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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 McGeoch, 1925; Thomas and Brown, 1972; Triplett, 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-

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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 (Stubbs, 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 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