Relative temporal representations in Pavlovian conditioning

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ABSTRACT

The transfer of relative temporal representations was assessed in a series of three experiments. In each experiment, rats (*Rattus norvegicus*) received one set of conditioned stimulus (CS) and intertrial interval (ITI) durations in Phase 1 and another set in Phase 2. The ratio between the CS and ITI intervals was either changed or maintained across phases. On the hypothesis that relative temporal representations are learned, groups receiving maintained temporal ratios across phases were expected to display greater change in responding upon encountering the new intervals. When the CS duration decreased across phases, maintaining the temporal ratio did lead to greater change in Day 1 of Phase 2 towards the final pattern of responding. However, when the CS increased across phases, maintaining the temporal ratio across phases did not facilitate adjustment to the new intervals, suggesting that extinction of previously reinforced times induced new learning. These results provide evidence that under some conditions, relative relationships in temporal maps may survive transformation-of-scale, like relative relationships in spatial maps.

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1. Introduction

In Pavlovian delay conditioning, there is an increased likelihood of a conditioned response (CR) during the CS as the time of the unconditioned stimulus (US) approaches. Animals learn that the CS signals the delivery of the US, in addition to learning the approximate time of US delivery (Balsam and Gallistel, 2009; Drew et al., 2005; Pavlov, 1927). It has been suggested that during Pavlovian conditioning, animals encode the temporal relationships between these events in temporal maps (Arcediano et al., 2005; Balsam and Gallistel, 2009; Honig, 1981).

Temporal maps may share properties with spatial maps, such as integration of separate maps via common elements. The integrative feature of temporal maps was successfully demonstrated by Arcediano et al. (2003, 2005). In their experiments, subjects integrated one map indicating the association US → S1 with a second map containing the association S2 → S1. By using the S1 element found in both maps, subjects formed a new association between S2 and US.

This integrative property has also been demonstrated in spatial maps. For example, spatial maps of large areas are acquired by integrating information across experiences (Collett et al., 2002; Gallistel and King, 2009; O'Keefe and Nadel, 1978; Shapiro et al.,

1997). In addition, Blaisdell and Cook (2005) showed that pigeons were able to integrate two separately learned spatial relationships, one between landmarks L1 and L2 and the other between L2 and a hidden food goal. The pigeons inferred the location of the hidden food goal when presented with L1 alone, demonstrating the successful combination of the two spatial relationships, using L2 as the integrative element.

There may be other similarities between spatial and temporal maps. For example, information in a spatial map is encoded in the relative relationships between landmarks, resulting in "transformation-of-scale," whereby relative relationships within a map are maintained regardless of the map's size. Whether a map has been shrunk to the size of a postage stamp or has been enlarged to the size of a billboard, it can still be effectively used for navigation, since the relative relationships contained within the map are preserved. It appears that animals can use transformation-of-scale in spatial maps to find new locations. Clark's nutcrackers, for example, can use relative geometric relationships between landmarks to find hidden food and can transfer these relationships to new interlandmark distances (Jones et al., 2002; Jones and Kamil, 2001; Kamil and Jones, 2000; Spetch et al., 2003). For example, the nutcrackers learned to find food that was hidden halfway between two landmarks even when they had not been previously trained on the particular absolute distance between the landmarks (Kamil and Jones, 2000). The ability to transfer acquired information about relative spatial relationships to new distances means that the nutcrackers

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do not have to approach each distance as a brand-new learning experience.

Do relative representations also guide behavior in the temporal domain? It is possible that animals may use relative relationships between intervals in temporal maps in the way that they use relationships between landmarks in spatial maps. There is some evidence consistent with this idea. Fetterman et al. (1989, 1993) found that pigeons are sensitive to relationships between intervals. The pigeons received a red light and a green light of various durations (T_1, T_2). They were then presented with a two-alternative, forced-choice procedure: One response was reinforced if the ratio of the light durations (T_1:T_2) was greater than a criterion ratio, and the other response was reinforced if the ratio was less than the criterion ratio. Surprisingly, the pigeons were as successful as humans in this relational temporal task. Molet and Zentall (2008) and Zentall et al. (2004) also demonstrated that animals make relative judgments about the durations of stimuli. Pigeons and humans were trained on temporal discrimination tasks and then presented with durations at the geometric mean of the acquired durations. The durations at the mean should have produced indifferent choices, but were in fact grouped with the shorter or longer alternative based on whether they had been presented as the shorter or longer choice in a separate discrimination.

