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A Comparison of Responses and Stimuli as Time Markers

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Abstract

A rat's behavior, as well as a stimulus, may be a time marker. But do they lead to similar performance? Eight rats were trained on a 20-s DRL procedure in which head-entry responses were time markers, i.e., each head-entry response indicated that food would not be delivered for 20 s. Concurrently, eight rats were trained on a control procedure in which light stimuli, yoked to the responses of a rat in the DRL procedure, were time markers, i.e., each light stimulus indicated that food would not be delivered for 20 s. A comparison of performance between the two groups showed a lower response rate in the DRL procedure than in the yoked control procedure. However, similar response patterns between the two groups were observed, suggesting that rats anticipated the food similarly with a stimulus or a response as the time marker.

Keywords

DRL; rat; time marker; timing; yoked control procedure

Introduction

Time markers are events that signal future events, such as the delivery of a food pellet or a shock, or that signal changes in the procedural state, such as whether or not a reinforcer will be delivered following a response. Examples of time markers are stimuli of different modalities, such as visual, auditory, or the reinforcer itself (e.g., food pellets); and the rat's responses, such as its lever presses.

Most timing studies have used *stimuli* as time markers (e.g., most fixed-interval schedules of reinforcement either have a stimulus or a reinforcer as time markers); there are not many studies on the properties of *responses* as time markers. The extensive use of stimuli as time markers in timing procedures may be due to the fact that external stimuli are procedurally controlled (and, therefore, easily manipulated by the experimenter), while responses are not. It may also be justified on the grounds that participants are assumed to equally use any particular time marker as a cue for future events, as long as the interval between the time marker and the future event is the most predictive feature. Thus, an underlying assumption of most theories of interval timing is that "participants are able to readily abstract from the input stimulus the temporal dimension and to tune their behavior according to this cue, irrespective of the real timed event" (Buhusi & Meck, 2000).

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In accordance with this assumption, a few experiments that used responses as time markers have found general properties of performance to be similar to those described by experiments in which stimuli were used as time markers. In these procedures, rats were trained in a fixed-interval (FI) schedule of reinforcement initiated by a response (a lever press, for example). One property of performance in timing tasks is the common “break-and-run” pattern of responding observed in individual trials of fixed-interval schedules of reinforcement. This pattern refers to the abrupt change in response rate from low to high at a time that is proportional to the time of reinforcement (Schneider, 1969). The same pattern has been observed in fixed intervals that were initiated by a response (Mechner, Guevrekian, & Mechner, 1963; Shull, 1970). Another example is the postreinforcement pause (PRP), which refers to a suppression of responding following reinforcement. The duration of this pause has been shown to increase as a function of the FI value not only in fixed intervals that are initiated by a stimulus, but also in fixed intervals initiated by a response (Chung & Neuringer, 1967; Lowe, Davey, & Harzem, 1974; Shull, 1970). These studies, however, did not explicitly attempt to describe similarities and differences on performance between the two types of time markers.

In addition to FI schedules, other types of reinforcement schedules could be used to study the properties of responses as time markers. One is the “differential reinforcement of low response rates” schedule (DRL; Ferster & Skinner, 1957; Wilson & Keller, 1953). In DRL schedules, the reinforcer is delivered if the interresponse time exceeds a certain value. Although, in this case, responses work as time markers and information about temporal properties could be obtained (e.g., Anger, 1956; Staddon, 1965), analyses and interpretations of performance on DRL schedules have usually focused on strengthening low rates of responding and not on its temporal properties. Rats that make premature responses in a DRL schedule are said to fail to withhold responding for the minimum interval required, and not to misjudge the interval timed. The measure commonly used to express how well rats time an interval in DRL schedules is “percent accuracy,” that is, percentage of reinforced responses. However, this measure is not very informative about the pattern of anticipation of the reinforcer, which can be evaluated by an inspection of when the premature responses occurred in the timed interval.

Finally, procedures involving DRL schedules of reinforcement have not been used to assess the properties of the response as a time marker, but instead to test the effects of drugs on timing performance (Paule, Meck, McMillan, McClure, Bateson, Popke, Chelonis, & Hinton, 1999), with “timing performance” being evaluated mostly by percent accuracy. As an illustrative example, a search on PsycINFO on August 14, 2008 with the words “DRL and Timing” returned 71 articles, out of which 54 were drug-related studies. Of the remaining 17 articles, most focused on the effects of other manipulations on timing performance (e.g., room temperature and water availability), and no study aimed on the description of the response as a time marker and its characteristics compared to a stimulus as a time marker.

