopes were compared statistically. The adjustment of performance observed was described by a significant interval \times cycle interaction, F(6, 66) = 7.43, p < .001, in a repeated measures ANOVA

with interval (30, 60, and 120 s) and cycle (1, 5, 10, and 20) as within-subjects factors. This significant interaction suggests that performance in the three intervals was different only later in the session, as shown in Fig. 4. A repeated measures ANOVA comparing the slopes for the three FIs during the second cycle yielded a significant effect of interval, F(2, 22) = 5.96, p = .009, indicating that the gradients were already discriminable in cycle 2, even though they continued to further space out as a function of cycles (see Fig. 4).

Discussion

In Experiment 2, rats were trained on a procedure in which both the stimulus and the temporal aspects of the task (based on previous cycles) were reliable cues to the interval in the current cycle. Even though performance could have been controlled by the different stimuli (as was observed with the fixed pairs in Experiment 1), responding was not a function of the stimuli early in the sessions, even after 35 sessions of training. Instead, the rats rapidly adjusted their performance as each session progressed.

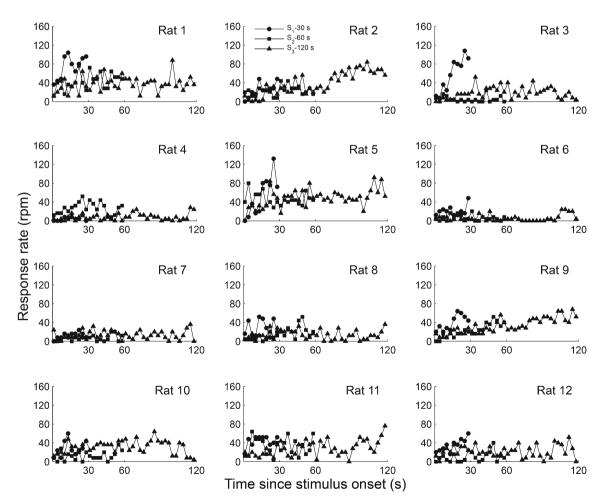


Fig. 5 Individual performance in cycle 1, Experiment 2. Responses per minute as a function of time since stimulus onset for each rat in cycle 1, averaged across the last five sessions of training of each stimulus–interval pair



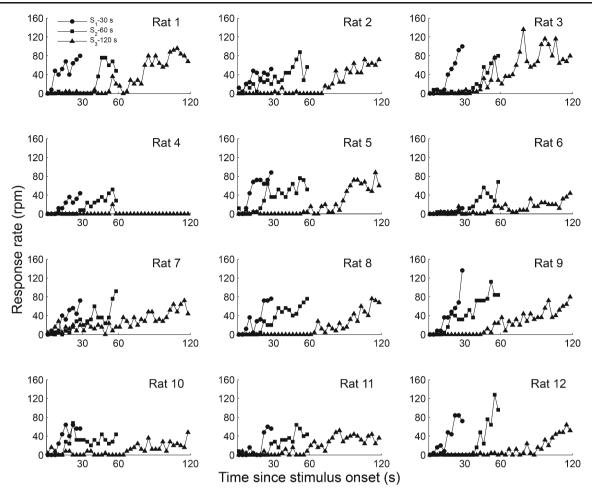


Fig. 6 Individual performance in cycle 60, Experiment 2. Responses per minute as a function of time since stimulus onset for each rat in cycle 60, averaged across the last five sessions of training of each stimulus–interval pair

These results conform with those described by Guilhardi et al. (2010), who showed that humans also rapidly adjusted performance when different stimuli signaled different intervals in a context in which the stimuli to be discriminated were made more and more similar to each other. As the discriminability among the stimuli decreased, participants switched from using the stimuli to using the temporal aspects of the previous cycle, even though they were still

Table 2 Means (and standard errors) of the slopes for the individual linear fits performed on the first $30~{\rm s}$ of each response gradient shown in Fig. 4

	Fixed pairs, Exp. 2			
	30 s	60 s	120 s	
Cycle 1	1.31 (0.37)	0.17 (0.14)	0.65 (0.14)	
Cycle 5	2.65 (0.32)	0.68 (0.12)	0.19 (0.08)	
Cycle 10	3.02 (0.29)	0.66 (0.18)	0.04 (0.07)	
Cycle 60	2.62 (0.31)	0.71 (0.22)	0.02 (0.05)	

able to discriminate the different stimuli in a simple stimulus discrimination test.

