



Temporal maps in appetitive Pavlovian conditioning



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ABSTRACT

Previous research suggests animals may integrate temporal information into mental representations, or temporal maps. We examined the parameters under which animals integrate temporal information in three appetitive conditioning experiments. In Experiment 1 the temporal relationship between 2 auditory cues was established during sensory preconditioning (SPC). Subsequently, rats were given first order conditioning (FOC) with one of the cues. Results showed integration of the order of cues between the SPC and FOC training phases. In subsequent experiments we tested the hypothesis that quantitative temporal information can be integrated across phases. In Experiment 2, SPC of two short auditory cues superimposed on a longer auditory cue was followed by FOC of either one of the short cues, or of the long cue at different times in the cue. Contrary to our predictions we did not find evidence of integration of temporal information across the phases of the experiment and instead responding to the SPC cues in Experiment 2 appeared to be dominated by generalization from the FOC cues. In Experiment 3 shorter auditory cues were superimposed on a longer duration light cue but with asynchronous onset and offset of the superimposed cues. There is some evidence consistent with the hypothesis that quantitative discrimination of whether reward should be expected during the early or later parts of a cue could be integrated across experiences. However, the pattern of responding within cues was not indicative of integration of quantitative temporal information. Generalization of expected times of reward during FOC seems to be the dominant determinant of within-cue response patterns in these experiments. Consequently, while we clearly demonstrated the integration of temporal order in the modulation of this dominant pattern we did not find strong evidence of integration of precise quantitative temporal information.

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1. Introduction

Learning about time is an integral part of associative learning (Balsam et al., 2010; Diaz-Mataix et al., 2013). Whether one considers such learning as the acquisition of a temporal map (Balsam and Gallistel, 2009; Honig and Urcuioli, 1981) or as the encoding of an attribute of the conditioned stimulus (CS) (Arcediano and Miller, 2002; Denniston and Miller, 2007; Molet and Miller, 2013) it is clear that temporal parameters have a large impact on learning and performance. The timing of events alters the speed with which anticipatory conditioned responses (CRs) emerge (Balsam and Gallistel, 2009; Gallistel and Gibbon, 2000; Gibbon and Balsam, 1981), the pattern of CR expression within the CS (Balsam et al., 2002; Brandon et al., 2003; Bitterman, 1965; Drew et al., 2005; Kirkpatrick and Church, 2003), and even the topography of the

CR itself (Silva and Timberlake, 1997; Vogel et al., 2003; Smith, 1968; Holland, 1980). Additionally, once this temporal learning has occurred the information can be used in flexible ways. One feature of this flexibility makes it analogous to spatial maps; subjects can integrate temporal information across separate experiences when there are common elements in the learning episodes (Molet et al., 2012). Spatial maps of large areas are built up through sequential experiences of overlapping subsets of the total map (Collett et al., 2002; Gallistel and King, 2009; O'Keefe and Nadel, 1978; Shapiro et al., 1997). Though acquired sequentially, an integrated representation of the information can guide behavior to new locations (Blaisdell and Cook, 2005) or be used to infer novel routes to a goal (Foo et al., 2005, 2007; Gallistel, 1990; Tolman, 1948).

Evidence for a similar ability to integrate temporal information across separate experiences comes primarily from both second-order conditioning and sensory pre-conditioning (SPC) studies which have shown that animals have the ability to superimpose temporal maps from different training phases provided there are common elements in each phase (Molet et al., 2012). In an SPC

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experiment animals are first presented with forward pairings of two neutral CS's, A and B, where A immediately precedes B ($A \rightarrow B$). In the next phase the value of one of these stimuli (B) is changed by pairing it with a motivationally significant event, for example a food unconditioned stimulus (US), $B \rightarrow \text{Food}$. Once the CR has been established to B ($B \rightarrow \text{CR}$), the integration of information across phases is evident when the changed value of B is reflected in a change in the value of A, even though A has never been directly associated with the US ($A \rightarrow \text{CR}$). This integration reflects the animal's knowledge of the order and perhaps timing of events. For example, in a variant of the SPC procedure Miller and colleagues (Arceidiano et al., 2003; Cole et al., 1995; Molet et al., 2012) showed that when B is backward paired with the US, B is not excitatory. Nevertheless, A controls a strong excitatory response as would be expected if subjects can infer that a US that comes before B would be expected just after A. Data like these encourage the view that animals are capable of integrating temporal information across experiences. Most studies have employed aversive conditioning paradigms and demonstrated that subjects can integrate order information. However the encoding and use of order information does not necessarily require a quantitative appreciation of time. The integration of temporal order and integration of quantitative temporal information may be separable processes mediated by different neural substrates (Buhusi and Meck, 2005; Eichenbaum, 2013; MacDonald et al., 2011; Ivry and Schlerf, 2008; Shapiro and Eichenbaum, 1999). Thus it is important to explore in more detail whether quantitative temporal information, like metric spatial information, can be integrated across experiences.

