A Comparison of Empirical and Theoretical Explanations of Temporal Discrimination

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ABSTRACT

The empirical goals were to describe the behavior of rats trained on multiple temporal discriminations and to use these descriptions to predict behavior observed under new training conditions. The theoretical goals were to fit a quantitative theory to behavior from one training condition, estimate parameters for the intervening perception, memory, and decision processes, and use these parameters to predict behavior observed under new conditions. Twenty-four rats were trained on a multiple peak-interval procedure with two stimuli that were presented individually (Stimulus A and B), or in compound (Compound AB); either different responses (Experiment 1) or the same response (Experiment 2) were reinforced during the presentations of Stimulus A, Stimulus B, and Compound AB. The patterns of correct and stimulus-error responses during Stimulus A and Stimulus B (Experiment 1) were used as elements that, with summation rules, predicted behavior under new conditions (Compound AB, Experiment 1 and Stimulus A, Stimulus B, and Compound AB, Experiment 2). A comparison of the success of the empirical and theoretical goals supported the use of a quantitative theory of behavior to explain the data.

The empirical goal was to describe the behavior of rats trained on multiple temporal discriminations (Experiment 1) and to use this description to predict behavior observed under new training conditions (Experiments 1 and 2). The theoretical goal was to fit a quantitative theory to behavior from one training condition, estimate parameters for the intervening perception, memory, and decision processes, and use these parameters to predict behavior observed under new conditions. A comparison of the success of the empirical and theoretical goals is provided in the General Discussion.

During one widely used temporal discrimination procedure, the peak procedure (Catania, 1970; Roberts, 1981), rats are presented with food following the first response after a fixed interval since the onset of a stimulus on some occasions; on others, no food is delivered and the stimulus remains on for a duration that is longer than the fixed interval. Rats may be trained on different intervals (e.g., Church, Meck, & Gibbon, 1994); or the same rats may be trained on multiple intervals that are signaled by different stimuli (e.g., Roberts, 1981; Yi, 2007). The standard results during the nonfood stimulus presentations are that response rate increases as a function of time, reaches a maximum at approximately the usual time of reinforcement, and then slowly decreases asymmetrically.

When performance on multiple intervals in the nonfood cycles in the peak procedure are compared, it is often observed that (1) the time at which response rate is at its maximum (peak time) is linearly related to the fixed interval (proportionality result); (2) the spread of the response rate gradient is also linearly related to the fixed interval (scalar property result); (3) since there is a linear relationship between the peak time and the spread of the response rate gradients and the fixed interval, the coefficient of variation, defined as the spread (standard deviation) divided by the peak time (mean) is constant (Weber’s law for timing result); and (4) the relative response rate (response rate divided by the maximum rate) as a function of relative time (time since stimulus onset divided by the stimulus onset to food interval) superposes for multiple intervals (timescale invariance result). The proportional timing, scalar property, Weber's law for timing, and timescale invariance results led to the explanation of timing behavior in terms of scalar timing theory. Scalar timing theory was initially described as a formal definition of these principles (Gibbon, 1977) and later developed as an information-processing model (Church, 2003; Church et al., 1994; Gibbon, Church, & Meck, 1984) to predict the relative response rate gradients for a wide range of procedures that also produced similar results, such as the bisection procedure (Church & Deluty, 1977) and temporal generalization procedure (Church & Gibbon, 1982).

Other theories with different cognitive and behavioral intervening variables have also been developed, and at least two of them have been used to account for the behavior observed when rats are trained on the peak procedure: learning to time (Machado, 1997), and a modular theory of learning and performance (Guilhardi & Church, 2005; Guilhardi, Yi, & Church, 2007; Kirkpatrick, 2002; Kirkpatrick & Church, 2003; Yi, 2007). Scalar timing theory, learning to time theory, and the modular theory each have specific intervening processes for perception, memory, and decision (See Church & Kirkpatrick, 2001 for a review). Closed-form equations that integrate these intervening processes have been developed for each of these theories and used to fit the response rate gradients. All three theories have satisfactorily accounted for the well established scalar principles (Gibbon, 1977, 1991; Gibbon & Church, 1990; Gibbon et al., 1984) based on the behavior observed in the peak procedure as well as in many other procedures.

The two experiments described in this article trained each rat in two peak intervals each signaled by a different stimulus (referred to as Stimulus A and Stimulus B), and was modified from the standard peak procedure in two ways: the presentation of the stimuli did not terminate with the delivery of food (on food cycles) but lasted as long as it did on non-food cycles; and in some cycles, both stimuli were presented concurrently as a compound (Compound AB) with the contingencies of reinforcement maintained consistent with Stimulus A and B. The two experiments manipulated the interval reinforced during Stimulus A and B (15, 30, or 60 s), and the responses reinforced during Stimulus A or B, that were the same (single responses) or different (multiple responses) in the two experiments. The empirical goal was to describe the behavior observed during Stimulus A and Stimulus B when multiple responses were used in order to predict (a) the behavior observed during the *Compound AB when multiple responses were used*, and (b) behavior during *Stimulus A, Stimulus B, and Compound AB when a single response was used*.

It is well know that rats can learn to discriminate multiple intervals whether the intervals are signaled by different stimuli (Guilhardi & Church, 2004; Guilhardi & Church, 2005; Hemmes, Brown, & Cabeza de Vaca, 1990) or by the same stimulus (Catania & Reynolds, 1968; Platt & Davis, 1983), even if these intervals are trained simultaneously within a session. This ability to learn multiple discriminations simultaneously is reflected in most theories, such as scalar timing theory, learning to time theory, and modular theory, with the assumption of independent memories for each of the temporal discriminations trained. The theoretical account will fit the modular theory to the behavior observed during Stimulus A and Stimulus B when multiple responses are used and then use these parameters to predict the behavior under the new conditions (Compound AB when two responses are used and Stimulus A, Stimulus B, and Compound AB when a single response is used).

For both procedures the modular theory assumes no interaction among memories when multiple temporal discriminations are trained simultaneously within a session. The question is whether this simple assumption is sufficient to account for the behavior observed when two stimuli are trained simultaneously within a session individually and as a compound. The prediction from the modular theory based on the current assumptions is that reinforcement of responses during the presentations of the compound stimuli would affect the memories of the individual stimuli. Therefore, when stimuli are presented by themselves, performance will be influenced by training in the compound.

EXPERIMENT 1: STIMULUS DISCRIMINATION WITH TWO RESPONSES

In Experiment 1, a food pellet was delivered to a rat with probability of 0.5 following a response on one lever (e.g., left) at a fixed interval after the onset of Stimulus A, and was delivered with the same probability following a different response on the other lever (e.g., right) at a fixed interval after the onset of Stimulus B. In addition, Stimulus A and Stimulus B were presented simultaneously in the Compound AB, with the contingencies of reinforcement of Stimulus A and Stimulus B maintained during the Compound AB.

The empirical goal was to describe the pattern and rate of lever press responses during Stimulus A and Stimulus B, and based on a description of the pattern and rate of responses during Stimulus A and Stimulus B predict the behavior observed during the Compound AB. The hypothesis was that this pattern and rate of responses during the Compound AB would be a simple function of the pattern and rate of responses during Stimulus A and B.

Method

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 and testing rooms. 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 libtum* 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 86 days old and occurred during the dark cycle.

Apparatus

The 12 chambers (25 x 30 x 30 cm) were located inside ventilated, noise-attenuating boxes (74 x 38 x 60 cm). Each chamber was equipped with a food cup, a water bottle, and two levers. Three stimuli, referred to as “noise,” “light,” and “clicker,” were generated from modules from Med Associates, St. Albans, VT. The noise was a 70-dB white noise with an onset rise time and termination fall time of 10 ms that was generated by an audio amplifier (Model ANL-926). The light was a diffused houselight (Model ENV-227M) rated to illuminate the entire chamber over 200 Lux at a distance of 3 in. The clicker (Model ENV-135M) was a small relay mounted on the outside of the chamber that was used to produce an auditory click at a rate of one per second. A pellet dispenser (Model ENV-203) delivered 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 & Zurn, 1989) controlled experimental events and recorded the time at which events occurred with 2-ms resolution.

Procedure

The 12 rats were pre-trained to lever press for one session (Session 1). At the beginning of the session, a food pellet was in the food cup, a house light was turned on, one of the levers was inserted into the box (left or right randomly selected for each rat), and a food pellet was delivered with probability of .5 every 140 s or contingent upon the first lever press response. After the occurrence of the first lever press, food was delivered only contingent upon each lever press. After 30 reinforced lever presses the lever was retracted, the other lever was inserted into the box, and 30 presses on this lever were each reinforced with the delivery of a food pellet. After a total of 60 lever presses (30 on the left and 30 on the right) the houselight went off, the second lever was retracted, the data were recorded, and the session ended.

The 12 rats were trained from Sessions 2 to 100 on a multiple schedule in which two stimuli, referred to as Stimulus A and Stimulus B (e.g., noise and clicker), were presented individually or in compound. At the beginning of each session the two levers were inserted into the box and remained in until the end of the session. Each session consisted of 60 cycles. Each cycle had a fixed 120-s presentation of Stimulus A, or Stimulus B, or the Compound AB (presented with equal probability) followed by a 20-s period of no stimulus. The contingencies of reinforcement during each of the stimuli and the compound are described below. For clarity of description, the left lever press will be designated as the response reinforced during Stimulus A and the right lever press as the response reinforced during Stimulus B.

Stimulus A. Fifteen seconds after the onset of Stimulus A (e.g., noise), the first *left* lever press response was reinforced with probability of .5.

Stimulus B. *d* s after the onset of Stimulus B (e.g., clicker), the first *right* lever press response was reinforced with probability of .5. The 12 rats were divided into three groups and randomly assigned to one of the three durations of *d*: 15, 30, or 60 s.

Compound AB. The Compound AB cycle was defined by the Stimulus A cycle and the Stimulus B cycle. Fifteen seconds after the onset of the Compound AB stimulus, the first *left* lever press response was reinforced with probability of .5. After *d* s following the onset of the Compound AB stimulus, the first *right* lever press response was reinforced with probability of .5. Therefore, on approximately 25% of the Compound AB cycles, two food pellets were scheduled to be delivered (at 15 s and at *d* s), on approximately 50 % of the Compound AB cycles one food pellet were scheduled to be delivered (15 s or *d* s), and on the remaining approximately 25% of the Compound AB cycles no food pellets were scheduled to be delivered. The interval *d* for each rat was same as the interval assigned to that rat for Stimulus B.

The stimulus presented for cycles with Stimulus A or Stimulus B was either the noise or the clicker. The noise stimulus was always associated with the left lever and the clicker stimulus always associated with the right lever. The assignment of the stimulus-response pair (noise-left and clicker-right) to Stimulus A and Stimulus B was counterbalanced between the three groups (*d* = 15, 30, or 60 s) and randomized within a group. Therefore, each group of four animals had two rats with noise stimulus and left levers assigned to Stimulus A and two rats with clicker stimulus and right levers assigned to Stimulus A. The assignment was consistent for each animal throughout the experiment. The three groups are referred to as FI 15/15, FI 15/30, and FI 15/60. The FI refers to the fixed-interval reinforcement distribution; the first value refers to the duration (15 s) from Stimulus A onset to reinforcement availability; and the second value refers to the duration (*d*) from Stimulus B onset to reinforcement availability.

Data Analysis

The results for the nonfood cycles during the last 50 sessions of the training during the individual stimuli (Stimulus A and Stimulus B) and compound (Compound AB) are described. The use of nonfood cycles for analysis prevented the influence of consummatory behaviors on the rate and pattern of the lever press responses. The data shown are the mean across rats. Absolute response rate gradients are described first, followed by the description of a measure of pattern (relative response gradient) and a measure of rate (overall response rate).

The absolute response rate gradient was defined as the response rate (responses per minute) as a function of time (in seconds) from stimulus onset to termination (duration of 120 s). The absolute response rate gradient was separated into two components: pattern and rate of responses. A measure of response pattern, the relative response rate gradient, was calculated by dividing the response rate by the maximum rate for each individual animal, defined as the highest rate over a 5-s period during the period from stimulus onset to termination. An index from these gradients, the time at which response rate reached its maximum, was used for statistical analysis. It was calculated using the running median over a 5-s period beginning 8 s after stimulus onset. This prevented responses immediately following stimulus onset as being used as an index of temporal control which would otherwise have occurred 2.8% of the time. A measure of response rate, the overall response rate during a stimulus, was defined as the sum of the rates of the reinforced and unreinforced responses for each individual rat.

Analysis of variance was performed on the measures of pattern and rate. There were two between-subjects factors, groups (with three levels: FI 15/15, FI 15/30, and FI 15/60) and counterbalancing (with two levels: assignment of stimulus-lever pair to Stimulus A and Stimulus

B), and one within-subjects factor, stimulus (with two levels: Stimulus A vs. Stimulus B). Because there were no significant effects of the stimuli-response counterbalancing, only main effects of group and stimulus factors, as well as their interaction, were reported.

Results

During the lever press pre-training, the median time required for the rats to press the lever for the first time was 1.0 min (the interquartile range was 4.0 min). The median time to complete the first 30 lever presses was 18.8 min (the interquartile range 24.5 min). The median time to complete the 60 lever presses in the session was 30.3 min (interquartile range 29.0 min), ranging from 16.7 to 59.2 min.

Stimulus A and Stimulus B

---------- Insert Figure 1 ----------

Response rate gradients (response rate as a function of time since stimulus onset) for the reinforced (rf) and unreinforced (unrf) lever press responses during nonfood cycles of Stimulus A and Stimulus B (rows) for the FI 15/15, FI 15/30, and FI 15/60 groups of rats (columns) are shown in Figure 1. The response rate for the reinforced responses (solid symbols) increased as a function of the time since stimulus onset, reached a maximum near the time of reinforcement, and then decreased. During Stimulus B, the time of the maximum response rate and the spread of the response gradient for reinforced responses increased as a function of the fixed interval. Response gradients during Stimulus A and Stimulus B for the FI 15/15 group were combined because any observed differences between these gradients would have been due to random error. (This was also done for any additional dependent measures described for this group during Stimulus A, Stimulus B, and Compound AB in all experiments.) The reinforced response rates (filled symbols) were higher than the unreinforced rates (empty symbols); both the reinforced and unreinforced response rates increased and then decreased.

---------- Insert Figure 2 ----------

Response pattern. The pattern of the response rate as a function of time since stimulus onset during Stimulus A and Stimulus B is shown in Figure 2. The panels show the mean relative response gradients for the reinforced (left panels) and unreinforced (right panels) lever responses during Stimulus A (top panels) and Stimulus B (bottom panels) for groups FI 15/15, 15/30, and 15/60.

For the reinforced responses, the maximum rate during Stimulus A was at approximately 15 s and the gradients for the three groups superposed. The reinforced responses during Stimulus B were related to the time from stimulus onset to reinforcement, with the maximum rate approximately at 15, 30, and 60 s for the different groups. Analysis of variance with two between-subjects factors (group and counterbalancing), and one within-subjects factor (Stimulus A vs. Stimulus B) was performed on the times at which the response rate gradients reached a maximum rate. There was a main effect of stimulus ($F_{(1,6)} = 129.73$, $p < .001$), a main effect of group ($F_{(2,6)} = 24.92$, $p < .001$), and a stimulus vs. group interaction ($F_{(2,6)} = 54.11$, $p < .001$) for the reinforced responses. The interaction described the different effect of group (FI 15/15, FI 15/30, and FI 15/60) for the two stimuli (A and B).

