Short communication

Do rats time filled and empty intervals of equal duration differently?

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Abstract

The goal was to determine whether rats time filled and empty intervals of equal duration differently. Each of five rats was trained for 50 sessions on an instrumental appetitive head entry procedure in which food was available (primed) every 120 s. On “empty” cycles, 30 s prior to the next food prime, a 0.5-s pulse of white noise was presented. On “filled” cycles, 30 s prior to the next food prime, white noise came on and stayed on until food was delivered. The two types of cycles were presented with equal probability. The results showed that the rats timed both the food-to-food interval and the stimulus-to-food interval. A comparison of the response gradients on filled and empty cycles following stimulus presentation showed better temporal discrimination on filled cycles. The results were modeled using a Packet theory of timing, with a linear averaging rule to combine the temporal information provided by the stimulus and food. The model fits to the individual response gradients were evaluated with a Turing test.

Keywords: Timing; Filled intervals; Empty intervals; Simultaneous temporal processing; Packet theory; Turing test; Rats

1. Introduction

“Tracts of time filled (with clicks of sound) seem longer than vacant ones of the same duration...” (James, 1890, p. 618).

In a timing procedure, an interval of time can be signaled by the continuous presentation of a stimulus during the interval duration to be timed, or it can be signaled by a brief pulse of the stimulus at the beginning and end of the interval duration. The former is referred to as a “filled” interval, and the latter is referred to as an “empty” interval. Although they can both signal the same interval duration, this presence or absence of the stimulus can influence the behavior from which conclusions about time perception are drawn. In his chapter on time perception in Principles of Psychology, William James described the perception of filled intervals as longer than empty intervals. This phenomenon, sometimes referred to as the “filled interval illusion,” has been the focus of many experiments on time perception throughout the 20th century (e.g., Goldfarb and Goldstone, 1963; Kane and Lown, 1986; Rammsayer and Lima, 1991; Roelofs and Zeeman, 1949; Steiner, 1968; Swift and McGeech, 1925; Thomas and Brown, 1972; Tripplett, 1931).

The research that has been conducted with humans has generally led to two conclusions: (1) the duration of a filled interval is perceived as longer than an empty interval of equal duration (e.g., Brown, 1931; Goldstone and Goldfarb, 1963; Long and Mo, 1970), and (2) timing of filled intervals is more precise than timing of empty intervals (e.g., Rammsayer and Lima, 1991; Rammsayer and Skrandies, 1998). The procedures implemented usually consisted of comparisons of responses made to filled and empty intervals. The mean time and variance of the responses to different stimuli provided information about how the intervals were being perceived. A higher mean time of response led to the conclusion that filled intervals were perceived as longer than empty intervals, and the lower variance in the time of the responses to filled intervals led to the conclusion that filled intervals were perceived more precisely than empty intervals.

Although temporal perception of filled and empty intervals has been studied extensively in humans (e.g., Buffardi, 1971; Ilhe and Wilsoncroft, 1983; Rammsayer and Skrandies, 1998), the study of filled and empty interval perception in animals began relatively recently (e.g., Grant and Talarico, 2004; Mantanus, 1981; Santi et al., 2005). Time perception of filled and empty intervals has been investigated in both pigeons (e.g., Grant and Talarico, 2004; Miki and Santi, 2005) and rats (Santi et al., 2005) with a bisection procedure. A bisection procedure is one in which the animal is trained to make different responses (e.g., left or right lever presses or key pecks) following two extreme target durations (e.g., 1 s and 4 s). During testing, unreinforced trials with stimuli of intermediate durations (e.g., 1.3, 1.6, 2.0, 2.5, and 3.2 s) are presented and the response (left or right) is recorded but unreinforced. The standard bisection results show that ani-
mals will shift from the short response to the long response (referred to as the bisection point or the point of subjective equality, PSE) at approximately the geometric mean of the two extremes (Stubb, 1976; Church and Deluty, 1977). A bisection procedure that measures performance on empty and filled intervals may be identical, except that both filled and empty intervals (intermixed throughout a session) are used for training and testing.