In the present experiment, however, the stimuli used were easily distinguishable, as shown by performance under the fixed condition in Experiment 1. In Experiment 2, by the end of the 35 sessions of 60 cycles, each stimulus–interval pair was trained 700 times. Still, temporal performance was not a function of the stimuli early on every session of training. This result is counterintuitive, since one would expect that the extensive training with each stimulus–interval pair would have led to learning of the respective associations and consequent control of performance by the different stimuli.

Caetano et al. (2007) described a similar counterintuitive finding in a secondary data analysis study, in which three fixed intervals were also signaled by three different stimuli. During training, one group of rats had the three stimulus—interval pairs trained intermixed within each experimental session. For a second group of rats, the pairs were trained in successive blocks of 10 sessions each. Rats in both groups were then put to a transfer test in which all pairs were



presented intermixed on each session (same procedure as that used for the first group of rats during training). Although performance was indistinguishable between groups during training, rats trained in blocks of 10 sessions did not discriminate the three stimuli early in the transfer test session. Instead, response rate gradients were almost identical for the three stimulus-interval pairs. This suggests that, in contrast to the rats trained with intermixed trials, rats trained with blocks of trials did not learn the different stimulusinterval associations. Those results, however, were based on only one transfer test session. Moreover, transfer test sessions differed from training sessions only for rats trained in blocks of trials, which could have interfered with performance during the first few trials of the transfer test session. Experiment 2 presented a situation in which each session could be viewed as a new transfer test session, during which rats consistently showed a rapid adjustment of performance, suggesting that the stimuli did not discriminatively control temporal performance.

General discussion

As described by Rescorla (1988), similar performance does not imply similar learning. In Experiment 1, performance at the end of each experimental session was similar with the fixed and varied stimulus-interval pairs, even though what was learned was different in the two conditions. Rats learned the associations between stimuli and intervals for the fixed pairs (S₁-30 s and S₃-120 s), as shown by the differential performance under each stimulus early in the sessions (Fig. 2). On the other hand, since S₂ was paired with different intervals on different days, the rats learned to use the previous cycle as a source of information about the time of food availability on the current cycle, evidenced by the fast within-session adjustments in performance. Interestingly, when the rats could use either the stimuli or the temporal cues from previous cycles to predict the interval imposed on the current cycle (Experiment 2), fast adjustment of performance was observed (Fig. 4). When the previous cycle was a reliable cue to the current interval, the strategy adopted was to quickly adjust performance instead of learning the stimulus-interval associations, which may be seen as a hierarchy of simplicity in which rapid adjustment of performance was the simplest option.

It is important to note that these results do not suggest that the rats were insensitive to the stimuli. In the fast adjustment case, the different stimuli simply set the context for the rats to respond (as opposed to responding during the intertrial interval, when no stimulus is presented), even though performance was not a function of the different stimuli early in each session. In that sense, those results allude to the *discriminative property* of a discriminative

stimulus and suggest that this property is enhanced when rats are exposed to different stimuli—those that they are supposed to learn to discriminate—successively within a short period of time. Under the conditions of the present experiments, training different intervals with different stimuli in blocks of 60 cycles of S₁-30 s, S₂-60 s, or S₃-120 s per session, spaced 24 h apart, did not lead to differential temporal performance given the different stimuli. Performance was a function of the stimuli only when different types of stimulus—interval pairs were intermixed within the same session.