Analysis of the unreinforced lever was performed by comparing the unreinforced response gradients during Stimulus A (top-right panel of Figure 2) and Stimulus B (bottom-right panel of Figure 2) to the reinforced response gradients for the 15-, 30- and 60-s intervals (bottom-left panel of Figure 2). These gradients were chosen as the asymptotic performance on a FI 15, FI 30, and FI 60 s schedules. The mean squared deviations from each of the unreinforced response gradients to each of the reinforced response gradients were used as a measure of similarity between the patterns of the unreinforced and reinforced gradients. This relationship is shown in Table 1. The smaller the mean squared deviation, the more similar the two response patterns.

---------- Insert Table 1 ---------

The response gradient for the unreinforced responses during Stimulus A approximated the response gradient for the reinforced responses during Stimulus B. The time of the maximum rate of the unreinforced responses during Stimulus A (top right panel of Figure 2) was at approximately 15 s for the FI 15/15 group, at approximately 30 s for the FI 15/30 group, and at approximately 60 s for the FI 15/60 group. The smallest sum of the mean squared deviations during Stimulus A (bold font for Stimulus A in Table 1), were a function of interval reinforced during Stimulus B (15, 30, or 60 s). That is, the unreinforced responses during Stimulus A were a function of the interval trained during Stimulus B. (Note the similarity between the top-right and bottom-left panels of Figure 2.)

The response gradients for the unreinforced responses during Stimulus B approximated the response gradients for the reinforced responses during Stimulus A. The unreinforced response gradients for the three groups during Stimulus B each reached a maximum response rate at approximately 15 s, the time at which responses were reinforced during Stimulus A. Moreover, the sum of the smallest mean squared deviations during Stimulus B (bold font for Stimulus B in Table 1) was a function of the interval reinforced during Stimulus A. That is, the unreinforced responses during Stimulus B were a function of the intervals trained during Stimulus A. (Note the similarities between the bottom-right and top-left panels of Figure 2.)

---------- Insert Figure 3 ----------

Overall response rate. The left panels of Figure 3 show the overall response rate during

Stimulus A (top panel) and Stimulus B (bottom panel). Analysis of variance with two between-subjects factors (group and counterbalancing), and one within-subjects factor (Stimulus A vs. Stimulus B) was performed on the overall response rate. The rates during Stimulus A were similar to those during Stimulus B ($F_{(1,6)} = 0.04$, $p = .84$). There was no effect of group on the overall rate ($F_{(2,6)} = 2.78$, $p = .14$) and no stimulus vs. group interaction ($F_{(2,6)} = 0.39$, $p = .69$). The overall response rate was approximately the same for the FI 15/30 and FI 15/60 groups (8.51 responses per minute for FI 15/30 and 8.26 responses per minute for FI 15/60 for Stimulus A; 9.21 responses per minute for FI 15/30 and 9.31 responses per minute for FI 15/60 for Stimulus B). Although the overall response rates appeared to be lower for the FI 15/15 group (6.32 responses per minute for Stimulus A and 5.24 responses per minute for Stimulus B), the difference was not significant.

The mean proportion of responses on the reinforced lever (rate of reinforced responses divided by the sum of the rates of reinforced and unreinforced responses) is shown in the right panels of Figure 3 for Stimulus A (top panel) and Stimulus B (bottom panel) for the three groups. The data shown are the mean across rats. The proportion of responses on the reinforced lever was approximately the same across the three groups ($F_{(2,6)} = 2.10$, $p = .20$) and the two stimuli ($F_{(1,6)} = 0.42$, $p = .54$). The median proportion of responses on the reinforced lever was 0.76. The proportion of reinforced lever presses was significantly above chance at 0.5 ($t_{(11)} = 9.27$, $p < .001$).

Compound AB

---------- Insert Figure 4 ----------

The response rate gradients during the Compound AB were similar to the gradients during Stimulus A and B. These gradients for the FI 15 schedule (Stimulus A, triangles) and FI *d* schedule (Stimulus B, squares) during the Compound AB for the FI 15/15, FI 15/30, and FI 15/60 groups (columns) are shown in Figure 4. The data shown are the mean across rats during the nonfood cycles of the last 50 sessions. The response rate increased as a function of time since stimulus onset, reached a maximum near the time of reinforcement, and then decreased. The time of the maximum response rate and the spread of the gradients increased as a function of the duration from stimulus onset. There was a reduction in the response rate for the FI *d* s at approximately 15 s (time of the reinforcement of the other response) in groups FI 15/30 and FI 15/60.

---------- Insert Figure 5 ----------

Response pattern. The patterns of the response rate gradients during the Compound AB are shown in Figure 5. The relative response rate gradients are shown for the FI 15 s (top panel) and for the FI *d* s (bottom panel) for the FI 15/15, FI 15/30, and FI 15/60 groups. The FI 15-s relative response rate gradients (top panel) increased, reached their maximum at approximately 15 s, and then decreased. These gradients were similar across the three groups. The time of the maximum response rate and the spread for the FI *d*-s gradients were a function of the interval from stimulus onset to food, *d* s (bottom panel). Analysis of variance with two between-subjects factors (group and counterbalancing), and one within-subjects factor (FI 15 s and FI *d* s) was performed on the time of maximum response rate. There was a main effect of group ($F_{(2,6)} = 7.46$, $p < .05$), a main effect of fixed interval FI 15 s and FI *d* s ($F_{(1,6)} = 58.92$, $p < .001$), and a group vs. fixed-interval interaction ($F_{(2,6)} = 23.11$, $p < .01$). The interaction indicated that there was a different effect of group (FI 15/15, FI 15/30, and FI 15/60) during the FI 15-s and FI *d*-s schedules.

---------- Insert Figure 6 ----------

Overall response rate. The overall response rate during the Compound AB stimulus is shown in the left panel of Figure 6 for the three groups. The overall response rate was defined as the sum of the rates during the FI 15-s and FI *d*-s schedules over the 120-s during which the Compound AB stimulus was on for each individual rat. Analysis of variance with two between-subjects factors (group and counterbalancing) was performed on the overall response rate. There was a main effect of group on the overall response rate ($F_{(2,6)} = 9.20$, $p < .050$). The overall rate was approximately constant for the FI 15/30 and FI 15/60 groups (12.84 and 14.32 responses per minute, respectively), but was lower for the FI 15/15 group (7.10 responses per minute). The proportion of the responses to the FI 15 s (responses to the FI 15 s, divided by the sum of the responses to the FI 15 s and FI *d* s) was similar across all groups ($F_{(2,6)} = 0.90$, $p = .456$). Moreover, the means were approximately 0.5 suggesting that the rates during the FI 15-s and FI *d*-s schedules were similar ($t_{(11)} = 1.04$, $p = .322$).

Rats from Group FI 15/15 responded at high rates on the reinforced and unreinforced levers at approximately the same time (15 s after stimulus onset) during the Compound AB stimulus; thus, the observed lower response rate for this group could be attributed to a cost for switching between levers. A measure of this cost was the difference between the shortest interresponse times from different responses (left-right and right-left) and from same responses (left-left and right-right). To exclude the influence of occasional very short interresponse times, the first 1% of the interresponse times was excluded. This was 0.45 s for the inter-response times of same responses and 1.00 s for inter-response times of different responses. The difference (0.55 s), is a measure of the extra time taken to switch between levers, which was significantly greater than zero ($t_{(11)} = 4.05$, $p < .005$).

The pattern and rate indices described in Figures 1 to 6 for individual rats are included in

Appendix A.

Discussion (Experiment 1)

Although the unreinforced responses occurred at a lower rate than the reinforced responses, they were reasonably frequent (with a median of 24% of the total number of responses).

Possible Sources of Error in Response Pattern

There are many possible sources of the error responses. Error responses can occur at random and bear no relationship with procedural events. It is also possible, that error responses are related to aspects of the procedural events, and if so, analysis of the response pattern may be indicative of the source of the errors. Analysis of the sources of error of the reinforced and unreinforced responses were performed by comparing predicted and observed response patterns under the different contingencies of reinforcement during Stimulus A and Stimulus B. The identification of the source of errors and their relationship to procedural manipulations identifies independent variables that may affect the error and, therefore, provide some possibility of error prediction and control.

---------- Insert Table 2 ----------

Table 2 describes an accurate response and three types of errors: interval, response, and stimulus, for one of the groups (FI 15/30 Group). For this group, accurate responses during Stimulus A were characterized by left responses with peak time at approximately 15 s, and during Stimulus B characterized by right responses with peak time at approximately 30 s. With an interval error, there is a reversal of the interval (i.e., left responses at 30 s during Stimulus A and right responses at 15 s during Stimulus B), with a response error there is a reversal of the response (i.e., right responses at 15 s during Stimulus A and left responses at 30 s during

Stimulus B), and with stimulus error, there is a reversal of the stimulus (i.e., right responses at 30 s during Stimulus A and left responses at 15 s during Stimulus B). Although the response pattern described as stimulus error could be viewed as a combination of response and interval errors, it is more parsimonious to consider this response pattern as determined by a single source of error until further experimental manipulations are used to distinguish among the two possibilities.

---------- Insert Figure 7 ----------

The errors described in Table 2 are shown as relative response rate gradients (relative response rate as a function of time) in Figure 7. The left column shows errors when Stimulus A is presented (reinforcement delivered for left responses at 15s) and the right column shows errors when Stimulus B is presented (reinforcement delivered for right responses at 30 s). The rows indicate the type of error (none, interval, response, and stimulus) with performance errors indicated by the bold italic font.

The pattern of errors described for the group FI 15/30 (Table 2 and Figure 7) also applies to the group FI 15/60. The identification of the sources of error for the FI 15/15 group, however, is confounded for interval duration. The conclusions regarding the identification of the sources of errors for this group are inferred from the conclusions for the other two groups. Below is a description of the sources of error in the pattern of reinforced and unreinforced relative response rate gradients.

Identification of the Sources of Error in the Data

A comparison of response pattern from the rats (Figure 2) with the patterns described in Figure 7, can determined whether the rats were responding accurately (no errors) or making interval, response, or stimulus errors.

Reinforced response. In Figure 2, the time of maximum relative rate of reinforced responses *(rf)* during Stimulus A (top left panel) for the FI 15/30 s group (filled square symbols) was at approximately 15 s, as in the top left panel of Figure 7, suggesting accurate performance. The time of maximum relative rate of reinforced *(rf)* responses during Stimulus B (bottom left panel of Figure 2) for the FI 15/30 s group (filled square symbols) was approximately at 30 s, as in the top right panel of Figure 7, suggesting accurate responding. The same pattern was observed for the remaining two groups. The time of maximum relative rate of reinforced responses during Stimulus A was at approximately 15 s and during Stimulus B was a function of the interval trained (15 s for the FI 15/15, and 60 s for the FI 15/60 s group).

Unreinforced response. In Figure 2, the time of maximum relative rate of the unreinforced responses (unrf) during nonfood cycles of Stimulus A (top right panel) for the FI 15/30 s group (empty square symbols) was at approximately 30 s as in the bottom left panel of Figure 7, suggesting the presence of stimulus error. The time of maximum relative rate of reinforced responses during nonfood cycles of Stimulus B (bottom right panel of Figure 2) for the FI 15/30 s group (empty square symbols) was approximately at 15 s as in the bottom panel of Figure 7, also suggesting the presence of stimulus error. The same pattern was observed for the remaining two groups: The time of maximum relative rate of unreinforced responses during Stimulus A was a function of the interval trained during Stimulus B (15 s for the FI 15/15, and 60 s for the FI 15/60 groups), and during Stimulus B was a function of the interval trained during Stimulus A (15 s for both FI 15/15 and FI 15/60 s groups).

In summary, reinforced responses were characterized primarily as accurate responses, while the unreinforced responses, characterized primarily as stimulus errors. Stimulus error can also be referred to as “cross-modal transfer,” that is, behavior that occurred during one stimulus was transferred to the other stimulus. Cross modal transfer has been reported across many stimulus and response modalities such as different intensities of visual and auditory stimuli (Meck & Church, 1982; Over & Mackintosh, 1969; Roberts, 1982) and visual and tactile perceptual modalities (Wilson & Shaffer, 1963).

Response Rate during Stimulus A and Stimulus B

Previous studies have suggested that measures of response strength (e.g., magnitude of conditioned responses and response rate) are a function of reinforcement density. For example, the magnitude of responses during a conditioned stimulus was a function on the CS-US interval (Bitterman, 1964; Gallistel & Gibbon, 2000; Gallistel & Gibbon, 2002; Schneiderman & Gormezano, 1964), the rate of responses was a function of trial time between successive food deliveries (Kirkpatrick & Church, 2003), and response rate was a function of reinforcement rate (de Villiers & Herrnstein, 1976; Herrnstein, 1970). Previous studies, have also suggested that response pattern is a function of reinforcement distribution (Catania & Reynolds, 1968; Gallistel & Gibbon, 2000; Gallistel & Gibbon, 2002; Kirkpatrick & Church, 2003). In Experiment 1, reinforcement density was the same across groups (food was delivery with p = .5 during both stimuli that lasted 120 s), but reinforcement distribution during Stimulus B (but not Stimulus A) varied across groups (FI 15, 30, and 60 s). The results were consistent with the previous studies in that the rate of responding was similar across all groups, and the response pattern was related to reinforcement distribution. Most consistent with the present results were those from an auto-shaping procedure using pigeons (Hemmes et al., 1990). The authors presented pigeons with two stimuli (i.e., keylights) that were followed by the delivery of a reinforcer (i.e., access to grain) after 6 s (first stimulus) and 14 s (second stimulus). As in the present experiment, both stimuli remained on after the delivery of reinforcement. This duration was the same for both stimuli (40-s on Hemmes et al, 1990 experiment), keeping the rate of reinforcement during each stimuli constant. The authors observed no effects of the delay to reinforcement on the overall rate of responding (rate during the 40 s of stimulus presentation), but observed a different pattern of responding during each stimulus that was a function of the delay to reinforcement. On some testing trials of selected sessions, the author presented the birds with both stimuli concurrently (compound) and observed similar patterns of responding during the individual and compound stimuli presentations.

The present experiment also reported rates of error responses. The proportion of the reinforced lever responses to the total reinforced and unreinforced lever responses was constant across all groups with a median of 0.76, indicating that approximately 76% of the responses were correct and approximately 24% of the responses were stimulus error. This suggested that error rate was not sensitive to changes in reinforcement distribution.

Compound AB as a Function of Stimulus A and Stimulus B

The pattern of responses during Stimulus A and Stimulus B were characterized most by accurate responses, but also by stimulus error responses. Can the accurate responses during one stimulus (e.g., left responses during Stimulus A) and stimulus error responses during the other stimulus (e.g., left responses during Stimulus B) be used to predict the pattern and rate of that response (e.g., left response) during Compound AB? The following section evaluates the assumption that the Compound AB behavior for the FI 15 s is composed of the summation of correct responses during Stimulus A, and stimulus error responses during Stimulus B. It also evaluates the assumption that the Compound AB behavior for the FI *d* s is composed of the summation of the correct responses during Stimulus B, and stimulus error responses during Stimulus A.