Further evidence consistent with the hypothesis that animals form both absolute and relative temporal representations comes from analyses of acquisition in Pavlovian conditioning. Animals show patterns of responding that indicate they have knowledge of the absolute duration of a CS (Balsam et al., 2002; Drew et al., 2005). However, acquisition speed, at least in some cases, depends on the duration of a CS relative to the duration of the time between trials (Balsam and Gallistel, 2009; Gallistel and Gibbon, 2000; Gibbon and Balsam, 1981). In explaining these results, it was assumed that animals learned the absolute durations of events and then compared them (Balsam et al., 2006; Balsam and Gallistel, 2009; Gibbon and Balsam, 1981). However, it is also possible that a relative representation is formed that directly captures the relationship between intervals and controls acquisition speed.

In the current study, we explored the idea that animals encode the relative relationships between intervals in Pavlovian conditioning. Specifically, we hypothesized that if animals use relative temporal representations, preserving the relative relationship between intervals will facilitate behavioral adjustment to new intervals. In Pavlovian conditioning, previous exposure to CSs, USs, or both stimuli strongly influences subsequent performance. This path dependence is observed if subjects are initially exposed to unsignaled USs or randomly presented CSs and USs prior to CS–US pairing. Not only is subsequent learning of a CS–US relationship slower, but asymptotic performance is also changed (Baker et al., 2003; Balsam and Schwartz, 1981; Claflin and Buffington, 2006; Tomie, 1976). Similarly, the exact parameters under which a CS–US association is acquired influence performance to the same CS and US when conditioning parameters are subsequently changed (Brown-Su et al., 1986; Lucas et al., 1981). Consequently, we would expect that subjects would be slow to change their behavior or display less change if they are switched from one set of conditioning parameters to new ones than if they are switched between equivalent conditions. We employed this strategy to investigate whether relative representations of time were acquired during Pavlovian conditioning.

In three experiments, rats were presented with one set of intervals (CS and ITI) in Phase 1 and a new set of intervals in Phase 2. Across phases, the relative temporal relationship, or ratio, between the CS and ITI interval durations was either maintained or changed. If the rats transfer their knowledge of the relative temporal relationship acquired in Phase 1 to the new intervals in Phase 2, then

a maintained ratio should facilitate this transfer. While all animals are expected to change their behavior in response to the new absolute intervals, those receiving a maintained ratio in Phase 2 should display greater change more rapidly than those receiving an altered ratio. In other words, when the groups are compared at the same point in the transfer phase, those receiving the maintained ratio should show greater adjustment away from the previously acquired pattern and towards a new pattern of responding. Alternatively, if only absolute durations, rather than relative temporal relationships, are learned, there should be no advantage to preserving the ratio between the CS and ITI in the transfer test.

2. Experiment 1

Experiment 1 was conducted to determine if rats would transfer the relative temporal relationship between an acquired CS and ITI to new intervals. All rats received a CS of 12 s in Phase 1 and a CS of 24 s in Phase 2, but the ITI durations were varied so that one group received a maintained temporal ratio in Phase 2, while the other group received a changed ratio.

2.1. Materials and methods

2.1.1. Subjects

Subjects were 16 male Sprague–Dawley rats from the Charles River laboratories. They were housed in pairs in Plexiglas cages and kept on a 12-h light–dark cycle. They were given free access to food for 1 h after each session and had continuous access to water. The rats were used in prior operant conditioning experiments unrelated to the current topic.

2.1.2. Apparatus

Eight Med Associates conditioning chambers were used. Each chamber measured 30 cm × 24 cm × 21 cm. The front and back walls and ceiling of the chamber were Plexiglas, and the sides were aluminum. The floor consisted of 19 stainless steel rods 4 mm in diameter and 1.5 cm apart. Pellets were dispensed in a food trough located 2.1 cm above the floor and centered on a sidewall. The house light was located 1.25 cm from the ceiling on the opposite wall. A photocell unit inside the trough automatically recorded the number of head entries per second. Data was saved on a computer in the same room as the conditioning chambers.

The stimuli consisted of a tone CS at 80 dB and 1000 Hz and a white noise CS at 80 dB.

2.1.3. Procedure

2.1.3.1. Phase 1. Subjects were divided into two groups of eight. All subjects received a 12-s CS followed by a pellet. Half of the rats in each group received the tone CS, while the other half received the white noise CS. One group received an average ITI of 180 s ranging from 105 to 255 s, and the other group received an average ITI of 360 s ranging from 210 to 510 s. Both groups received 11 sessions of 15 trials (CS–US pairings).

2.1.3.2. Phase 2. For all rats, the CS duration was changed to 24 s. The group that previously received a 180 s ITI received a 360 s ITI. The other group continued to receive a 360 s ITI. Both groups received 20 sessions of 15 trials.

Table 1 shows the intervals received by each group throughout the experiment. In one group (15–15), the relative relationship, or ratio, between the CS and ITI intervals was maintained at 15 across phases, and in the other group (30–15), the relative relationship was changed. The group names indicate the ratios between the CS and ITI in Phase 1 and Phase 2 of the experiment.