These results can also be interpreted as an instance in which the temporal features of the cycle *overshadowed* the stimulus. Most experiments on overshadowing used two stimuli that competed for control of performance (e.g., Jennings et al., 2007; McMillan & Roberts, 2010). Of course, a time interval itself could be treated as a stimulus (Ferster & Skinner, 1957). The memory of the duration to food may be more salient than the stimulus (e.g., light, white noise, or clicker). As a result, the time stimulus would overshadow the other stimuli, leading to a superposition of the temporal gradients in the first cycle of the sessions and a separation of the gradients starting on cycle 2. Thus, from an overshadowing perspective, an explanation of the results would be that time cues block the conditioned stimulus (CS) but the CS does not block time cues (Williams & LoLordo, 1995).

Some timing theories emphasize the importance of the expected time to reinforcement from a time marker, such as the onset of a stimulus. These theories include packet theory (Kirkpatrick, 2002; Kirkpatrick & Church, 2003) and the closely related modular theory of learning and performance (Guilhardi, Yi, & Church, 2007). In the fixed condition of Experiment 1, both the stimulus and the expected time from stimulus onset to reinforcement were reliable cues; in the varied condition, only the temporal cues provided a basis for differential responding. In Experiment 2, however, both the stimulus and the expected time to reinforcement were reliable cues. Despite 2,100 exposures to this procedure (35 sessions of 60 cycles), the rats showed no evidence of using the stimulus but rapidly adjusted performance to the temporal interval of the session.

References

Balsam, P. D., Drew, M. R., & Yang, C. (2002). Timing at the start of associative learning. *Learning and Motivation*, 33, 141–155.

Caetano, M. S., Guilhardi, P., & Church, R. M. (2007). Differences between simultaneous and blocked training detected by a transfer test. *Behavioural Processes*, 75, 176–181.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In
 W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1–42). New York: Appleton-Century-Crofts.



- Ferster, C. B., & Skinner, B. F. (1957). Schedules of reinforcement. New York: Appleton-Century-Crofts.
- Gallistel, C. R., Mark, T. A., King, A. P., & Latham, P. E. (2001). The rat approximates an ideal detector of changes in rates of reward: Implications for the law of effect. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 354–372.
- Guilhardi, P., & Church, R. M. (2005). Dynamics of temporal discrimination. *Learning & Behavior*, 33, 399–416.
- Guilhardi, P., Menez, M., Caetano, M. S., & Church, R. M. (2010). The effect of stimulus discriminability on strategies for learning multiple temporal discriminations. *Behavioural Processes*, 84, 476–483.
- Guilhardi, P., Yi, L., & Church, R. M. (2007). A modular theory of learning and performance. *Psychonomic Bulletin & Review*, 14, 543–559.
- Higa, J. J. (1996). Rapid timing of a single transition in interfood interval duration by rats. *Animal Learning & Behavior*, 25, 177–184.
- Jennings, D. J., Bonardi, C., & Kirkpatrick, K. (2007). Overshadowing and stimulus duration. *Journal of Experimental Psychology: An*imal Behavior Processes, 33, 464–475.

- Kirkpatrick, K. (2002). Packet theory of conditioning and timing. Behavioural Processes, 57, 89–106.
- Kirkpatrick, K., & Church, R. M. (2003). Tracking of the expected time to reinforcement in temporal conditioning procedures. *Learning & Behavior*, 31, 3–21.
- McMillan, N., & Roberts, W. A. (2010). The effects of cue competition on timing in pigeons. *Behavioural Processes*, 84, 581–590.
- Pavlov, I. P. (1927). Conditioned reflexes (G. V. Anrep, Trans.). London: Oxford University Press.
- Rescorla, R. A. (1988). Behavioral studies of Pavlovian conditioning. Annual Review of Neuroscience, 11, 329–352.
- Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 7, 242–268.
- Tatham, T. A., & Zurn, K. R. (1989). The MED-PC experimental apparatus programming system. Behavioral Research Methods, Instruments, & Computers, 21, 294–302.
- Williams, D. A., & LoLordo, V. M. (1995). Time cues block the CS, but the CS does not block time cues. *Quarterly Journal of Experimental Psychology*, 48B, 97–116.