The results of the bisection task with filled and empty intervals in rats (Santi et al., 2005) showed a later PSE for filled intervals than for empty intervals, which suggests that they were perceived as longer than the empty intervals. Additionally, the functions for the filled cycles had steeper slopes, which indicates that performance was less variable on the filled cycles than on the empty cycles. Both results have been interpreted as changes in specific parts of the “internal clock,” as it is described by scalar expectancy theory (Gibbon, 1977; Gibbon et al., 1984). Proposed alterations include changes in pacemaker rate or differences in switch operation.

A comparison of time perception on filled and empty intervals can also be investigated with a simple fixed-interval (FI) procedure in which the task is to “reproduce” an interval (e.g., 30 s) by making a response 30 s following some procedural event (e.g., stimulus onset for a filled interval, or a brief stimulus presentation for an empty interval). In this case, the procedures can be identified by terms consistent with those used in the conditioning literature: delay and trace conditioning respectively. It is widely reported that performance on delay conditioning procedures is better than performance on trace conditioning procedures (e.g., Domjan, 2006). This conclusion is usually based on a comparison of the number of responses that are emitted in the presence of the stimulus (in the case of a delay procedure), or of the number of responses that are emitted following stimulus presentation (in the case of a trace procedure).

Packet theory (Kirkpatrick, 2002; Kirkpatrick and Church, 2003; Guilhardi et al., 2005) is a real-time model of timing that predicts times of responses on simple conditioning procedures. While it has some components that are similar to those in SET, such as a threshold, it does not include a pacemaker with a variable rate or a switch, which suggests that, if it can account for differences on filled and empty cycles, the differences may not be due to either changes in pacemaker rate or a switch-closure latency. The relationships between parameters in the model can be used to further explain the behavior observed on the different cycle types. Simulations of individual data can be compared to the observed individual data, based on any dependent measure the experimenter chooses. The model can also be evaluated based on a cycle-by-cycle comparison of model and rat data.

The purpose of this article is to replicate, with a simple FI head-entry procedure in rats, the Santi et al. (2005) bisection results which indicated that filled intervals were timed more precisely and were perceived to be longer than empty intervals of the same duration. The data will be modeled with Packet theory (Packet theory version 2, with a linear averaging combination rule, as presented in Guilhardi et al., 2005), a model that does not have a variable rate pacemaker or a switch, two components of the internal clock that have been investigated as possible causes of the filled interval illusion. The model will be evaluated using a Turing test.

2. Materials and methods

2.1. Subjects

Five male Sprague Dawley rats (Taconic Laboratories, Germantown, NY) were used in the experiment. They were 35 days old upon arrival, and were handled daily from arrival to the onset of the experiment. The rats were housed individually in a colony room on a 12:12 h light/dark cycle (lights off at 9:30 a.m.). Dim red light illuminated the colony room and the testing room. In addition to the reinforcers obtained in the experimental chambers, the rats were fed 15 g of FormuLab 5008 food after the daily testing session. Water was available ad libitum in both the home cages and the experimental chambers. Testing began when the rats were 67 days old.

2.2. Apparatus

Five operant chambers (25 cm × 30 cm × 30 cm), each located inside a ventilated, noise-attenuating box (74 cm × 38 cm × 60 cm), were used in testing. Each chamber was equipped with a food cup (5 cm × 5 cm × 2 cm) and a water bottle. A magazine pellet dispenser (Model ENV-203, Med Associates, St. Albans, VT) delivered 45-mg Dustless Precision Pellets (Bio-Serv, Rodent Grain-Base Formula, Frenchtown, NJ) into the food cup. Each head entry into the food cup was transduced by a LED-photocell. The water bottle was mounted on the outside of the experimental chamber. Water was available through a tube that passed through a hole in the middle of one of the walls. The food cup was located in the center of the wall opposite the wall with the water bottle. A diffused houselight (Model ENV-227M) rated to illuminate the entire chamber over 200 lx at a distance of 3 in. was mounted near the ceiling of the chamber to the right of the water bottle. A 70-db white noise, with an onset rise time and termination fall time of 10 ms was generated by an audio amplifier (Model ANL-926). Two Gateway Pentium computers, running the Med-PC Medstate Notation Version 2.0 (Tatham and Zurn, 1989), controlled experimental events and recorded the time at which events occurred with 2-ms resolution.