Summation

---------- Insert Figure 8 ----------

The reinforced and unreinforced response rate gradients during Stimulus A and Stimulus B were used to determine the FI 15-s and FI *d*-s behavior during the Compound AB. Figure 8 shows the response rate gradients for the FI 15 s (triangles) and for the FI *d* s (squares) for the FI 15/15 (left panel), FI 15/30 (second panel), and FI 15/60 (right panel) groups. The lines are the summation of the reinforced response rate gradient during Stimulus A and the unreinforced response rate gradient during Stimulus B (for the FI 15 s) and the reinforced response rate gradient during Stimulus B and the unreinforced response rate gradient during Stimulus A (for the FI *d* s). The summation considers that when the Stimulus A and Stimulus B are presented together, the rats respond appropriately to both stimuli and also make stimulus errors that are not dissociable during the compound. The proportion of the variance accounted for by the summation (ω^2) for the FI 15 s (training during Stimulus A) was 0.44 for the FI 15/15 group, 0.95 for the FI 15/30 group, and 0.96 for the FI 15/60 group. The goodness of fit for the FI *d* s (training during Stimulus B) was 0.44 for the FI 15/15 group, 0.37 for the FI 15/30 group, and 0.36 for the FI 15/60 group. The overall goodness of fit was 0.80. The fits were satisfactory especially considering that no free parameters were estimated and that the predictions were determined directly by the responding during Stimulus A and Stimulus B, and no response competition rule (as described below) was used.

These summation fits suggest that the behavior during compounds is composed of correct responses and stimulus error for both Stimulus A and Stimulus B. Much of the systematic unexplained variance accounted for could be attributed to response competition, as described in the next section.

Response Competition

The increased difference of the time between successive responses on different levers (left-right and right-left responses) relative to the time between successive responses on the same lever (left-left and right-right responses) may reflect, among other factors, a difference in travel-time between levers relative to travel-time to the same lever and a difference between making the decision to switch levers relative to the decision to stay on the same lever.

The possibility of the observed difference between times of successive same and different responses occurs due to the tendency of rats to response in bouts (Guilhardi et al., 2005; Kirkpatrick, 2002; Shull, Gaynor, & Grimes, 2001) was minimized by ignoring the very short differences (the third percentile from the distributions was used to compare time between successive same and different responses), suggesting response competition. Response competition can account for the unexpected lower response rate observed during the Compound AB for the FI 15/15 Group compared to the other two groups (described in Figure 6) when the overall reinforcement density was the same across all three groups and no differences were expected.

The summation overpredicted the observed data during the times at which the summation indicated that both responses would occur at a high rate (times at which reinforcement occurred on reinforced cycles, indicated by the vertical dotted lines in Figure 8). Nonetheless, the summation captured the essential features of the response rate gradients during Compound AB. Moreover, it indicated that the obtained response rate gradients during Compound AB are composed of correct responses and responses generated by stimulus error.

Experiment 1 used a summation of correct responses and stimulus error responses to the alternatives (Stimulus A and Stimulus B) to account for the compound behavior when two responses are used. The next experiment reduces the complexity of the procedure by using only a single response instead of two responses. Such simplification is likely to mask some of the determinants of the pattern as described by the contingency table.

---------- Insert Table 3 ----------

Table 3 summarizes the predictions from the summation described in Experiment 1 (columns labeled “Two responses”) and extends the summation predictions to a similar procedure in which a single response is used during Stimulus A, Stimulus B, and Compound AB (column labeled “One response”). Predictions that can be derived from behavior observed during Stimulus A and Stimulus B when two responses are used (a_{rf}, a_{unrf}, b_{rf}, and b_{unrf}) are shown in bold font. When a single response is used, the four gradients observed during a procedure in which two responses are used should predict the behavior during Stimulus A ($a_{rf} + a_{unrf}$), Stimulus B ($b_{rf} + b_{unrf}$), and Compound AB ($a_{rf} + a_{unrf} + b_{rf} + b_{unrf}$). These predictions are shown in italicized bold font in the last column of Table 3. Such a procedure and predictions were explored in Experiment 2.

EXPERIMENT 2: STIMULUS DISCRIMINATION WITH ONE RESPONSE

In Experiment 2, a food was delivered to a rat with probability of 0.5 following a response on one lever (e.g., left) at a fixed interval after the onset of Stimulus A, and was delivered with the same probability following the same response at a fixed interval after the onset of Stimulus B. In addition, Stimulus A and Stimulus B were presented simultaneously in the Compound AB, with the contingencies of reinforcement of Stimulus A and Stimulus B maintained during the Compound AB.

The empirical goal was to predict the pattern and rate of the behavior observed during Stimulus A, Stimulus B, and Compound AB when a single response was used, based on the description of the pattern and rate of behavior during Stimulus A and Stimulus B from

Experiment 1, when two responses were used (a_{rf}, a_{unrf}, b_{rf}, and b_{unrf}, Table 3). The hypothesis was that this pattern and rate of responses during Stimulus A, Stimulus B, and Compound AB when a single response was used would be a simple function of the pattern and rate of correct and error responses during Stimulus A and B observed during when two responses were used.

Method

Subjects

Twelve male Sprague Dawley rats (Taconic Laboratories, Germantown, NY) maintained under the same conditions as the rats in Experiment 1 were used. The rats arrived in the colony at 35 days of age and were handled daily until the onset of the experiment. The animals arrived on the same day as the animals in Experiment 1. Training began when they were 86 days old and occurred simultaneously with training in Experiment 1.

Apparatus

The same 12 standard boxes with two levers used in Experiment 1 were used in Experiment 2.

Procedure

Lever press pre-training (Session 1) was the same as in Experiment 1, except that a single lever (e.g., left or right) was used. The difference from Experiment 1 is that after the first 30 reinforcements of lever presses the lever was retracted and the same lever was immediately re-inserted into the box and the next 30 lever presses were each reinforced with the delivery of a food pellet. The lever inserted was randomly assigned such that six rats had the left lever and the other six rats had the right lever.

As in Experiment 1, the 12 rats were trained from Sessions 2 to 100 on a multiple schedule in which two stimuli, referred to as Stimulus A and Stimulus B (e.g., noise and clicker), were presented individually or in compound. The difference between Experiment 1 and Experiment 2 was that in the latter, the same lever response (e.g., left) was reinforced during Stimulus A, Stimulus B, and Compound AB cycles. Half of the rats were assigned to the left lever and the other half to the right lever. The three groups are also referred to as FI 15/15, FI 15/30, and FI 15/60. The FI refers to the fixed-interval reinforcement distribution; the first value refers to the duration from Stimulus A onset to reinforcement; the second value refers to the duration (*d*) from Stimulus B onset to reinforcement. The 12 rats in Experiment 2 were run daily intermixed with the rats in Experiment 1 in two squads (12 rats each) allowing for comparisons between the two experiments.

Data Analysis

As in Experiment 1, the results for the nonfood cycles during the last 50 sessions of the two-response training during the individual stimuli (Stimulus A and Stimulus B) and compound (Compound AB) are shown. Absolute response rate gradients are described first, followed by the description of a measure of pattern (relative response gradient) and a measure of rate (overall response rate).

Results

During the lever press pre-training, the median time required for the rats to press the lever for the first time was 0.67 min (the interquartile range was 2.1 min). The median time to complete the first 30 lever presses was 17.3 min and the interquartile range was 7.0 min. The median time to complete the 60 lever presses was 21.0 min (the interquartile range was 8.4 min), ranging from 14.0 to 41.6 min.

Stimulus A and Stimulus B

---------- Insert Figure 9 ----------

Response rate gradients (response rate as a function of time since stimulus onset) during Stimulus A and Stimulus B (rows) for the FI 15/15, FI 15/30, and FI 15/60 groups of rats are shown in Figure 9. The response rate increased as a function of time since stimulus onset, reached a maximum near the time of reinforcement, and then decreased. During Stimulus B, the time of the maximum response rate and the spread of the response gradient increased as a function of the fixed interval d.

---------- Insert Figure 10 ----------

Response pattern. The left panels of Figure 10 show the pattern of the response rate as a function of time since stimulus onset during Stimulus A (top panel) and Stimulus B (bottom panel). The relative response gradients are shown for the FI 15 s (top panel) and FI d s (bottom panel) for the FI 15/15, FI 15/30, and FI 15/60 groups. The relative response rate during Stimulus A (top panel) increased, reached a maximum at approximately 15 s, and then decreased. These gradients during Stimulus A superposed for the different groups. The relative response rate during Stimulus B (bottom panel) increased, reached a maximum at approximately the time of reinforcement, and then decreased. The time of maximum response rate and the spread during Stimulus B was a function of interval from stimulus onset to food, d s. Analysis of variance with two between-subjects factors (group and counterbalancing), and one within-subjects factor (Stimulus A and Stimulus B) was performed on the times at which the response rate gradients reached the maximum rate as defined above. There was a main effect of group ($F_{(2,6)} = 37.50$, $p < .001$), a main effect of stimulus ($F_{(1,6)} = 104.30$, $p < .001$) and a group vs. stimulus interaction ($F_{(2,6)} = 59.54$, $p < .001$). The interaction indicated a different effect of group (FI 15/15, FI 15/30, and FI 15/60) during Stimulus A and Stimulus B.

Overall response rate. The right panels of Figure 10 show the overall response rate during Stimulus A (top panel) and Stimulus B (bottom panel). Analysis of variance with two between-subjects factors (group and counterbalancing) and one within-subjects factor (Stimulus A and Stimulus B) was performed on the overall response rate. The response rates during Stimulus A were similar to those during Stimulus B ($F_{(1,6)}$ = 0.05, p = .831). There was no effect of group on the overall rate ($F_{(2,6)}$ = .06, p = .935).

Compound AB

---------- Insert Figure 11 ----------

Figure 11 shows response rate gradients during the Compound AB for the FI 15/15 (left panel), FI 15/30 (second panel), and FI 15/60 (right panel) groups of rats. The response rate gradients increased as a function of stimulus onset, reached a maximum, and then decreased. The time of the maximum response rate was approximately 15 s. This is the time of reinforcement during Stimulus A for all three groups. The decrease in response rate was a function of the interval *d* s.

---------- Insert Figure 12 ----------

Response pattern. The patterns of the response rate gradients during the Compound AB are shown in the left panel of Figure 12 for the FI 15/15, FI 15/30, and FI 15/60 groups. The relative response rate gradients during Compound AB increased, reached their maximum approximately at 15 s, and then decreased. Analysis of variance with two between-subjects factors (group and counterbalancing) was performed on the time of maximum response rate. The time at which response rate reached its maximum was similar across all groups ($F_{(2,6)}$ = 0.168, p = .849). Analysis of variance with two between-subjects factors (group and counterbalancing) was also performed on the mean relative rate during the last 10 s of the 120-s interval as a measure of the decrease in response rate. The decrease in response rate was a function of the time from stimulus onset to reinforcement during Stimulus B. ($F_{(2,6)} = 41.59$, $p < .001$).

Overall response rate. The overall response rates during Compound AB are shown in the right panel of Figure 12 for the three groups. Analysis of variance with two between-subjects factors (group and counterbalancing) was performed. There was a main effect of group on the overall response rate ($F_{(2,6)} = 9.05$, $p < .05$). The overall rate increased as a function of the groups FI 15/15, FI 15/30, and FI 15/60.

The pattern and rate indices described in Figures 9 to 12 observed from individual rats are included in Appendix B.

Discussion (Experiment 2)

Response Pattern and Rate during Stimulus A and Stimulus B

The pattern of responses during Stimulus A and Stimulus B increased until a maximum at approximately the time of reinforcement and then decreased. The gradients were a function of the interval trained, suggesting that correct responses occurred at a rate that was sufficient to differentiate the effects of training. Whether there were stimulus error responses or not, could not be directly determined since a single response was used.

The pattern of responding was similar for groups FI 15/15, 15/30, and 15/60 during Stimulus A, and was related to the duration d s during Stimulus B. As in Experiment 1, the rate of responding during the stimulus was similar for all groups.

The results are consistent with previous results suggesting that measures of response strength are not related to reinforcement distribution but measures of response pattern are (Hemmes et al., 1990; Kirkpatrick & Church, 2003). Previous research have shown that measures of response strength are related to reinforcement density (Bitterman, 1964; de Villiers & Herrnstein, 1976; Gallistel & Gibbon, 2000; Gallistel & Gibbon, 2002; Herrnstein, 1970;

Kirkpatrick & Church, 2003; Schneiderman & Gormezano, 1964).

Predicting Response Pattern and Rate during Stimulus A and Stimulus B

---------- Insert Figure 13 ----------

Because a single response was used, it is not possible to directly dissociate correct responses from stimulus error responses. It is, however, plausible to assume that the same sources of error (none and stimulus error) were also present. The reinforced and unreinforced response rate gradients for Stimulus A and Stimulus B observed in Experiment 1 were summed as described in column labeled “One response” and rows labeled “A” and “B” in Table 3, and compared to the data of the single response case. The comparison is shown in the top panels of Figure 13 for Stimulus A (top panels) and Stimulus B (bottom panels) for the FI 15/15 (left panels), FI 15/30 (second panels), and FI 15/60 (right panels) groups of rats. The proportion of the variance accounted for (ω^2) by the summation of reinforced and unreinforced response rate gradients from Experiment 1 during Stimulus A (a_{rf} + a_{unrf}) was 0.72 for the FI 15/15 group, 0.98 for the FI 15/30 group, 0.97 for the FI 15/60 group, and during the Stimulus B (b_{rf} + b_{unrf}) was 0.72 for the FI 15/15 group, 0.93 for the FI 15/30 group, 0.25 for the FI 15/60 group.

These fits suggested that stimulus error responses were also present in the case of a single response, but these stimulus error responses could not be dissociated from correct responses during training on Stimulus A and Stimulus B. Although the summation of reinforced and unreinforced responses from Experiment 1 accounted for most of the variance for the FI 15/30 group during Stimulus A and Stimulus B, and FI 15/60 group during Stimulus A, it did not account for the FI 15/15 s group during Stimulus A and Stimulus B, and for the FI 15/60 s group during Stimulus B. The variance accounted for by the summation of reinforced and unreinforced response from Experiment 1 for the FI 15/60 s group during Stimulus B is low most likely because the mean of the data is also good predictor of the gradient that approximates a line with slope zero. The unexplained variance accounted for by the FI 15/15 s group during Stimulus A and Stimulus B can be attributed to response competition as described below. Nonetheless, the goodness of fit is impressive considering that there were no free parameters and the gradients used were estimated during Experiment 1 with different rats.

The summation of reinforced and unreinforced response rate gradients from Experiment 1 underpredicted the observed data at the times at which both responses would occur at a high rate (times at which reinforcement occurred on reinforced cycles, the vertical dotted lines on the top-left panels of Figure 13). The underprediction of the summation of reinforced and unreinforced response rate gradients from Experiment 1 suggested that response competition produced a decrease in rate of responding when correct and stimulus error responses were different responses but not when they were the same response. Nonetheless, the summation of reinforced and unreinforced response rate gradients from Experiment 1 remarkably captured the shape of the response rate gradients during Stimulus A and Stimulus B. Moreover, it indicated that the obtained response rate gradients during Stimulus A and Stimulus B are composed of correct responses and also by responses generated from stimulus error.

Compound AB as a Function of Stimulus A and Stimulus B

The remaining question is whether the Compound AB in the single response case can also be predicted by the summation of the correct and stimulus error responses during Stimulus A and Stimulus B. The pattern and rate during Compound AB were quite complex. The pattern of the response rate gradients increased similarly for all three groups, reached a maximum at approximately 15 s, and then decreased. The magnitude of the decrease was a function of the groups and it was smaller for longer durations of *d*. Overall response rate was a function of groups and it was higher for longer durations of *d* s.

