



Reinforcement probability modulates temporal memory selection and integration processes[☆]



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ARTICLE INFO

Article history:

Received 17 December 2012
Received in revised form 28 May 2013
Accepted 17 June 2013
Available online 27 July 2013

PsycINFO classification:

2400 Animal Experimental & Comparative Psychology
2420 Learning & Motivation

Keywords:

Time perception
Rats
Multimodal

ABSTRACT

We have previously shown that rats trained in a mixed-interval peak procedure (tone = 4 s, light = 12 s) respond in a scalar manner at a time in between the trained peak times when presented with the stimulus compound (Swanton & Matell, 2011). In our previous work, the two component cues were reinforced with different probabilities (short = 20%, long = 80%) to equate response rates, and we found that the compound peak time was biased toward the cue with the higher reinforcement probability. Here, we examined the influence that different reinforcement probabilities have on the temporal location and shape of the compound response function. We found that the time of peak responding shifted as a function of the relative reinforcement probability of the component cues, becoming earlier as the relative likelihood of reinforcement associated with the short cue increased. However, as the relative probabilities of the component cues grew dissimilar, the compound peak became non-scalar, suggesting that the temporal control of behavior shifted from a process of integration to one of selection. As our previous work has utilized durations and reinforcement probabilities more discrepant than those used here, these data suggest that the processes underlying the integration/selection decision for time are based on cue value.

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1. Introduction

Life unfolds in time, and the perception of time in the seconds to minutes range (i.e., interval timing) is essential to an animal's survival (Gallistel, 1990). Given the importance of temporal expectation, some have proposed that temporal perception is carried out by neural circuits dedicated to processing specific sensory/motor information (Ivry & Spencer, 2004). In support of this notion, Shuler and Bear (2006) have demonstrated that firing rates in primary visual cortex encode light-reward delays. In contrast, evidence of cross-modal transfer of duration information (Meck & Church, 1982a, 1982b; Roberts, 1982; Tees, 1999) suggests that inputs from sensory structures are sent to a central structure that is responsible for generating temporally controlled behavior. One approach that might provide some traction on this argument is assessing how subjects respond when temporal expectations associated with different modality cues conflict with one another.

Recent work from our lab has demonstrated a behavioral phenomenon, temporal memory averaging, in which two different temporal memories are combined into a single expectation (Swanton, Gooch,

& Matell, 2009; Swanton & Matell, 2011). Specifically, rats were trained on a dual-duration, dual-modality, peak-interval procedure in which one modality stimulus (e.g., a tone) indicated probabilistic reinforcement availability after a short duration (e.g., 10 s), whereas a different modality stimulus (e.g., a house light) indicated probabilistic reinforcement availability after a long duration (e.g., 20 s). Following training, rats were tested under extinction contingencies with the simultaneous compound stimulus (i.e., tone + light). Remarkably, robust peak-shaped responding occurred at a time between the two criterion durations (i.e., around 16 s), despite subjects never being reinforced at this time. Importantly, this compound peak exhibited the normal Gaussian shape, and clear superimposition of all three peak functions was seen after normalizing response rate and peak time, indicating scalar variability of the compound peak. These data were interpreted as resulting from the retrieval of the component temporal memories, which were then integrated into a single expectation that was timed in a normal manner. As it relates to the above question about the neural processes underlying temporal control, this finding of scalar averaging is largely incompatible with a temporally modulated output signal from visual and auditory cortices, as the sum of these temporal output signals (i.e., the sum of the two individual peak functions) would not be scalar.

Our initial observation of temporal memory averaging occurred in the context of an electrophysiological investigation (Matell, Shear-Brown, Gooch, Wilson, & Rinzel, 2011), and the experimental design required that response rates for the two cues be equal. Because longer durations produce diminished peak rates when tested within subjects,

[☆] This research was supported in part by grants from the National Institute on Drug Abuse and Villanova University.

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we utilized a higher reinforcement probability for the long duration (50%–20 s), than for the short duration (25%–10 s) to equate peak rates. In subsequent work exploring this phenomenon with different durations and duration ratios, we continued to equate incentive value of the cues by offsetting the longer reinforcement delay with an increased reinforcement probability. In all of these studies, the peak time on compound trials fell closer to the long criterion duration than the short criterion duration. Remarkably, post-hoc analyses suggested that the time of the compound peak could be accurately predicted by a weighted average of the criterion durations, in which the relative probability of reinforcement for each cue served as the weights. However, in all of these experiments, the reinforcement probabilities co-varied with the duration ratios, and therefore this relation might have been fortuitous.

The purpose of the present study was to evaluate whether rats utilize the reinforcement probabilities of the component cues as weights when integrating discrepant temporal memories. To this end, we directly varied the reinforcement probabilities of the component cues while keeping the criterion durations constant. In this way, any differences in peak times on compound trials would be tied to the reinforcement probabilities rather than to differences in absolute durations or duration ratios.