Procedures in which a response or a stimulus is a time marker may indeed lead to similar performance, but this is not the only possibility. Performance could be a function of attentional factors to some extent, and this could be a distinguishing factor between the two types of time markers. It is possible to claim that rats are attending to the beginning of the FI if they are required to initiate it. Following this rationale, it is common that experiments with pigeons and monkeys, for example, require a key peck or a gaze at a specific location before the beginning of a trial. If, on the other hand, the trial is automatically initiated regardless of the position or behavior of an animal at that moment, it is possible that it will not attend to the cue that indicates the beginning of the trial right away, or even miss the cue completely. For example, a rat might be grooming when a visual stimulus is presented. If attention plays an important role in performance, it would be plausible that performance in a task in which a response is a time marker would be better than performance in a task in which a stimulus is a time marker.

In contrast, in a DRL task, or in response-initiated FI schedules that use only one response, the same response that initiates the interval also delivers the reinforcer, so there are two distinct functions attributed to the same response. It is plausible that this could lead to some confusion, and that rats could lose track of which response initiated the interval. Under these circumstances, performance in a task in which a response is a time marker could be worse than performance in a task in which a stimulus is a time marker. Therefore, the question of whether or not responses and stimuli lead to similar performances as time markers is an empirical one.

The aim of the present paper was to answer the empirical question of whether responses and stimuli as time markers lead to similar performances. In doing so, this experiment uses a yoked DRL procedure to directly compare the two types of time markers.

Materials and methods

Animals

Sixteen experimentally naïve male Sprague Dawley rats were used. They were fed with 45-mg Noyes pellets (Improved Formula A) in the experimental sessions, and 18 g of Formulab 5008 food in the home cage after the experimental sessions. Water was available *ad libitum* in both home cages and experimental chambers. They weighed between 75–100 g at the time of arrival in the laboratory, and training began 18 days later.

Apparatus

Sixteen standard operant chambers were used. Each chamber was equipped with a food cup, a water bottle, a food pellet dispenser, LED-photocells that record head entries into the food cup and modules that generate two stimuli, referred to as “noise” and “light.” The noise was a 70-dB white noise with an onset rise time and termination fall time of 10-ms, which was generated by an audio amplifier (Model ANL-926). The light was a diffused houselight (Model ENV-227M) rated to illuminate the entire chamber over 200 Lux at a distance of 3 inches. 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 a 2-ms resolution.

Procedure

Rats were randomly assigned to two groups of eight rats each, named the Response Group and the Stimulus Group. The group names indicate whether a response or a stimulus was used as a time marker. Each rat in one group was randomly paired with a rat in the other group. They were trained for 78 2-hr sessions.

The rats in the Response Group were trained on a differential reinforcement of low response rate (DRL) schedule of reinforcement (see Figure 1, top line). A cycle began with the onset of the noise stimulus; food was made available (primed) 20 s after the last head-entry response into the food cup. Each response made before 20 s from the previous response restarted the 20 s interval. After the food was primed, the next head-entry response within the next 20 s (limited hold) was reinforced and the noise terminated; if no responses occurred during the limited hold, the noise was terminated and no food was delivered. The next cycle began after a mean of 60 s from the previous prime (a fixed 20 s plus a random 40 s sampled from an exponential distribution with mean and standard deviation equal to 40).

Each rat in the Stimulus Group was yoked to one rat in the Response Group (see Figure 1, bottom line). The cycles for each pair of rats started at the same time. Prior to the time of prime, each rat in the Stimulus Group received 0.5-s light presentations at the times of head-entry responses of the rat it was paired with in the Response Group. Each rat in the Stimulus Group

also had the same time of food prime as its paired rat in the Response Group, but it received food and had the noise stimulus terminated at the time of its own first head-entry response prior to termination of the limited hold. The cycle ended for the rat in the Stimulus Group at the same time as it did for the rat in the Response Group.

The primary difference between the groups was that food was primed 20 s after the last *head-entry response* for the Response Group and 20 s after the last *light stimulus* for the Stimulus Group.

Data analyses

Anticipatory responses to the time of food availability (food prime) were compared between groups. The times of head entries from the previous time marker up to (a) the next time marker or (b) the time of food prime, whichever comes first, for the last 15 sessions of training, were used in the exploratory and inferential data analyses with MATLAB® v.7.4.0 (R2007a) and SPSS® 16.0, respectively. Therefore, analyzed responses consisted of interresponse times (IRTs) shorter than 20 s for the Response Group, and of response times from the last light presentation up to the next light presentation or up to the time of food prime for the Stimulus Group.