The reinforced and unreinforced response rate gradients observed in Experiment 1 for Stimulus A and Stimulus B were summed to predict the behavior of Compound AB in the single response case. This is the summation of a_{rf}, a_{unrf}, b_{rf}, and b_{unrf} shown in the column labeled "One response" and row labeled "Compound AB" in Table 3. The comparison of the summation of all responses during Stimulus A and Stimulus B in Experiment 1 to the data from Compound AB (Experiment 2) is shown in the bottom panels of Figure 13 for Compound AB for the FI 15/15 (left panels), FI 15/30 (middle panels), and FI 15/60 (right panels) groups of rats.

The proportion of the variance accounted for (ω^2) by the summation of correct and stimulus error response rate gradients during Stimulus A and Stimulus B from Experiment 1 was 0.92 for the FI 15/15, 0.82 for the FI 15/30, and 0.89 for the FI 15/60 groups. The goodness of fit was also impressive considering that there were no free parameters and the gradients used were obtained during Experiment 1. Moreover, the assumption of this summation was simple and predicted the Compound AB complex pattern. Some of the unexplained variance accounted for can be also be attributed to response competition: The summation of correct and stimulus error response rate gradients during Stimulus A and Stimulus B from Experiment 1 overpredicted the observed data at the times at which the summation indicated that both responses would occur at a high rate (times at which reinforcement occurred on reinforced cycles, indicated by the vertical dotted lines on bottom panels of Figure 13). Nonetheless, the summation of correct and stimulus error response rate gradients during Stimulus A and Stimulus B from Experiment 1 captured the essential features of the response rate gradients during Compound AB. Moreover it indicated that the obtained response rate gradients in the Compound AB were composed of correct responses and also by responses generated by stimulus error from both Stimulus A and Stimulus B.

The most complex procedure in which two responses were used (Experiment1) provided the components to predict the behavior during Stimulus A and Stimulus B in a single response case (Experiment 2), and the Compound AB in a single response case (Experiment 2) and a multiple response case (Experiment 1).

GENERAL DISCUSSION

Empirical Explanations of Behavior

One standard approach to explain experimental data is to fit known functions to a particular dependent measure. For example, the average of two Gaussian functions (each with parameters for mean, μ, standard deviation, σ, and a scaling rate) could be used to describe the response gradient functions for the experimental conditions described in Table 3. With this approach, however, the number of free parameters may become excessively large. Considering three parameters for each Gaussian function, two Gaussian functions averaged per gradient, and a total of ten gradients (rows and columns of Table 3), there would be a total of 24 free-parameters. It is likely that there would be systematic deviations under some conditions since the functional forms for some of the gradients may not be in the functional form spectrum of the sum of two Gaussian functions. In addition to an excessive complexity and lack of adequacy, this descriptive approach would likely lack generality by failing to account for results from many additional dependent measures (e.g., post-reinforcement pause, indices from a break-run-break pattern of responding, or bout structure of responses), and from many procedures (e.g., random-interval procedure).

Theoretical Explanations of Behavior

An alternative to the empirical approach is one in which a theory of the process generates times of responses. As in the empirical approach, a process theory simplifies the number of parameters used to generate a particular summary measure and can be evaluated using measures of adequacy (e.g., variance accounted for) based on the fits of closed-form equations to the dependent measure. Unlike the empirical approach, a process model may also be simulated to generate times of responses from which any summary measure can be calculated and compared to the data. Moreover, predictions for many new procedures can be determined with both methods: simulations from the process model or through explicit solution.

At least three theories of temporal discrimination processes with cognitive and behavioral intervening variables have been developed and used to account for the behavior observed when rats are trained under a peak procedure: Scalar timing theory, learning to time, and a modular theory of learning and performance. The theoretical goal was to contrast the empirical approach with a theoretical approach that fit a quantitative theory to behavior from one training condition, estimated parameters for the intervening perception, memory, and decision processes, and used these parameters to predict behavior observed under new conditions.

A modular theory of learning and performance

The modular theory was first introduced to predict times of responses for fixed-time, random-time, and tandem fixed- plus random-time procedures (Kirkpatrick, 2002; Kirkpatrick & Church, 2003). More recently, it has been used to explain the dynamics of temporal discrimination (Guilhardi & Church, 2005): The theory predicted, with a single set of parameters, different patterns of results produced by different dependent measures of acquisition (Guilhardi & Church, 2004). The theory was also extended to account for the pattern and rate of responses under schedules with response contingency (e.g., fixed- and random-interval schedules), and under schedules in which multiple time-markers were used as cues for the delivery of reinforcement (Guilhardi, Keen, MacInnis, & Church, 2005). Recently, explicit solutions of the theory to predict behavior under the fixed-interval (Guilhardi et al., 2007) and peak (Yi, 2007) procedures have been developed as described below.

---------- Insert Figure 14 ----------

A flow diagram of the modular theory is shown in the top of Figure 14 for the two-responses (left) and one-response (right) procedures. The diagram contains the basic elements of the theory and the inputs and outputs of each element. The *time markers* refer to the stimuli that, in the two experiments, were Stimulus A or Stimulus B. The onset of the stimulus starts a *clock* and the information provided by the clock is available to the entire system at all times. The delivery and non-delivery of a reinforcer strengthens and weakens the association between the time marker and the response in *strength memory*. Strength memory is primarily responsible for the observed overall response rate. The delivery of a reinforcer also affects *pattern memory* which is the representation of the expected time from the onset of the time marker to the next reinforcer based on experience. Pattern memory is primarily responsible for the observed distribution of responses in time, such as the observed peak response rate gradients. A decision to respond is based on pattern memory, the current value of strength memory, and an operant level. Once the decision to respond is made, a packet of responses is initiated.

The modular theory considers independent pattern and strength memories for each stimulus. Moreover, the theory considers independent strength and response memories for each operant response that is reinforced in the presence of a stimulus. The independent modules for each operant response is shown in the diagram labeled “Two responses” on the top of Figure 14. The simple assumption of independent memories for stimuli and responses is sufficient to account for stimulus error and summation, features not described in previous applications of the theory, as described below.

Modular Theory Predictions: Stimulus Errors. When the Compound AB (Stimulus A and Stimulus B) is presented, the strength and pattern memories of both Stimulus A and Stimulus B for each of the responses (or a single one in the case of the one-response procedure) are modified with respect to the contingencies of reinforcement operating during the Compound AB. Therefore, training during Compound AB will create, in pattern and strength memories for Stimulus A and Stimulus B for each of the responses, a mixture of information about the contingencies of reinforcement that were learned during both Stimulus A and Stimulus B. The response rate results observed during Stimulus A and Stimulus B will contain stimulus errors that were trained during the presentations of the Compound AB stimulus. The amount of stimulus error will be less than the amount of correct responses because correct responses are strengthened in pattern and strength memory during the presentations of individual stimuli and compound, and stimulus errors are only strengthened during presentations of compound stimuli.

Modular Theory Predictions: Summation with Response Competition. Similar learning rules provide similar learned content during training under the two-response and the one-response procedure. The difference is that the memory in the two-response procedure case is separate for each of the two responses (see left top panel of Figure 14). This separation allows for differentiation of correct and error responses (produced by the Compound AB training). However, because the learning during the two-response procedure with separate memory for each response is the same as the learning during the one-response procedure with single memory storage, the observed sum of different responses are expected to be the same as the observed same responses. The difference between learning in the two- and one-response procedures lies in how the information is stored in memory, not in the output behavior. Of course, there is a need for consideration of loss of observed responses due to response competition (i.e., increase in travel time, increase in decision processes) when there is a decision to start packets of two different responses at approximately the same time. Similarly, summation of observed responses (with some loss due to response competition) is predicted to occur during the presentation of Compound AB since two processes, those learned in the presence of Stimulus A and B, are both independently generating responses.

Modular Theory: Explicit Solution for the Peak Procedure. The functional forms for all of the elements from the modular theory are shown in the bottom of Figure 14 with procedure as the input, perception, memory, and decision as intervening modules, and packet of responses as the output. This description is limited to the processes occurring during the presentation of a single stimulus and for a single response, but it applies to conditions in which any stimuli was presented and for both responses. Subjective time is linearly related to physical time, t (the "Clock" in the perception module shown in Figure 14). During cycles in which reinforcement is delivered, perception is a function that starts at zero (time of stimulus onset) and increases linearly with physical time until it reaches the subjective time of reinforcement $\hat{T}$. The subjective time of reinforcement $\hat{T}$ is defined as the linear transformation of physical time of reinforcement T multiplied by K (a normally distributed variable with mean μ_k and coefficient of variation γ_k). During cycles in which no reinforcement is delivered, perception is a function that starts at zero (time of stimulus onset) and increases linearly with physical time until the time of the stimulus termination.

After each cycle, these perception functions are transformed into expected time to reinforcement functions. After the delivery of reinforcement (on cycles with reinforcement), the expected time to reinforcement is a function that starts at $K\hat{T}$ and decreases in time to zero (the

“Perceptual Store” in the perception module in Figure 14). After cycles with no reinforcement, the expected time to reinforcement is a function that starts at the mean subjective time of reinforcement, decreases in time to zero, and then increases until the subjective time of stimulus termination. Pattern memory is the weighted average of expected time to reinforcement functions (the “Reference” in the memory module in Figure 14).

Strength memory changes in time with experience, simultaneously with pattern memory. Response strength weakens during extinction and strengthens with reinforcement (the “Strength Memory” in the memory module in Figure 14). The strengthening and weakening of response strength is defined by a linear operator rule (Bush & Mosteller, 1951, 1955), similar to the rule used in the Rescorla & Wagner (Rescorla & Wagner, 1972) and learning to time models (Machado, 1997). See Guilhardi, et al. (2007) for a detailed description of strength memory in the modular theory of learning and performance. Consistently with previously published results (Guilhardi, Yi, & Church, 2006; Rescorla, 2002), the rate of acquisition of response strength in the modular theory is assumed to be faster than the rate of extinction of response strength (Guilhardi et al., 2007).

The decision to respond is based on a thresholded pattern memory (the “State” in the memory module in Figure 14), the current strength (the “Strength Memory” in the memory module in Figure 14), and a constant operant rate of responding (the “Operant Rate” in the decision module in Figure 14). The threshold (the “Threshold” in the memory module in Figure 14) is set at a percentile of pattern memory, B (normally distributed with a mean μ_b and coefficient of variation γ_b).

The explicit solution of the modular theory to the peak procedure is described in Equations 1 and 2. For a description of how the functional forms described in Figure 14 are solved into Equations 1 and 2, refer to Yi (2007) and Guilhardi, et al. (2007).

Equation 1 describes the explicit solution for pattern memory $E_{SR}[H(t)]$ for stimulus S and response R:

$$E_{SR}[h(t)] = \frac{1}{2\pi\gamma_k\gamma_b KT}\int_0^\infty dy\int_{|y-t|}^\infty dx\,\frac{1}{B(y)}\exp\left(\frac{-(x-B(y))^2}{2\gamma_b{}^2B^2(y)}\right)\exp\left(\frac{-(y-KT)^2}{2\gamma_k{}^2(KT)^2}\right) \qquad \text{(Eq. 1)}$$

The function used to fit the observed response rate gradients for stimulus S and response R, is described in Equation 2:

$$E[R(t)] = A\cdot E[h(t)] + R_0 \qquad \text{(Eq. 2)}$$

where $E[R(t)]$ is the response rate as a function of time, R_0 is the operant rate, and $E[R(t)]$ is the explicit solution for pattern memory (Equation 1). A is a response rate parameter that contains the multiplication of two constants, the number of responses per packet and the strength values in strength memory, that determines the overall rate of packet initiation (and therefore, the rate of stimulus error). For the present experiments, T was defined as 15 (T_{15}), 30 (T_{30}), or 60 s (T_{60}), depending on the stimulus, response, and experimental group. In order to account for the rising of response rate late into the cycle, a second peak function was also used with T defined as approximately 175 s, the mean time to the next food delivery (T_{175}). A second function has also been used by other researchers (Buhusi & Meck, 2000; Machado, 1997; Taylor, Horvitz, & Balsam, 2007). The rising of response rate late in the cycle was shown to be a function of manipulations in the time of reinforcement, the duration of the intertrial interval, and in the duration of the nonfood trials, and suggested to occur as an anticipation of the next food delivery and to produce the asymmetry in the peak gradient (Church, Miller, Meck, & Gibbon, 1991; Sanabria & Killeen, 2007).

Response competition is expected to produce a loss of responses at times during which the theory predicted packet initiation of two mutually exclusive responses at approximately the same time. Response competition was only used to account for the response gradients during the Compound AB when two responses were used (Experiment 1). The corrected the probability of occurrence of a particular response ($\hat{P}_{R_1}$) is described in Equation 3.

$$\hat{P}_{R_1} = P_{R_1} - \left[(P_{R_1} \cdot P_{R_2}) \cdot \frac{P_{R_2}}{P_{R_1} + P_{R_2}} \right] \qquad \text{(Eq. 3)}$$

The corrected probability of a particular response $\hat{P}_{R_1}$ is defined as the initial probability that the response would occur if there was no competition (P_{R_1}), minus the probability that both responses (R_1 and R_2) would occur at the same time ($P_{R_1} \cdot P_{R_2}$) multiplied by the initial probability of occurrence of the other response ($\frac{P_{R_2}}{P_{R_1} + P_{R_2}}$). This response competition rule will predict greater loss of responses when both responses are likely to occur and greater loss of responses by the response that is less likely to occur.

Application of the Modular Theory: Response Gradients from Experiment 1 and Experiment 2

---------- Insert Figure 15 ----------

First, the a_{rf} function (response rate gradient for the reinforced response during Stimulus A, see Table 3) for the FI 15/30 Group was fit with two parameters set as constants (operant rate R_0, was set to zero, and mean of the memory bias, μ_k, was set to one) and three free parameters (coefficient of variation of memory, $\gamma_k = 0.34$, mean of the threshold, $\mu_b = 63.33$, coefficient of threshold, $\gamma_b = 0.47$). These parameters were restricted to be the same for the functions with T_{15} and T_{175}, and the values estimated from the a_{rf} function were used to fit all remaining functions from Experiment 1 and Experiment 2, reducing the number of free parameters and, mostly importantly, reducing the overall number of parameter estimates.

In addition, two parameters (A_{15} and A_{175}) were free to vary for the different stimuli (Stimulus A and Stimulus B), and for each of the responses, to account for the different rates of correct and stimulus error responses. The A_{15} parameter had a median of 9.35 responses per minute, ranging from 1.54 to 35.49 responses per minute. This wide range is due to the wide range between the rate of correct and stimulus error responses. The parameter A_{175} had a median of 2.32 responses per minute ranging from 1.04 to 4.07 responses per minute. The fits of the modular model based on these parameters are shown as solid lines in the top-six panels of Figure 15 (Stimulus A and Stimulus B, Groups FI 15/15, 15/30, and 15/60).

---------- Insert Figure 16 ----------

No other parameters were estimated to account for any of the gradients shown in the bottom panels of Figure 15 (Compound AB, FI 15/15, 15/30, and 15/60 groups). These gradients were predicted using summation (based in a_{rf}, a_{unrf}, b_{rf}, and b_{unrf} as predicted by the modular theory and described in Table 3) with response competition (Equation 3). Moreover, no other parameters were estimated to account for the Stimulus A, Stimulus B, and Compound AB response rate gradients shown in Figure 16 (response rate gradients for Stimulus A, Stimulus B, and Compound AB response rate gradients from the one-response experiment) using the summation predictions from the modular theory.