2. Experiment 1

2.1. Method

2.1.1. Subjects and apparatus

Thirty adult male Sprague–Dawley rats (*Rattus norvegicus*; Harlan, Indianapolis, IN) approximately 6 months of age at the beginning of the experiment were used. Rats were housed in pairs with a 12 h light:dark cycle (lights on at 8 a.m.). All behavioral testing was conducted during the light phase. The rats had ad libitum access to drinking water, but were kept on a restricted feeding schedule (Harlan 2019 Rat Diet) to maintain their body weights at 85–90% of free-feeding levels, adjusted for growth. Rodent chow was provided immediately following each daily session. Training and testing took place in 10 standard operant-conditioning chambers (30.5 × 25.4 × 30.5 cm, Coulbourn Instruments, Allentown, PA). The sides of the chambers were ventilated Plexiglas, and the front and back walls and ceiling were aluminum. The floor was composed of stainless steel bars. A pellet dispenser delivered 45-mg sucrose pellets (Formula F; Noyes Precision, Lancaster, NH) to a food magazine on the front wall of the chamber. Three nosepoke response apertures (2.5 cm opening diameter) with photobeam detection circuits were placed on the back wall of the chamber, and had yellow and green LED cue lights in their interior. The operant chambers were also equipped with an 11 lx houselight on the front wall of the chamber and a seven-tone audio generator which could play 95 dB tones through a speaker on the back wall of the chamber. Stimulus control and data acquisition were achieved using a standard operant-conditioning control program (Graphic State, Coulbourn Instruments), with a temporal resolution of 20 ms.

2.1.2. Procedure

The rats progressed through a sequence of nosepoke training, fixed-interval (FI) training with two stimuli/durations, peak-interval (PI) training with two stimuli/durations, and compound testing. Compound testing was identical to PI training, but with the addition of non-reinforced compound stimulus presentations on a small proportion of the trials. The discriminative stimuli were the houselight and a 4 kHz tone, and the modality–duration relationship was counter-balanced in each group (tone short/light long; light short/tone long). The short duration was 4 s and the long duration was 12 s. Upon reaching PI training, the rats were randomly divided into three groups with each group having different reinforcement probabilities in terms of the ratio of FI trials to PI trials. One group (20%/80%) was trained

with a 20% reinforcement probability for the short duration and an 80% reinforcement probability for the long duration (2 short FI: 8 short PI; 8 long FI: 2 long PI), as this ratio led to equivalent mean response rates in our previous work (Swanton & Matell, 2011). Group 10%/90% was trained with a 10% reinforcement probability for the short duration and a 90% reinforcement probability for the long duration (1 short FI: 9 short PI; 9 long FI: 1 long PI). Group 50%/50% was trained with a 50% reinforcement probability for both durations (5 short FI: 5 short PI; 5 long FI: 5 long PI). Short and long trials were presented in equal numbers. Rats were run five days per week at approximately the same time each day. Two days before training commenced, rats were given twenty 45 mg sucrose pellets in their home cage to acclimate them to the sucrose pellets.

2.1.3. Nosepoke training (5 sessions)

Rats were reinforced with a sucrose pellet on a fixed ratio 1 schedule on the center nosepoke aperture. A 2 s “timeout” followed the delivery of each pellet to prevent subjects from breaking the photobeam multiple times in rapid succession (therein possibly jamming the food delivery port). Training continued until rats earned 60 reinforcements on two sequential sessions.

2.1.4. Fixed-interval training (10 sessions)

Trials commenced with the presentation of either the “short” stimulus (either a 4 kHz steady tone or illumination of the houselight; counter-balanced) or the “long” stimulus (the stimulus not used for the short duration). The first nosepoke entry into the center nosepoke aperture after the associated criterion duration elapsed was reinforced and the stimulus terminated. Responses made prior to the criterion duration had no programmed consequences. A variable, uniformly distributed 60–90 s inter-trial interval (ITI) separated trials. Sessions lasted 2 h in this and in all subsequent procedures.

2.1.5. Peak-interval training (45 sessions)

PI training was identical to FI training, except that non-reinforced probe trials were presented in addition to the reinforced trials. Probe trials were 3–4 times the criterion duration for the corresponding signal and terminated independently of behavior. The probability of reinforcement was as described above.

2.1.6. Compound testing (5 sessions)

Compound testing was identical to PI training, with the addition of compound stimulus probe trials composing 20% of all trials. On these trials, both the 4 kHz tone and the houselight commenced simultaneously, and terminated without reinforcement in a response-independent manner at a duration equivalent to the probe length for the long cue.

2.1.7. Analysis

The mean response rate (discrete nosepoke infrared beam breaks) as a function of signal duration on probe trials was computed using 1 s bins. The data from each rat were pooled over 5 sessions to obtain sufficient trials to generate peak functions. Due to the skewed pattern of responding sometimes seen on compound trials (see results), rather than using a standard symmetrical Gaussian to describe the data, we fit (curve fitting package of MATLAB, Cambridge, MA) the pooled responses with the dual asymmetric sigmoid function, $Y = Y_0 + A * (1 / (1 + \exp(-1 * ((x - B + C/2)/D)))) * (1 - (1 / (1 + \exp(-1 * ((x - B - C/2)/E)))))$, with a lower bound of 0.25 for parameters D and E to prevent occasional fits with a sharp triangular shape (e.g., Swanton & Matell, 2011). This function captured the shape of the raw data irrespective of its skew (mean $R^2 = 0.84, 0.97, 0.93$ for the short, compound and long response functions, respectively). The maximal height of each fitted function was taken as the peak rate, and the time of the peak rate (i.e., the mode of the function) was taken as the peak time. The width at half maximal responding served as a measure of peak spread. Because single trials analyses are quite

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