2.3. Procedure

All rats were trained as follows: the houselight was illuminated at the beginning of each session, and terminated approximately 2 h later when the session ended. Food was made available (primed) 120 s after the most recent food delivery (or session start), and delivered contingent upon a head entry into the food cup. In addition, a stimulus was presented 90 s following the most recent food delivery. The stimulus was either a 0.5-s burst of white noise (“empty cycles”), or a white noise that came on and stayed on until food delivery (“filled cycles”). On filled cycles, the noise was terminated with the head entry that
delivered the food. The two cycle types were presented with a probability of 0.5. The animals were tested 60 cycles a session for 50 sessions (one session a day).

2.4. Data analysis

The data analyses were based on the last 10 sessions of training. The dependent measures presented in the results section include mean response rate, curvature index, and response rate as a function of time.

The mean response rate following stimulus presentation was defined as the mean response rate since stimulus onset (i.e., the mean response rate during seconds 90–120 of the cycle).

The curvature index (CI) is a measure that is calculated on the cumulative record of responses (Fry et al., 1960; Guilhardi and Church, 2004). The CI is a measure of how much area is between the cumulative record and a straight line that connects the first and last data point. It ranges between zero and one, where a straight line produces a CI of zero, and perfect timing (a single response exactly at the time of reinforcement) produces a CI of one.

Response rate as a function of time since the last food is calculated as number of responses per second divided by opportunities to respond. This produces an unbiased calculation of responses per minute.

For fits of Packet theory to the data, the data were divided into a calibration sample and a validation sample. The calibration sample consisted of the five odd sessions from 41 to 50 (sessions 41, 43, 45, 47 and 49); the validation sample consisted of the five even sessions from 41 to 50 (sessions 42, 44, 46, 48, and 50). Parameters were estimated based on fits to the calibration sample, and the model was evaluated based on how well the data simulated by the model (with the previously determined parameters) fit the validation sample. Two individual simulations, each with the same parameters, were run for each rat, and were used in model evaluation.

3. Results

3.1. Mean response rate and curvature index

Fig. 1 shows the mean response rate following stimulus presentation or onset (top panel) and the curvature index (bottom panel) for the empty (white bars) and filled (gray bars) cycles for the rat data (left side of each panel) and the model data (right side of each panel). The error bars show the standard error of the mean.

The mean response rates for the rat data were 71.01 and 52.09 for the empty and filled cycles respectively, $t(4) = 3.82, p < 0.02$; these may be compared to the mean response rates for the simulated data which were 75.14 and 54.95 for the empty and filled cycles respectively, $t(4) = 3.75, p < 0.02$.

The mean curvature indices for the rat data were 0.27 and 0.43 for the empty and filled cycles respectively, $t(4) = 4.90, p < 0.01$; these may be compared to the mean curvature indices for the model data which were 0.28 and 0.41 for the empty and filled cycles respectively, $t(4) = 5.08, p < 0.01$.

3.2. Response gradients

Fig. 2 shows response rate as a function of time since food delivery for the mean (large, top left panel) and the individual rats (five smaller panels) for the filled (black circles) and empty (white circles) cycles. The line near each function is the model fit. The dashed vertical line indicates the 0.5-s noise burst, and the gray shaded area indicates the time during which the white noise was on for the filled cycles. Response rate dropped following food delivery (time zero on the abscissa), and slowly increased until stimulus presentation similarly for both filled and the empty cycles. Following stimulus presentation the response gradients show that, on filled cycles, following the onset of the white noise, there was a pause in responding, followed by a sharp increase in response rate, while on empty cycles there was a brief decrease in response rate followed by a steady increase.