The median goodness-of-fit for the conditions under which parameters were estimated was 0.95 (Top panels of Figure 15). The overall median goodness-of-fit (ω^2) of the modular theory fits to the mean response rate gradients shown in Figures 15 and 16 was 0.85. Although most of the goodness-of-fit indices to the mean functions were above 0.80, they were considerably smaller for conditions in which the response rate gradient was flat and low (FI 30 and 60 s error responses) because the mean of the data under those conditions is also a good predictor of the data. Although some systematic deviations were observed, the overall goodness of fit was impressive, considering the fact that the pattern parameters estimated under one gradient were used on many other gradients for other stimuli, responses, and groups of rats, considerably reducing the total number of parameters estimated by the model.

Strengths and Weaknesses of the Modular Model

The Stimulus A and Stimulus B gradients for Group FI 15/15 trained on the one-response procedure (top-left panels of Figure 16) were systematically higher than predicted by the model. These systematic deviations may be due to the fact that response competition occurred during the Stimulus A and Stimulus B for Group FI 15/15 (less for the remaining groups since error responses occurred at different intervals) during the two-response procedure (Figure 15, top-left panels). Because these functions were used as the source functions, any response competition was not taken into account when fitting the modular theory.

The assumption of independence between strength and pattern memories for different stimuli and different responses was sufficient to predict data from this experiment. Under some conditions, however, rats may use a configural representation (Pearce, 1987, 1994) of the compound stimulus instead of using it as a combination (such as the sum) of the elements (Bush & Mosteller, 1951, 1955; Rescorla, 1997; Rescorla & Wagner, 1972). More complex assumptions of interaction among distinct memories, as well as the identification of properties of the training multiple stimuli simultaneously that will generate separate memories (as reported by Caetano, Guilhardi, & Church, 2007), will be necessary to account for results indicating rats may under some conditions use configural representations and under other conditions elemental representations of the stimuli. One important feature of the modular theory is that it attempts to relate the intervening variables of response pattern and strength to each other, and map this relationship onto the observed response rate.

The parameters of the modular theory are closely related to behavioral and cognitive processes and the predictions of the theory can be generalized to alternative dependent variables and procedures without increase in complexity or parameter estimations. Although the explicit solution was used to fit the response rate gradients, the modular theory could be simulated to generate times of responses that can be used to evaluate predictions of the theory to any particular dependent measure. This is an important feature of the theory that may be used to integrate the theory with fields often considered to be very different from each other.

Integration among theories of choice, conditioning, and timing

A standard feature of a choice procedure is the use of more than one response; the standard feature of a conditioning procedure is the use of stimuli presented individually or in compounds; and the standard feature of a timing procedure is the use of multiple interval durations. The dependent measure often reported in choice is the relative proportion of responses on the response alternatives (de Villiers & Herrnstein, 1976; Herrnstein, 1961, 1970, 1974); in conditioning it is the ordinal relationships among rates of responding during individual stimuli and compounds (Bush & Mosteller, 1951, 1955; Kamin, 1968, 1969; Rescorla, 1969); and in timing it is the pattern of behavior shown as the relative response rate as a function of the onset of a time marker (Church, 2003; Church et al., 1994; Gibbon et al., 1984). A standard theory of choice is the matching law (de Villiers & Herrnstein, 1976; Herrnstein, 1961, 1970, 1974; Herrnstein, Rachlin, & Laibson, 1997); a standard theory of conditioning is the Rescorla & Wagner model (Rescorla, 2003; Rescorla & Wagner, 1972); and a standard theory of timing is scalar timing theory (Church et al., 1994; Gibbon, 1977; Gibbon et al., 1984). The theories are often used to explain different procedures; even when the procedures are similar, the theories are typically used to explain different dependent measures. Moreover, even if the same procedures and dependent variables are used, there are still differences among experiments that were run independently, such as the type of responses used, the species of the subjects, and the apparatus. Therefore, although all of these theories have provided some contribution to the overall understanding of behavior resulting from the manipulation of number of responses, stimuli presented, and interval duration, none have provided an integrative description and explanation of behavior.

The two experiments described in this article involved features of choice, conditioning, and timing procedures. Three independent variables were manipulated: the number of responses (one or two responses, i.e. a choice procedure), which stimuli were presented (Stimulus A, Stimulus B, and Compound AB, i.e. a conditioning procedure), and the interval durations (fixed intervals 15-, 30-, and 60 s, i.e. a timing procedure). A combination of the predictions from a process model accounts for the components and the principles can be used for the explanation and prediction of behavior described by many dependent measures under many choice, conditioning, and timing procedures. For example, the absolute response rate gradients were used as a measure that provided a description of the pattern and rate of multiple responses. From the absolute response rate gradients many dependent measures, such as the ones often used by theories of timing, conditioning, and choice, can be also derived: proportion of responses on the response alternatives (as used by choice theories), overall response rate (as used by conditioning theories), and relative response rate gradient (as used by timing theories). Because of this generality, the absolute response rate was used as the measure to be explained and fitted by a process model. Ideally, an explanation should account for any dependent variable.

Conclusions

Performance on a discriminated peak interval procedure was characterized by correct and error responses that were related to the interval duration trained. The correct and error responses during individual stimuli were used as primary components to predict the pattern and rate of responses on many other conditions, including compound stimuli with two responses, and individual and compound stimuli with a single response. A simple summation of the components, with the addition of response competition rule, was sufficient to account for the behavior under these new conditions. The dissociation between correct and error responses was possible only when two responses were used. The fact the sum of these correct and error responses predicted rate and pattern during individual stimuli when a single response was used suggested the same errors occurred, although they could not be directly observed.

In addition to the identification of the rules that relate the correct and error response components to other conditions, the present paper presented a process model to account for the data. A modular theory was used to fit the data, but alternative process models, such as learning to time (Machado, 1997), could also be used. A Turing test may be used as a tool for model evaluation (Church, 2001; Church & Guilhardi, 2005). In addition to the simplification of the description of the correct and error response components, the modular theory provided a psychological process with perception, memory, and decision modules that can be also used to predict alternative dependent measures and procedures within its domain. The integration provided by the empirical analysis presented is the foundation necessary for a process model, such as the modular theory, to explain fundamental cognitive and behavioral processes.

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APPENDIX A

Pattern and rate indices for the individual rats described during Experiment 2. The columns for Stimulus A and Stimulus B are the overall response rate during stimulus (Rate), proportion of responses reinforced p(rf), and time of maximum response rate (Time max R) for the reinforced (rf) and unreinforced (unrf) responses. The columns for the Compound AB are the overall response rate during the compound (Rate), the proportion of reinforced responses during the FI 15 relative to the total number of reinforced responses on FI 15 and FI *d*, p(15), and time of maximum response rate (Time max R) for FI 15 and FI *d* s.

	Stimulus A				**Stimulus B**				**Compound AB**			
			Time max R				Time max R				Time max R	
	Rate	p(rf)	rf	unrf	Rate	p(rf)	rf	unrf	Rate	p(15)	FI 15	FI *d*
Group FI 15/15												
Rat 727	8.24	.82	16.0	16.0	5.55	.47	15.0	13.0	8.61	.58	14.5	17.0
Rat 729	5.43	.89	14.0	28.0	4.81	.64	18.0	29.5	6.43	.45	32.7	25.5
Rat 730	5.21	.62	14.5	15.0	5.26	.56	15.0	14.5	6.61	.57	17.0	15.0
Rat 743	6.42	.58	14.3	19.0	5.35	.76	13.0	25.5	6.77	.53	18.0	16.0
Mean	6.33	.73	14.7	19.5	5.24	.61	15.25	20.6	7.11	.53	20.5	18.4
Group FI 15/30												
Rat 731	7.10	.78	16.0	34.0	7.57	.91	25.5	27.5	11.51	.59	14.5	33.0
Rat 741	12.16	.92	13.5	32.5	13.17	.71	26.0	10.0	16.37	.60	10.0	27.0
Rat 746	6.13	.57	13.0	8.0	9.71	.65	33.5	15.0	11.79	.47	15.0	32.0
Rat 747	8.07	.75	14.0	27.0	6.37	.80	25.0	20.5	11.69	.60	11.0	32.0
Mean	8.37	.76	14.1	25.4	9.21	.77	27.5	18.3	12.84	.56	12.62	31.0
Group FI 15/60												
Rat 732	8.89	.70	14.0	36.0	5.60	.73	66.0	16.0	12.72	.55	16.0	34.5
Rat 738	7.72	.86	18.5	111.0	7.26	.79	55.5	12.5	12.86	.54	16.0	55.5
Rat 742	8.34	.66	10.0	68.5	17.06	.97	46.0	24.0	19.74	.30	8.5	51.0
Rat 745	8.08	.84	14.5	9.5	7.32	.68	49.0	14.3	11.99	.53	15.0	51.0
Mean	8.26	.77	14.3	56.3	9.31	.79	54.1	16.7	14.33	.48	13.9	48.0

APPENDIX B

Pattern and rate indices observed for the individual rats described in Experiment 2. The columns are the overall response rate (Rate) and time of maximum response rate (Time of max R) during Stimulus A and Stimulus B, and Compound AB for the FI 15/15, FI 15/30, and FI 15/60 groups of rats.

	Stimulus A		**Stimulus B**		**Compound AB**	
	Rate	Time of max R	Rate	Time of max R	Rate	Time of max R
Group FI 15/15						
Rat 733	14.29	15.5	10.19	16.0	11.86	14.0
Rat 736	6.67	11.5	6.37	12.0	7.36	12.0
Rat 739	9.83	10.5	8.67	11.5	10.7	11.0
Rat 744	5.73	15.5	5.4	16.0	7.27	16.5
Mean	9.13	13.3	7.66	13.9	9.30	13.4
Group FI 15/30						
Rat 734	11.46	14.5	13.9	24.0	16.43	14.5
Rat 735	9.21	14.0	10.94	25.0	13.53	15.0
Rat 749	6.71	13.5	6.97	24.0	10.3	11.5
Rat 750	6.32	12.0	4.88	12.5	10.57	15.0
Mean	8.43	13.5	9.17	21.4	12.71	14.0
Group FI 15/60						
Rat 728	10.45	14.0	11.03	42.0	19.92	15.0
Rat 737	9.31	14.0	6.18	58.0	14.32	14.5
Rat 740	6.97	14.5	10.32	59.0	16.04	12.5
Rat 748	6.72	10.0	7.57	59.5	12.44	14.5
Mean	8.36	13.1	8.78	54.6	15.68	14.1

AUTHOR NOTES

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The raw data (time of occurrence of each response and reinforcer on each session for each rat) are available at http://www.brown.edu/Research/Timelab. This makes it possible for other to examine alternative dependent variable, and evaluate theories of timing and conditioning (Church, 2002).

Table 1

Mean squared deviations from the unreinforced response gradients during Stimulus A and Stimulus B and reinforced response gradients during Stimulus B. The values that produced the smallest sum (rows or diagonals) are in bold font.

	Unreinforced							
	Stimulus A				Stimulus B			
Interval	15	30	60	Sum	15	30	60	Sum
Reinforced								
15	**0.013**	0.039	0.394	0.446	**0.007**	**0.018**	**0.066**	**0.091**
30	0.126	**0.028**	0.232	0.386	0.062	0.057	0.041	0.160
60	0.447	0.282	**0.052**	0.781	0.344	0.302	0.193	0.839
		Sum of diagonal		**0.093**		Sum of diagonal		0.257

Table 2

Three types of error: Stimulus, interval, and response. This example is for the FI 15/30 Group, with reinforcement following a left response during Stimulus A after 15 s, and a right response during Stimulus B after 30 s. Performance errors are indicated by the bold italic font.

Error	Stimulus A		Stimulus B	
	Time of maximum rate	Lever	Time of maximum rate	Lever
None	15 s	Left (rf)	30 s	Right (rf)
Interval	***30 s***	Left (rf)	***15 s***	Right (rf)
Response	15 s	***Right*** (unrf)	30 s	***Left*** (unrf)
Stimulus	***30 s***	***Right*** (unrf)	***15 s***	***Left*** (unrf)

Table 3

Contingency table for procedures with one or two responses for Stimulus A, Stimulus B, and Compound AB. The table shows predictions from a summation assumption for cases in which multiple responses (Experiment 1) or a single response (Experiment 2) are used. The predictions are in bold font.

	Two Responses		One response
Stimulus	Left	Right	Left
A	a_{rf}	a_{unrf}	$\boldsymbol{a_{rf} + a_{unrf}}$
B	b_{unrf}	b_{rf}	$\boldsymbol{b_{rf} + b_{unrf}}$
Compound AB	$\mathbf{a_{rf} + b_{unrf}}$	$\mathbf{a_{unrf} + b_{rf}}$	$\boldsymbol{a_{rf} + a_{unrf} + b_{rf} + b_{unrf}}$

FIGURE CAPTIONS

Figure 1	Response rate gradients for the reinforced (rf) and unreinforced (unrf) lever press responses during Stimulus A and Stimulus B (rows) for the FI 15/15, FI 15/30 and FI 15/60 groups of rats (columns). Response rate was calculated for the nonfood cycles during the last 50 sessions of the multiple schedule training.
Figure 2	Relative response gradients for the reinforced (left panels) and unreinforced (right panels) responses during Stimulus A (top panels) and B (bottom panels) for groups FI 15/15, FI 15/30, and FI 15/60.
Figure 3	Overall response rate (left panels) and proportion of reinforced lever press responses (right panels) during the Stimulus A (top panels) and Stimulus B (bottom panels) for the FI 15/15, FI 15/30, and FI 15/60 groups. The overall response rate is the sum of the rates of the reinforced and unreinforced responses obtained on nonfood cycles. The proportion of reinforced lever responses is the rate of reinforced responses divided by the sum of the reinforced and unreinforced rates.
Figure 4	Response rate gradients for the fixed interval 15 s (triangles) and the fixed interval *d* s (squares) during the Compound AB. The variable *d* was 15 s (left panel), 30 s (second panel), or 60 s (right panel) for the FI 15/15, FI 15/30, and FI 15/60 groups respectively. Response rate was calculated for the nonfood cycles during the last 50 sessions of the multiple schedule training.
Figure 5	Relative response rate gradients for the FI 15-s (top panel) and FI *d*-s (bottom panel) responses during the Compound AB.
Figure 6	Overall response rate (left panels) and proportion of FI 15 s responses during the

Compound AB for the FI 15/15, FI 15/30, and FI 15/60 groups. The overall response rate is the sum of the rates during the FI 15 s and FI *d* s obtained on nonfood cycles. The proportion is the rate of FI 15 s responses divided by the sum of the rates during the FI 15 s and FI *d* s.

Figure 7 Hypothetical relative response gradients during Stimulus A (left columns) and Stimulus B (right columns). The rows represent none (top panel), interval (second panel), response (third panel), and stimulus (bottom panel) discriminative errors that are based on the discrepancy between the actual contingencies of reinforcement and the relative response rate gradients. Left lever press responses are indicated by the solid black line and the right lever presses indicated by the dotted line.

Figure 8 Response rate gradients for the FI 15 s (triangles) and FI *d* s (squares) during the Compound AB. The variable *d* was 15 s (left panel), 30 s (second panel), or 60 s (right panel). The lines are the predictions of responding during the Compound AB as calculated by the sum of responses during Stimulus A and Stimulus B.