Responses per minute (RPM) as a function of time from the last time marker (i.e., the last response for rats in the Response Group and the last light presentation for rats in the Stimulus Group), also referred to as “temporal gradients,” are shown. The same method was used to calculate the temporal gradients for the two groups. For the Response Group data, interresponse times per opportunity (IRTs/Op; Anger, 1956; Odum & Ward, 2004) were used to calculate the gradients; for the Stimulus Group, head entries per opportunity were used. A detailed description of the calculations is provided in the Appendix.

For statistical comparisons of response rate, individual overall response rates were used, which were defined as the mean RPM for the 20 s preceding food prime on the last 15 sessions of training. For statistical comparisons of response pattern, normalized RPMs were used. Individual temporal gradients normalized for response rate were calculated as follows:

$$Y_{\min} = Y_i - \min(Y), \quad \text{Equation (1)}$$

$$Y_{\text{norm}} = Y_{\min} / \max(Y_{\min}), \quad \text{Equation (2)}$$

where Y_i is RPM on second i , and $4 \leq i \leq 20$. Note that the gradient was restricted to 4–20 s to ignore high frequencies of short IRTs for the Response Group (responses that occurred within a bout) and the immediate reaction to the presentation of a light stimulus for the Stimulus Group (therefore, focusing only on the anticipation of the next reinforcer).

From the individual normalized temporal gradients, three different summary measures were used to compare response pattern between rats in the Response and Stimulus Groups: the *sum of the distance* between normalized gradients (i.e., the area in between the gradients); the *curvature index* (a measure of the curvature of the gradients); and the center parameter from *ogive fits*, which were calculated by

$$f(t) = \frac{1}{(1 + e^{-\frac{(t-c)}{b}})}, \quad \text{Equation (3)}$$

where t is time since the time marker, b is the slope parameter, and c is the center parameter. A nonlinear search algorithm that minimized the sum of squares was used for the estimation of the parameters b and c . This was done with the `nlinfit` function of MATLAB®. The estimate of the center (parameter c) was used in the response pattern comparison because it represents the time at which response rate reached half of the way to its estimated maximum response rate.

Results

Performance of rats was analyzed in terms of response rate (a measure of the amount of responding) and response pattern (a measure of the location of responding). These results are presented and discussed separately.

Response rate

The upper panel of Figure 2 shows the temporal gradients for the Response Group (open circles) and the Stimulus Group (filled circles), averaged across all rats in each group. The temporal gradient of the Stimulus Group was always higher than the gradient of the Response Group, and this was the case for all paired rats (individual data not shown). In order to quantify this difference, overall response rates of individual rats were used. The mean overall response rate (and standard error) for the rats in the Stimulus Group was 46.8 (4.3), while for the rats in the Response Group it was 4.2 (0.3). Therefore, rats in the former group had a higher overall response rate than rats in the latter group (Paired t -test, $t_7 = 10.35$, $p < .001$).

Response pattern

The bottom panel of Figure 2 shows relative response rate (normalized gradients) for the Response Group (open circles) and the Stimulus Group (filled circles), averaged across all rats in each group (the average gradients across rats was taken after individual normalized gradients were obtained). The mean normalized gradients are representative of the individual pairs of normalized gradients (individual data not shown). To quantify the difference between the groups, the distance between the two gradients for each pair was calculated. A positive distance indicates a lower gradient for the Response Group than the gradient for the Stimulus Group; a negative distance indicates the opposite; and a distance equals to zero indicates overlapping gradients. The mean observed area was not significantly different than zero (Paired t -test, $t_7 = 1.56$, $p = .163$), with a mean (and standard error) of 0.7 (0.4).

A curvature index analysis was also performed on the normalized gradients. This dependent measure expresses the magnitude of the deviation of a cumulative response record from a straight line starting at the number of responses at 4 s into the interval and ending at the number of responses at 20 s into the interval. The curvature index ranges between -1 (more responses at the beginning of the interval than at the end) and 1 (more responses at the end of the interval than at the beginning), passing through 0 (constant response rate throughout the interval; for a complete description of the curvature index, see Fry, Kelleher, & Cook, 1960). The mean observed curvature index was not significantly different for the two groups (Paired t -test, $t_7 = .53$, $p = .613$), with a mean (and standard error) of 0.43 (0.2) for the Response Group and 0.41 (0.2) for the Stimulus Group.