4. Discussion

The present study suggests that, when timing filled and empty intervals of the same duration, rats time more precisely on filled than on empty cycles. An examination of the mean response rate in the presence of the stimulus (or the interval following
stimulus presentation) shows higher rates on empty cycles than on filled cycles (Fig. 1). This result contradicts the generally accepted conclusion that stronger stimulus conditioning (i.e., more responding) takes place in delay procedures (filled cycles) than in trace procedures (empty cycles). A traditional interpretation of such results would be that there was stronger stimulus conditioning to the 0.5-s burst of noise than to the continuous presentation of the noise.

The curvature index (CI), however, was significantly higher for the filled cycles than for the empty cycles. This indicates that on filled cycles the rats were waiting longer to start responding following stimulus onset than on the empty cycles. This result, better temporal discrimination on filled cycles than on empty cycles, is consistent with the results reported by Santi et al. (2005) in a bisection procedure with filled and empty intervals.

These two results combined, higher CIs and lower overall response rates for the filled cycles and the opposite for the empty cycles, suggest that although there was generally more responding on empty than filled cycles, the responses were more focused towards the end of the 30-s stimulus on the filled cycles. This can be better viewed as a response gradient, with responses per minute as a function of time since the last food. The response gradients in Fig. 2 show that on the filled cycles the rats were pausing for a longer time following stimulus onset on the filled cycles than they were following stimulus presentation on the empty cycles. This can be seen in the shape of the gradients. On empty cycles (empty circles) the response gradient dips down at the time of stimulus presentation (indicated by the dashed line) and then increased in an approximately linear fashion until the time of reinforcer prime. On filled cycles (filled circles) the response gradient drops at the time of stimulus onset (gray shaded area), and does not increase linearly, but stays low for some time before increasing closer to the end of the interval, near the time of reinforcer prime. The length of the pause following stimulus onset can also be seen as an indication of how long the duration is perceived to be: a longer pause indicates a longer interval (i.e., the filled interval must be physically longer to be perceived as long enough). The steepness of the curve can be seen as the precision of timing, where a steeper gradient indicates more precise behavior.

In their chapter on fixed-interval schedules of reinforcement, Ferster and Skinner observed that ‘‘...the pause after reinforcement is extended, and it usually gives way to an abrupt shift to a higher rate,’’ (Ferster and Skinner, 1957, p.158). This shift from very low or no-responding state (low response state) to a steady, relatively fast rate of responding (high response state), has been referred to as a break-run pattern. It has been observed on many fixed-interval schedules, especially after substantial training (Schneider, 1969). If the rat shifts from a low response state to a high response state at exactly the same time on each cycle, the overall response gradient would be a step function. However, as more variability is introduced into the time of state change, the more gradually the function increases. This would suggest that there was less variability in the timing of the filled interval (a gradient that shows an initial slow increase followed by a faster increase in response rate) than of the empty interval (a gradient that shows a relatively steady increase from the time of stimulus presentation).

4.1. Packet theory (calibration versus validation)

This difference between behavior on filled and empty intervals can also be described by the parameters from Packet theory, an information-processing model that predicts times of responses based on the procedure implemented (version 2, Guilhardi et al., 2005). As described in Guilhardi et al. (2005), a linear averaging rule was used to combine the temporal information from the food-to-food interval (120 s) and the stimulus-to-food interval (30 s).
Packet theory was used to simulate data based on the procedure described in the present paper. Parameters were fit by hand and based on goodness-of-fit ($\omega^2$) of the model to the calibration sample response gradients. Simulations were run for each of the individuals, and the means were calculated from the individual simulations. Fig. 1 shows the model-generated response rates following stimulus onset in the right two bars of the top panel, and the model-generated CIs in the right two bars of the bottom panel. In Fig. 2, the solid lines near the data points are the model-generated data.