Figure 9 Response rate gradients for lever responses during Stimulus A and Stimulus B (rows) for the FI 15/15, FI 15/30 and FI 15/60 groups of rats (columns). Response rate was calculated for the nonfood cycles during the last 50 sessions of the multiple schedule training.

Figure 10 The left panels show the relative response rate gradients during Stimulus A (top panel) and B (bottom panel) for groups FI 15/15, FI 15/30, and FI 15/60. The right panels show the overall response rate during Stimulus A (top panel) and Stimulus B (bottom panel) for the FI 15/15, FI 15/30, and FI 15/60 groups.

Figure 11 Response rate gradients during Compound AB. The variable *d* was 15 s (left panel),

	30 s (second panel), or 60 s (right panel) for the FI 15/15, FI 15/30, and FI 15/60 groups respectively. Response rate was calculated for the nonfood cycles during the last 50 sessions of the multiple schedule training.
Figure 12	Relative response rate gradients (left panel) and overall response rate (right panel) during Compound AB for the FI 15/15, FI 15/30, and FI 15/60 groups.
Figure 13	Response rate gradients for lever press responses during Stimulus A and Stimulus B (top rows) and Compound AB (bottom row) for the FI 15/15, FI 15/30 and FI 15/60 groups of rats (columns). The lines are the predictions based on the summation assumption that responding during Stimulus A, Stimulus B, and Compound AB is the sum of reinforced responses and unreinforced responses during Stimulus A and Stimulus B from Experiment 1 (Figure 1) as described in Table 3.
Figure 14	A flow diagram of the modular theory of learning and performance(adapted from Guilhardi et al., 2007).
Figure 15	Application of the modular theory of learning and performance to the response rate gradients obtained from the FI 15/15, FI 15/30, and FI 15/60 groups of rats (columns) in the two-response experiment (Experiment 1). Top panels: Stimulus A and Stimulus B. Bottom panels: Compound AB.
Figure 16	Application of the modular theory of timing to the response rate gradients obtained for the FI 15/15, FI 15/30, and FI 15/60 groups of rats (columns) in the one-response experiment (Experiment 2). Top panels: Stimulus A and Stimulus B. Bottom panels: Compound AB.

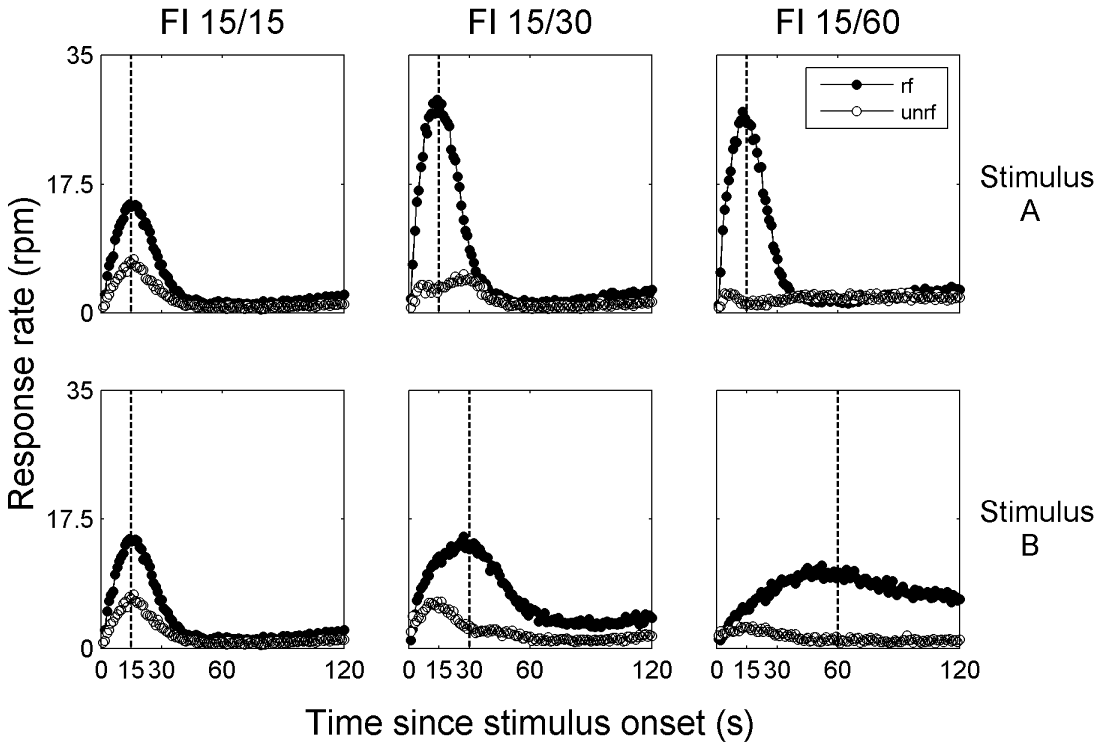
FI 15/15
FI 15/30
FI 15/60
rf
unrf
Stimulus A
Stimulus B
Response rate (rpm)
35
17.5
0
35
17.5
0
0 15 30 60 120
0 15 30 60 120
0 15 30 60 120
Time since stimulus onset (s)

Figure 1

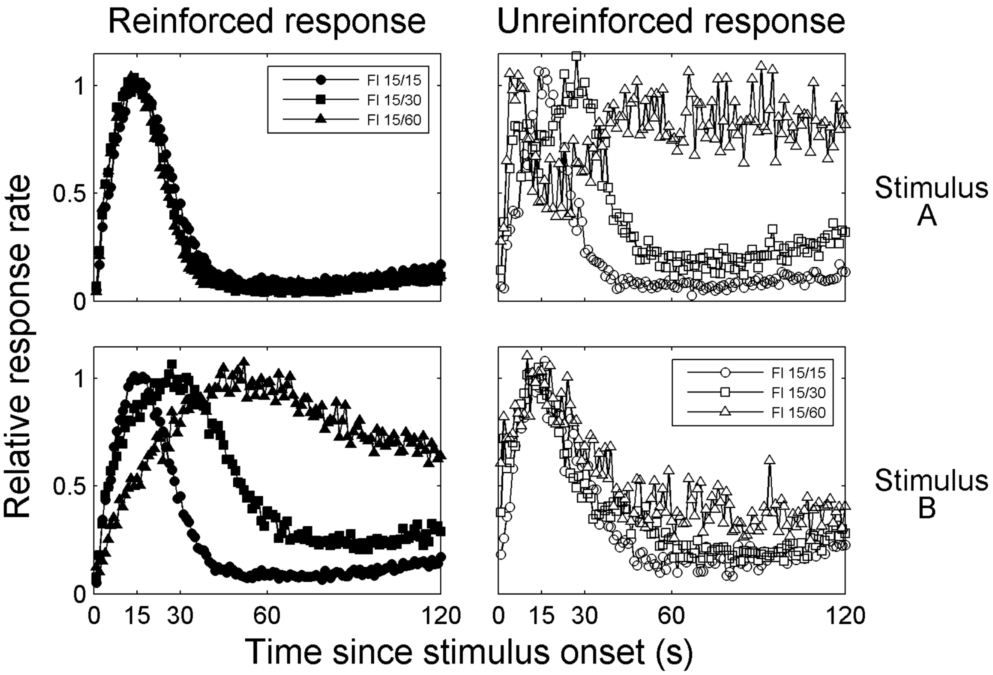
Reinforced response
Unreinforced response
Relative response rate
Time since stimulus onset (s)
Stimulus A
Stimulus B
FI 15/15
FI 15/30
FI 15/60
0
0.5
1
0
15
30
60
120

Figure 2

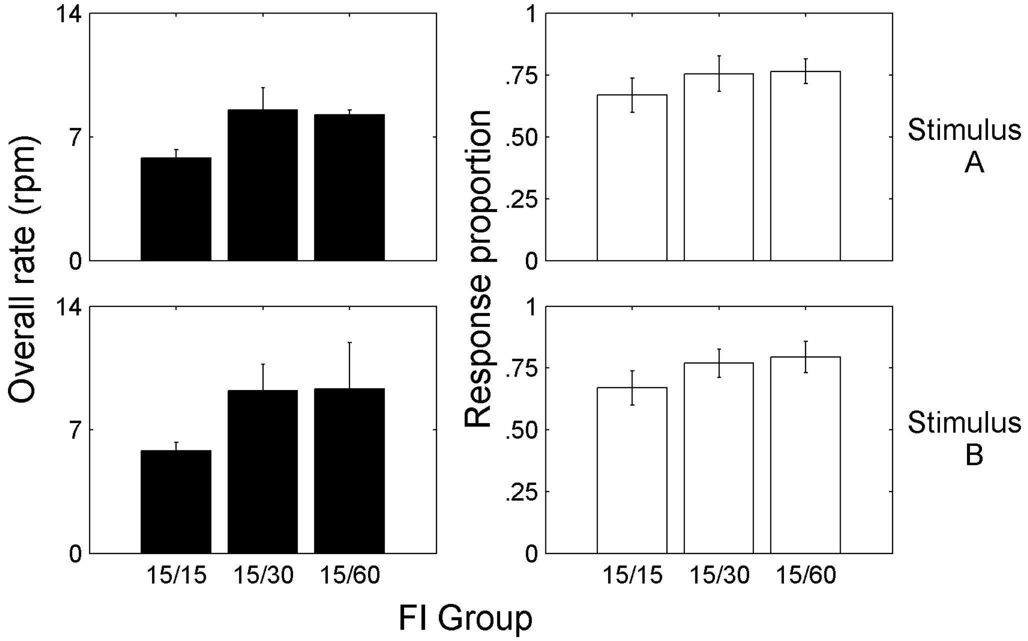
14
7
0
Overall rate (rpm)
14
7
0
15/15
15/30
15/60
1
.75
.50
.25
0
Response proportion
1
.75
.50
.25
0
15/15
15/30
15/60
Stimulus A
Stimulus B
FI Group

Figure 3

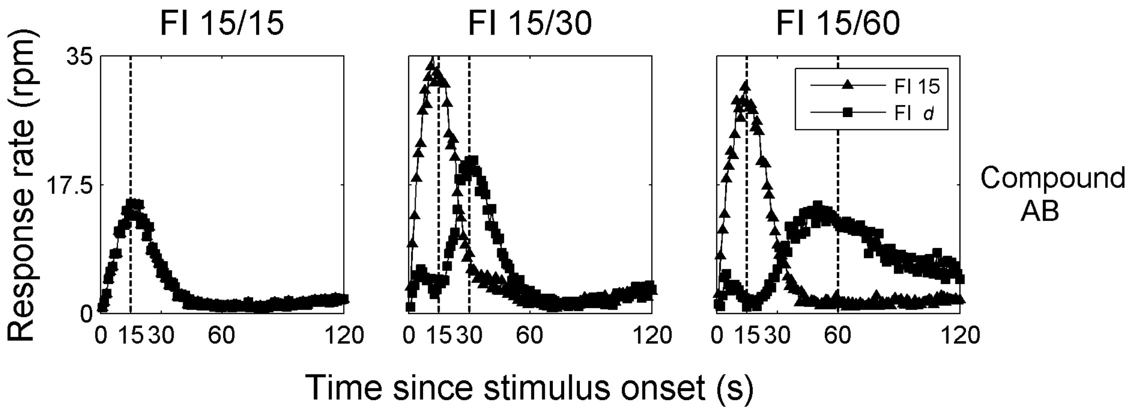
FI 15/15
FI 15/30
FI 15/60
Response rate (rpm)
35
17.5
0
0 15 30 60 120
0 15 30 60 120
0 15 30 60 120
FI 15
FI d
Compound AB
Time since stimulus onset (s)

Figure 4

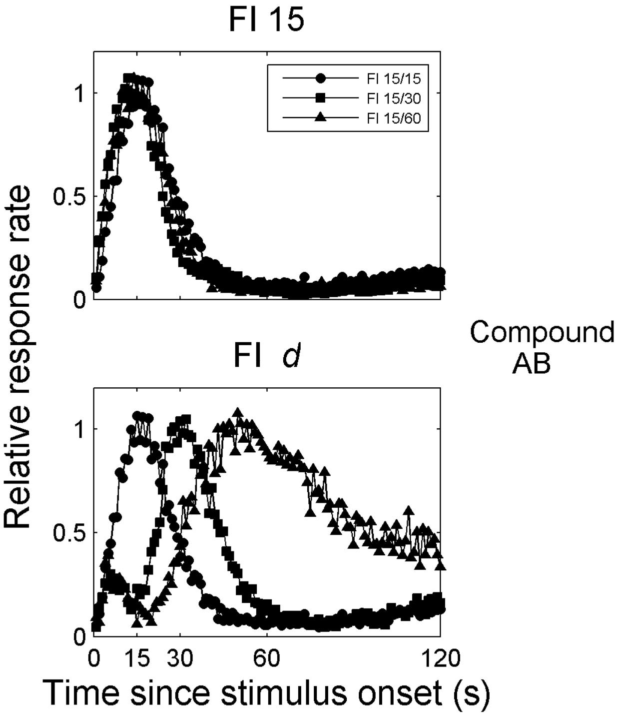
FI 15
FI 15/15
FI 15/30
FI 15/60
1
0.5
0
Relative response rate
Compound
AB
FI *d*
1
0.5
0
0
15
30
60
120
Time since stimulus onset (s)

Figure 5

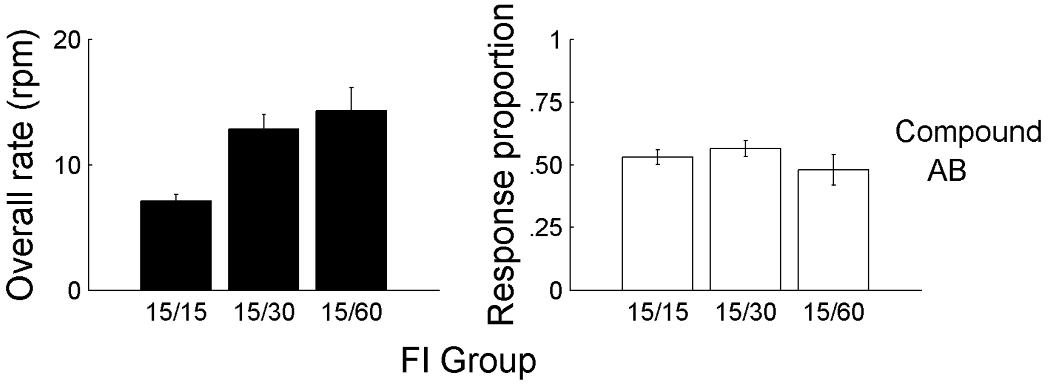
Overall rate (rpm)
20
10
0
15/15
15/30
15/60
Response proportion
1
.75
.50
.25
0
15/15
15/30
15/60
Compound
AB
FI Group