Finally, a comparison of the center parameter from individual ogive fits on the normalized gradients did not reveal significant differences between groups (Paired t -test, $t_7 = 1.71$, $p = .13$), with a mean (and standard error) of 14.5 (0.5) for the Response Group and 13.5 (0.4) for the Stimulus Group. Taken together, the three measures of response pattern indicate that rats in the Response Group increased responding at a rate similar to rats in the Stimulus Group.

Discussion

In this yoked DRL-20 s task, rats in the Response Group that used their own head entry responses as time markers showed a lower response rate than rats in the Stimulus Group that used light presentations as time markers. However, when the temporal gradients were normalized for response rate, performance of the two groups was similar, which indicates that rats anticipated the time of food prime in a similar manner regardless of the type of time marker used.

The difference in rates of responding is expected based on the different schedules of reinforcement. In the Response Group, rats were penalized for premature responses (i.e., responses that occurred before 20 s from the previous response) by the restart of the 20-s interval and consequent delay in the time of food prime. In contrast, in the Stimulus Group, responses that occurred before the time of food prime had no consequence.

Although the different schedules of reinforcement did not allow an investigation of differences in response rate due to the time marker used, they did allow a direct comparison of the response pattern, i.e., the distribution in time of the responses made (timing performance) between the different time markers. The results of this comparison suggest that the timing performance was not strongly affected by the nature of the time marker and that, therefore, responses (or response-produced stimuli) might be comparable to (external) stimuli as time markers.

A limitation of conclusions from the present findings is that they are based on the comparison of a single response and a single stimulus, head entries and light presentations. It could be that a different response-stimulus combination produces a different result. For example, different stimuli have been shown to produce different timing performances: Bright lights are judged to be longer than dim lights (Kraemer, Brown, & Randall, 1995), and filled intervals are judged to be longer than empty intervals (Santi, Miki, & Hornyak, 2005). Therefore, the authors don't rule out the hypothesis that different results could be observed with different pairings. However, the choice of head entries and light stimuli as the response and stimulus used in the present study was based on the extensive literature in timing behavior in which both have been shown to work well in timing tasks, that is, to produce good temporal discrimination.

In summary, the present study used a method that directly compared responses and stimuli as time markers and suggested that responses and stimuli lead to similar timing performance. Important additions to the present findings would be to extend the range of responses and stimuli, as well as the range of procedures (schedules of reinforcement), used.

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Appendix

This is a description of how the temporal gradients (RPMs) were calculated from the times of responses (head entries) for the Stimulus and Response Groups:

First, a list of times of responses since the time marker (the last head entry for the Response Group and the last light presentation for the Stimulus Group) was obtained for each session. Multiple responses could be given by the rats in the Stimulus Group, but there was only one response in each timed fixed interval (FI) for the Response Group because each head entry either restarted the 20-s FI (premature response) or delivered the reinforcer. Therefore, for the Response Group, this list of times of responses since the last response (time marker) is equivalent to a list of interresponse times (IRTs).

Next, for both groups, a histogram from 0 to 20 s in 1-s bins of the list of response times provided responses-per-second (RPS) gradients for each session. Because not all FIs lasted for 20 s (each FI restarted upon a premature response by the Response Group rat), the RPS gradients were normalized by the opportunities to make a response at each 1-s bin, as follows:

$$R/Op(j) = \frac{R(j)}{O(j)}, \quad \text{Equation (A1)}$$

where $R(j)$ is the number of responses at bin j and $O(j)$ is the number of opportunities to make a response at bin j for which $j = 1, 2, 3 \dots 20$. For the Response Group, $R(j)$ is equivalent to $IRT(j)$, which refers to the number of IRTs that are greater or equal to $(j-1)$ seconds and less than j seconds; and $O(j)$ is the number of IRTs in bin j plus the number of all longer IRTs (Odum & Ward, 2004). For the Stimulus Group, $O(j)$ is the frequency of different durations in between

light presentations, and also in between a light presentation and food prime (i.e., for how long each FI lasted).

Finally, responses-per-minute (RPM) gradients for the Stimulus and Response Groups were obtained by

$$\text{RPM} = 60 * (\text{R}/\text{Op}).$$

Equation (A2)

Figure 1.

The yoked DRL-20 s procedure. For the Response Group (top line) a head entry was the best predictor of the time of food availability; for the Stimulus Group (bottom line) a 0.5-s light was the best predictor of the time of food availability. See text for details.

Figure 2.

Upper panel: Responses per minute as a function of time from the last time marker averaged across the last 15 sessions of training. Lower panel: Normalized response rate as a function of time from the last time marker. For the Response Group, the last time marker refers to the last head entry, while for the Stimulus Group, it refers to the last light presentation.