For all dependent measures presented here, the mean response rate, the CI, and the response gradients, Packet theory provided good fits to both the individual data and the mean data validation samples (with no significant difference between the model data and rat data for the mean rate or curvature index, and $\omega^2$ values ranging from 0.93 to 0.99 for the response gradients, with a mean of 0.97 and a standard error of the mean of 0.01). Previously, models have accounted for the difference in behavior on filled and empty cycles by explaining the difference as a difference in pacemaker speed. Packet theory can predict these results without having to make changes in the components of an internal clock.

For each rat, seven parameters were estimated to fit the two response gradients: a mean and variance of a threshold for the two cycle types for the stimulus onset-to-food intervals, mean response rates for the two cycle types for the stimulus onset-to-food intervals, and an overall mean response rate for the food-to-stimulus interval. The mean threshold was significantly later for the filled cycles (a mean of 21 s following onset) than for the empty cycles (a mean of 15 s following onset) for all rats ($t(4) = 6.71, p < 0.01$; the variance of the threshold was significantly lower for the filled cycles (mean of 0.77) than for the empty cycles (mean of 0.97) for all rats, $t(4) = 2.97, p < 0.05$). The later, less variable threshold parameters for the gradients on the filled cycles suggests that the rats perceived the filled intervals as longer than the empty intervals (later threshold), and that timing was more precise on filled cycles than on empty cycles (smaller variance).

4.2. Turing test

A model can be evaluated based on its fits to certain dependent measures, but this can be a biased evaluation if the dependent measures chosen to evaluate the model were ones that the model was expressly designed to account for. As data are summarized more (i.e., going from times of individual response, to response gradients that show responding as a function of time, to curvature indices and mean response rates that show only a single index for responses emitted following stimulus onset) it becomes simpler to predict what the results will be based on the procedure implemented.

A Turing test (Church and Guilhardi, 2005; Turing, 1950) is a matching-to-sample test that takes the primary data from both the rats and the model and compares it cycle by cycle, a method for comparison that is even less summarized than the response gradient described above. The cycle-by-cycle comparison is based on the local response rate during a cycle. A rat cycle and a model cycle are both compared to the same sample cycle by taking the sum of the absolute differences between the sample and the rat, and the sample and the model. The sample cycle is designated as “model” or “rat” based on the smaller of the two sums. Because all sample cycles are generated from the model, if it is designated as “model” then this is considered a correct identification; if it is designated as “rat” then this is considered as an incorrect identification. A perfect model would produce data that could only be correctly identified 50% of the time (chance identification). Two simulations were run for each animal and a Turing test was conducted for each of the rats based on comparisons between the rat data and the data from the two simulations (“model” and “sample”). On average, for both the filled and the empty cycles, the samples were correctly identified as “model” 58% of the time (the standard error of the mean was less that 0.03 for both cycle types), slightly above the “ideal” score of 50%.

4.3. General conclusions

The data collected in this simple conditioning procedure replicated the results that Santi et al. (2005) reported: filled intervals are perceived as longer than empty intervals of equal duration and the behavior on filled intervals is less variable than the behavior on empty intervals. The former result is consistent with the ideas presented by James (1890) more than a century ago, and replicates the results obtained by Santi et al. (2005) with a bisection procedure. Previous interpretations of the filled interval illusion result have involved an examination of the components of the internal clock (as described by SET) including the switch operation and the pacemaker rate, as a function of stimulus (filled or empty). Packet theory accounted for the data both on the empty cycles and on the filled cycles without changing any of the assumptions about the internal clock for the two cycle types. Only seven parameters were estimated to fit the 36,000 data points that were fit in the Turing test, which showed a 58% correct identification rate, 8% higher than the “ideal” 50%. Overall, these results suggest that the perception of filled intervals was longer and less variable than empty intervals, and that changes in components of the internal clock are not needed to account for the data.

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