Figure 6

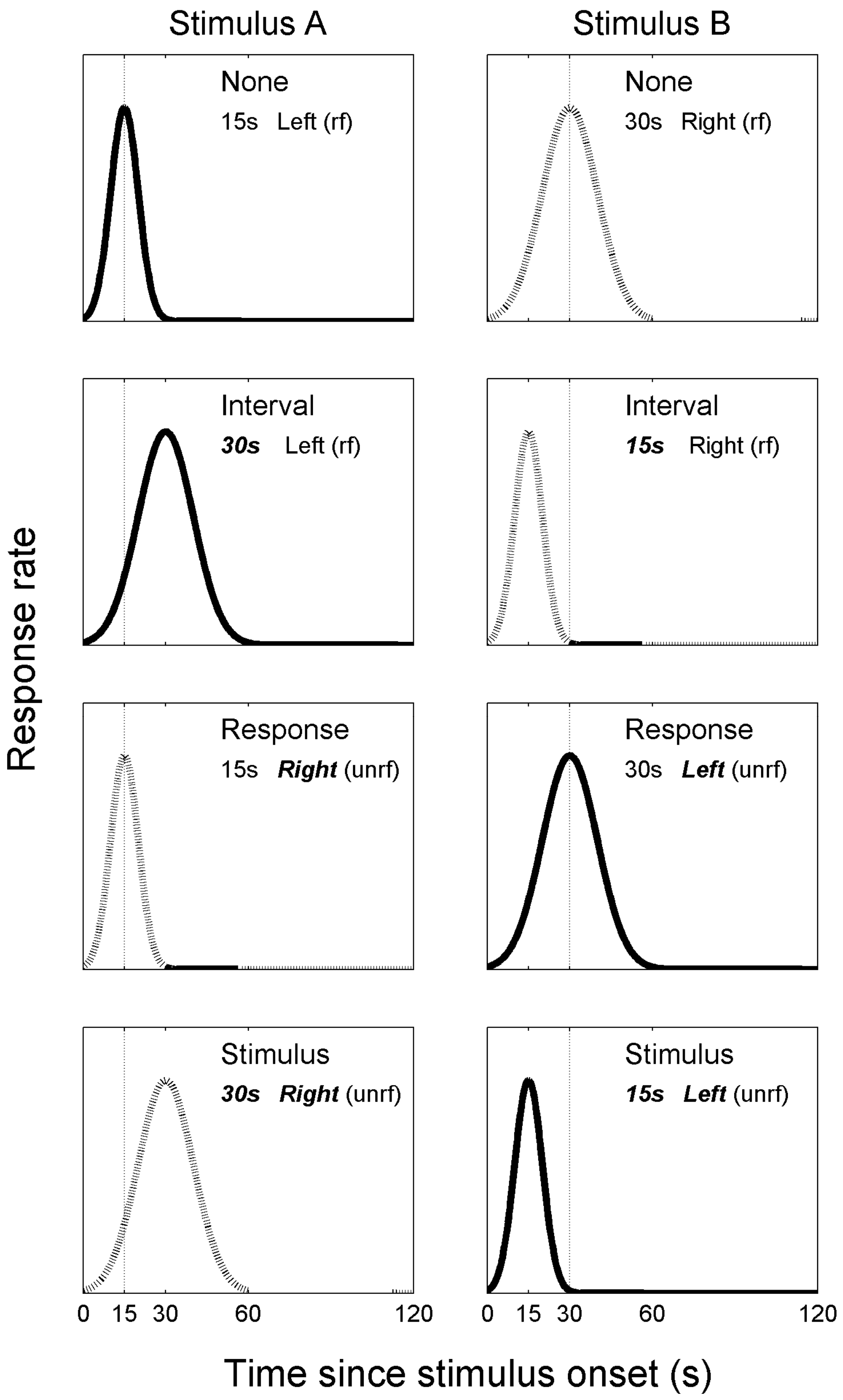
Stimulus A
Stimulus B
None
15s Left (rf)
None
30s Right (rf)
Interval
30s Left (rf)
Interval
15s Right (rf)
Response
15s Right (unrf)
Response
30s Left (unrf)
Stimulus
30s Right (unrf)
Stimulus
15s Left (unrf)
Response rate
0
15
30
60
120
0
15
30
60
120
Time since stimulus onset (s)

Figure 7

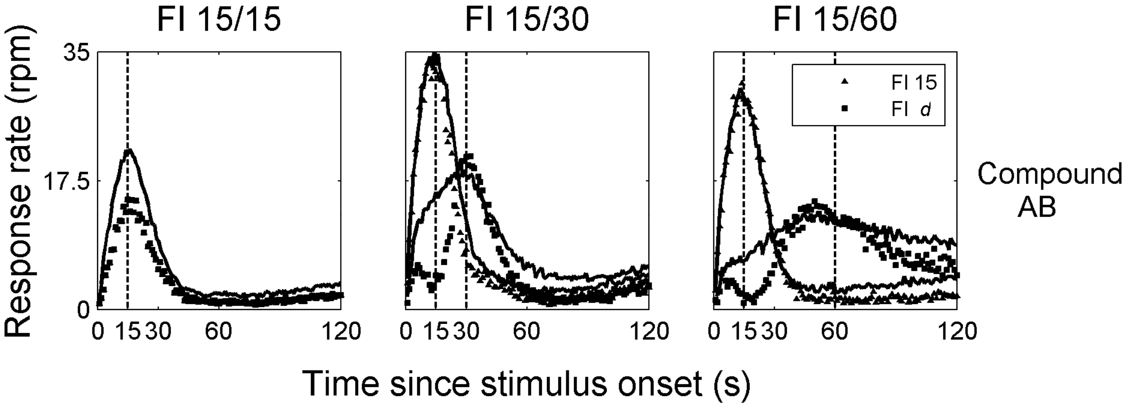
FI 15/15
FI 15/30
FI 15/60
Response rate (rpm)
35
17.5
0
0
15
30
60
120
▲ FI 15
■ FI d
Compound AB
Time since stimulus onset (s)

Figure 8

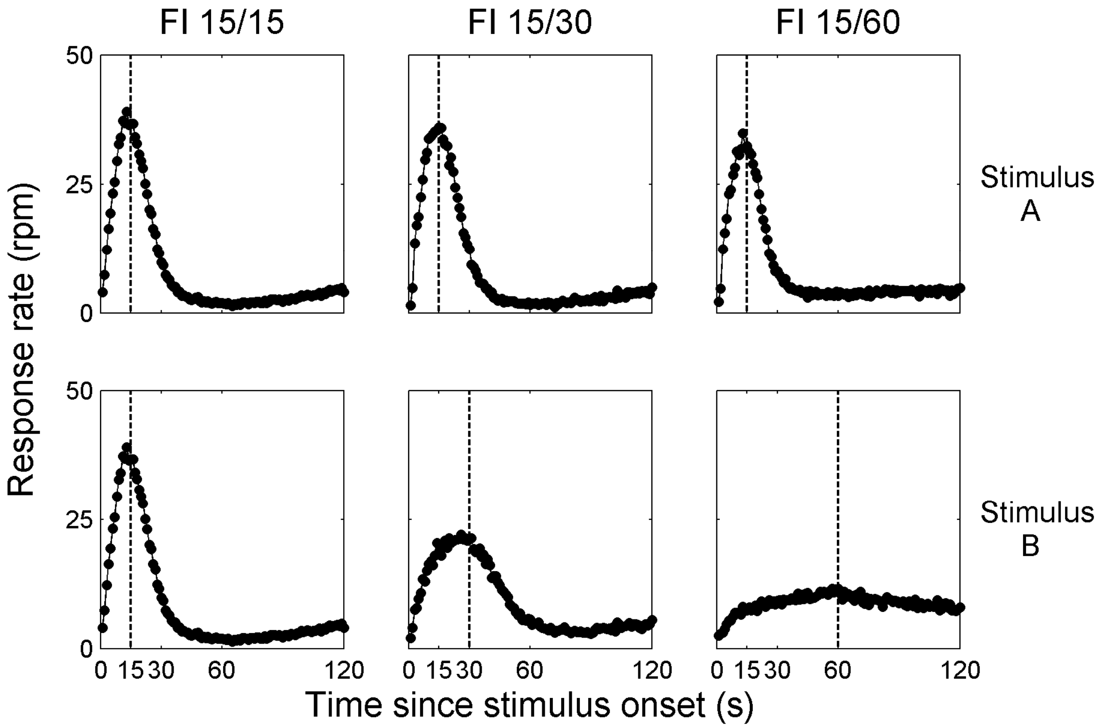
FI 15/15
FI 15/30
FI 15/60
Response rate (rpm)
50
25
0
Stimulus A
Stimulus B
0
15
30
60
120
Time since stimulus onset (s)

Figure 9

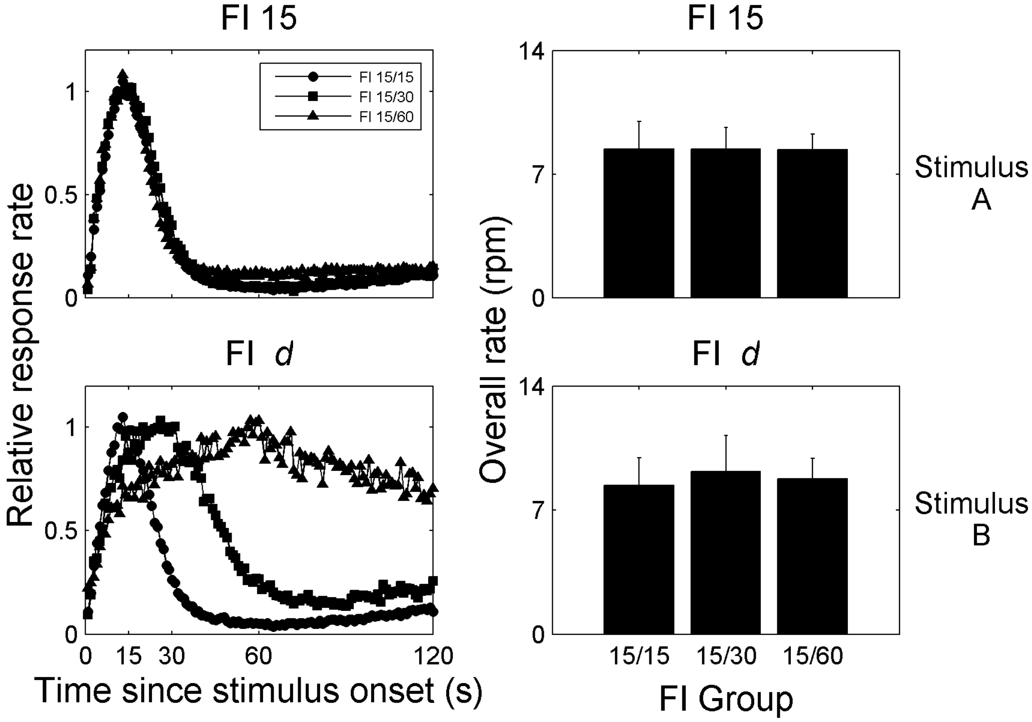
FI 15
FI 15/15
FI 15/30
FI 15/60
1
0.5
0
Relative response rate
FI d
0
15
30
60
120
Time since stimulus onset (s)
FI 15
14
7
0
Overall rate (rpm)
Stimulus A
FI d
Stimulus B
15/15
15/30
15/60
FI Group

Figure 10

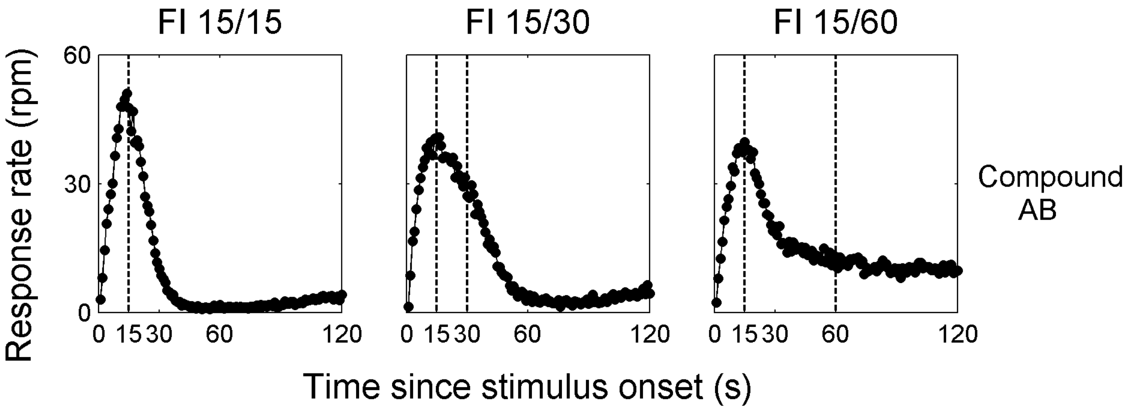
FI 15/15
FI 15/30
FI 15/60
Response rate (rpm)
60
30
0
0
15
30
60
120
Compound
AB
Time since stimulus onset (s)

Figure 11

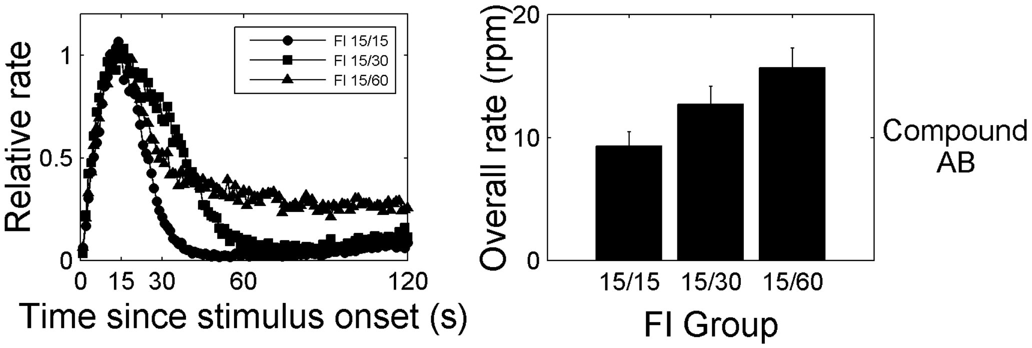
Relative rate
1
0.5
0
0
15
30
60
120
Time since stimulus onset (s)
FI 15/15
FI 15/30
FI 15/60
Overall rate (rpm)
20
10
0
15/15
15/30
15/60
FI Group
Compound
AB

Figure 12

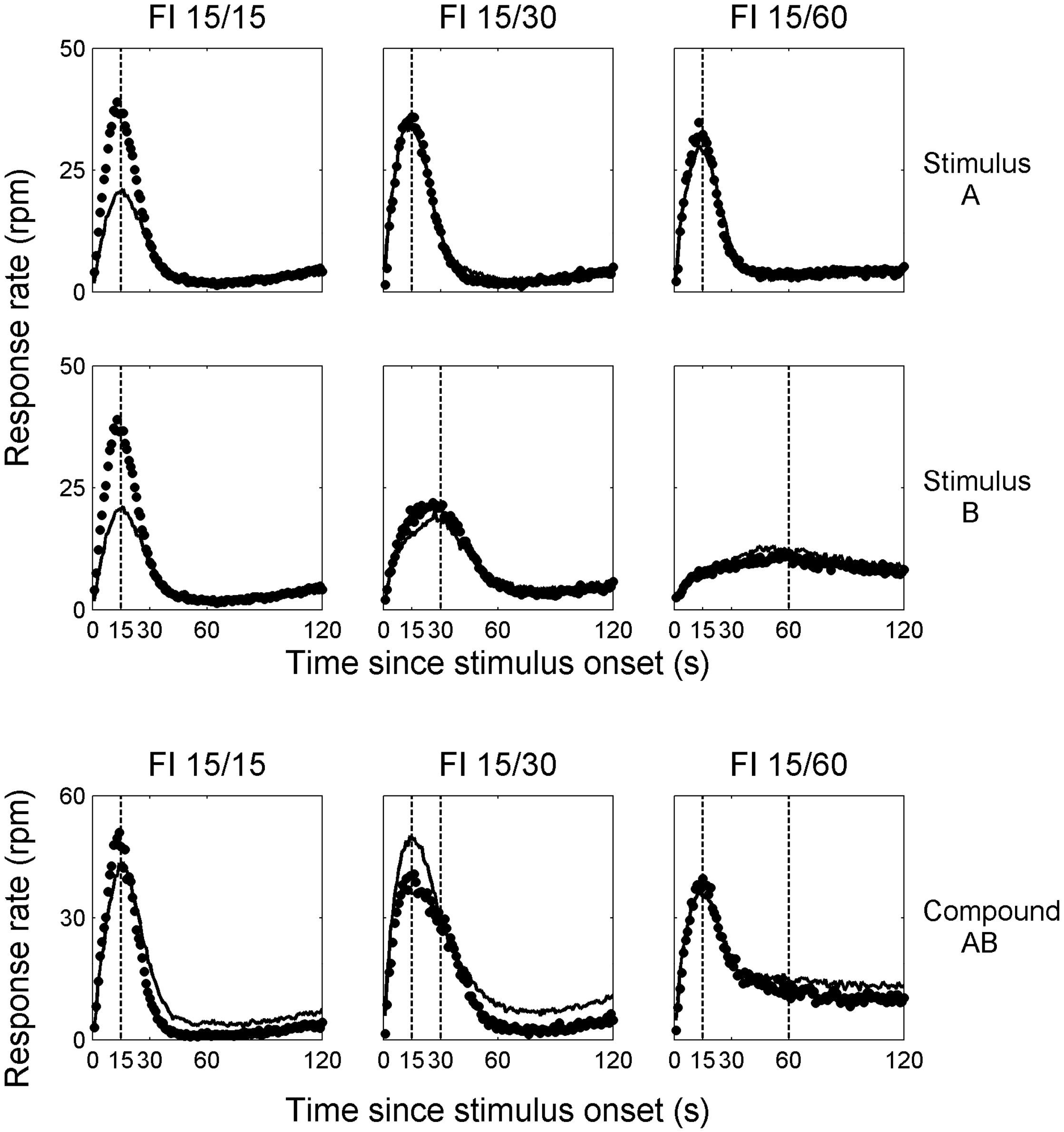
FI 15/15
FI 15/30
FI 15/60
Stimulus A
Stimulus B
Response rate (rpm)
50
25
0
0
15
30
60
120
Time since stimulus onset (s)
FI 15/15
FI 15/30
FI 15/60
Compound AB
Response rate (rpm)
60
30
0
Time since stimulus onset (s)

Figure 13

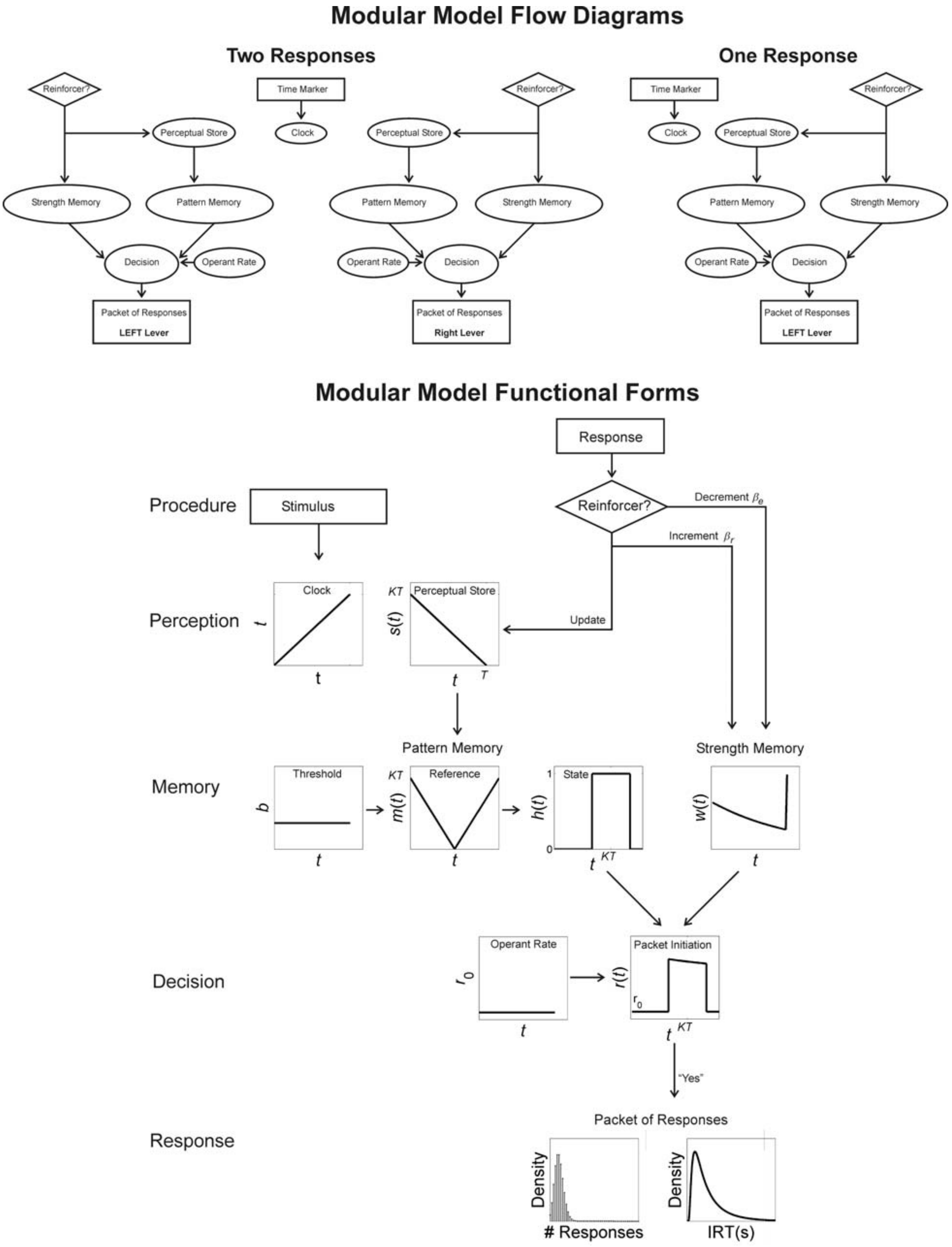
Modular Model Flow Diagrams
Two Responses
One Response
Reinforcer?
Time Marker
Clock
Perceptual Store
Strength Memory
Pattern Memory
Decision
Operant Rate
Packet of Responses
LEFT Lever
Right Lever
Modular Model Functional Forms
Response
Procedure
Stimulus
Reinforcer?
Decrement β_e
Increment β_r
Perception
Clock
t
t
KT
Perceptual Store
s(t)
Update
t
T
Pattern Memory
Strength Memory
Memory
Threshold
b
t
KT
Reference
m(t)
t
1
State
h(t)
0
t KT
w(t)
t
Decision
Operant Rate
r_0
t
Packet Initiation
r(t)
r_0
t KT
"Yes"
Response
Packet of Responses
Density
Responses
Density
IRT(s)

Figure 14

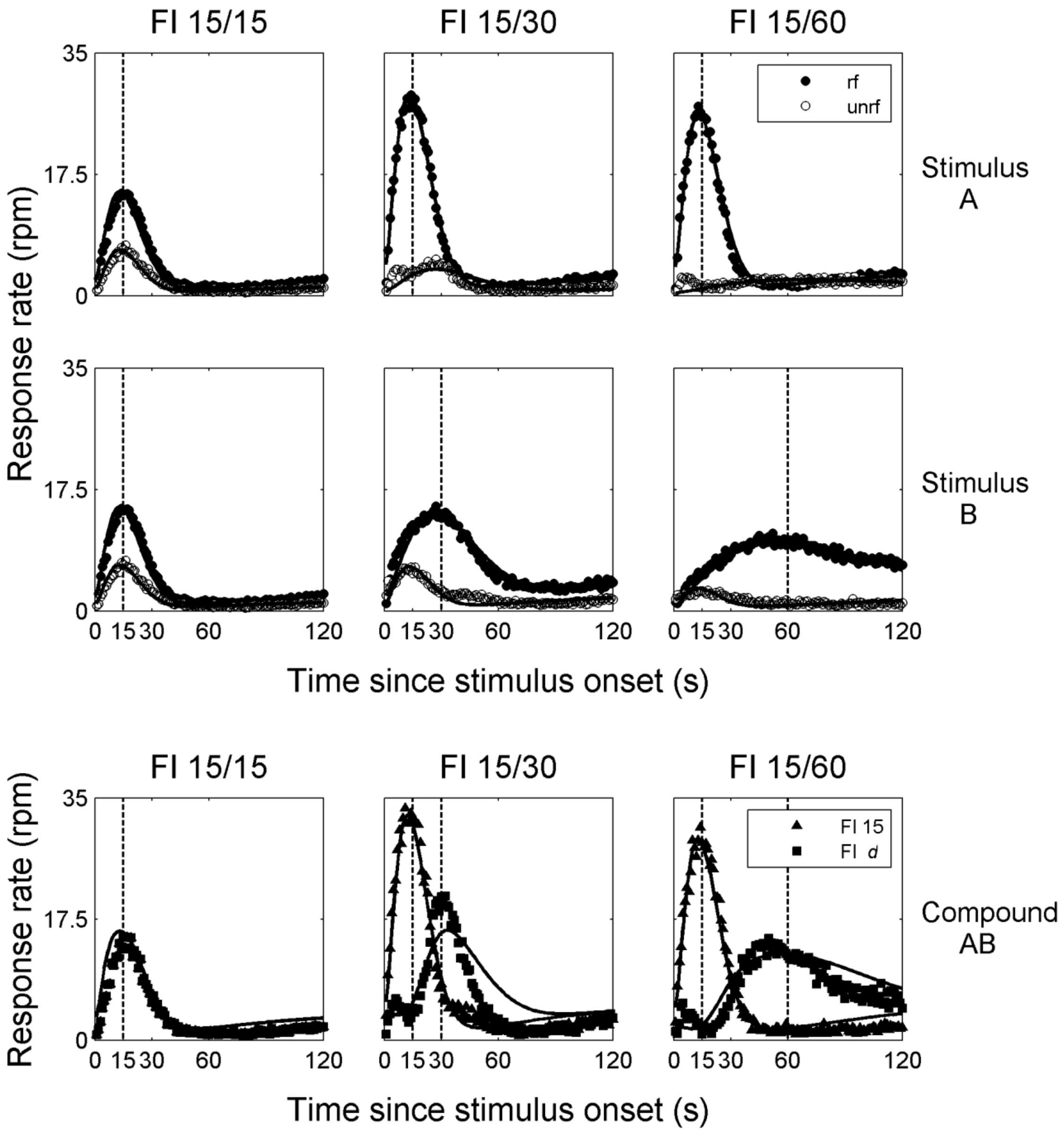
FI 15/15
FI 15/30
FI 15/60
rf
unrf
Stimulus A
Stimulus B
Response rate (rpm)
35
17.5
0
0 15 30 60 120
Time since stimulus onset (s)
FI 15/15
FI 15/30
FI 15/60
FI 15
FI d
Compound AB
Response rate (rpm)
35
17.5
0
0 15 30 60 120
Time since stimulus onset (s)

Figure 15

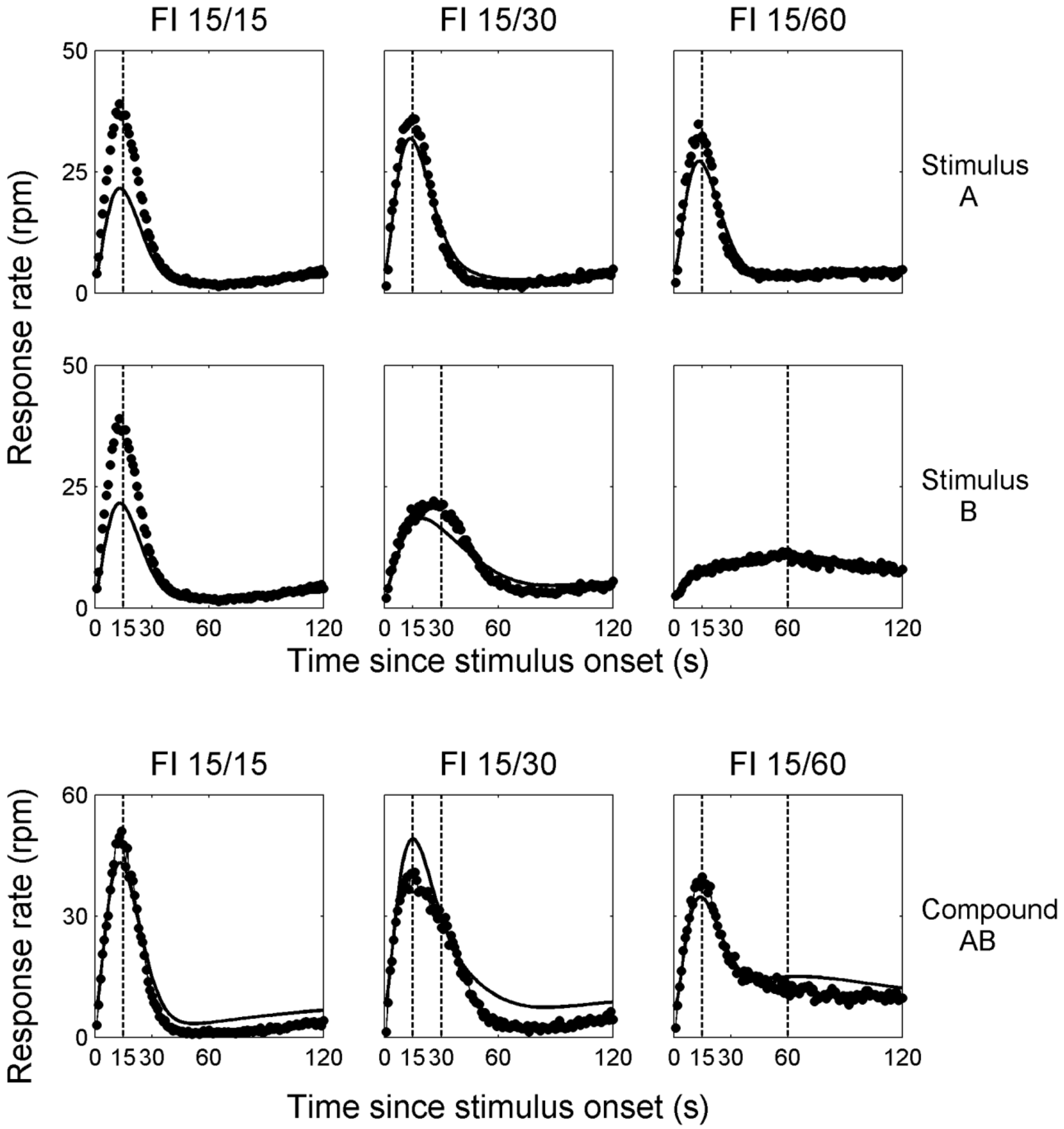
FI 15/15
FI 15/30
FI 15/60
Stimulus A
Stimulus B
Response rate (rpm)
50
25
0
0
15
30
60
120
Time since stimulus onset (s)
Compound AB
60
30

Figure 16