Only one appetitive conditioning study indicates that integration of quantitative temporal knowledge is possible (Leising et al., 2007). Here we explore this possibility in more detail. Experiment 1 sought to demonstrate temporal order integration in appetitive conditioning with a method similar to the aversive conditioning procedures of Arceidiano et al. (2003). In subsequent experiments we explored the conditions that give rise to integration of quantitative temporal information across experiences.

2. Experiment 1

Experiment 1 sought to establish that temporal order information could be integrated across experiences in appetitive conditioning as demonstrated in aversive conditioning. Subjects were exposed to temporal information in two separate training phases as illustrated in Fig. 1. During the first phase of training two auditory cues (A and B) were presented in sequence. Two groups were exposed to these cues in forward order ($A \rightarrow B$) as in a standard SPC experiment, while two groups experienced backward pairings ($B \rightarrow A$). First-order conditioning occurred in the second phase, where B was presented either before or after the delivery of a food pellet. One forward-ordered SPC group and one backward-ordered SPC group received forward CS-US pairings ($B \rightarrow \text{US}$) while the two remaining groups received backward CS-US pairings ($\text{US} \rightarrow B$) of B with food. From the traditional associative point of view which assumes weak learning as a result of backward pairing, only the subjects that received forward pairings in both phases of the experiment should show an excitatory response when tested with A. However, if animals integrate temporal knowledge across experiences, then each group of animals would each have different expected times of reinforcement (Fig. 1). Group Post-A received SPC of $A \rightarrow B$ followed by first order conditioning of $B \rightarrow \text{Food}$. If the animal is responding based on temporal expectation, there may be little excitatory conditioning to A as the temporal expectation for food would be well after the end of the A. However, Group Late-A, with identical SPC training ($A \rightarrow B$), received backward pairings of the food US and B ($\text{Food} \rightarrow B$). In this case, the integrated temporal

information would lead to the expectation of food at the end of the A. The prediction here is somewhat counterintuitive. We expected greater excitatory conditioning to A, even though there is very little excitatory conditioning to B based on the backward pairing of food and B ($\text{Food} \rightarrow B$). In the groups given backward SPC training with $B \rightarrow A$, similar predictions follow. During FOC, Group Pre-A receives backward pairings of $\text{Food} \rightarrow B$, and the temporal expectation induced by the presentation of A is that the time for the delivery of the food US has passed, as B precedes A in SPC and occurs after food is delivered in FOC. Therefore, we expected to see very little response to A. In Group Early-A animals are given forward paired $B \rightarrow \text{Food}$ during FOC, and the temporal expectation would be for food to be available at the beginning of A. Consequently, if the animals integrate temporal information across phases we predict higher responding when tested with A in Groups Early-A and Late-A, both of which should expect food during A, and less responding in groups Pre-A and Post-A, both of which should not expect the food to be available during A. These predictions were tested in the first experiment.

2.1. Methods

2.1.1. Subjects

Male Sprague Dawley rats (CD:CrI Charles River Laboratory, Raleigh, NC; $N=40$) were pair housed in clear polycarbonate cages, and maintained on a 12:12-h light/dark cycle in a controlled environment with temperatures of $22 \pm 2^\circ\text{C}$. Animals were acclimated to the animal colony for at least one week after arrival and were weighed and handled at least 3 times prior to training. Beginning 3 days prior to training, rats were restricted to 1 hour per day of food with unlimited access to water. Training consisted of one session per day. All behavioral training occurred after light onset (7 am), and feeding occurred after all animals had completed the training for that day but prior to light offset. These animal husbandry procedures were maintained for each of the experiments reported here. All husbandry and testing procedures were approved by the Columbia University Institutional Animal Care and Use Committee.

2.1.2. Behavioral apparatus

In each experiment the subjects were trained and tested in modular operant test chambers (MedAssociates, Georgia, VT, model ENV-008, 30 cm \times 24 cm \times 21 cm). The chambers were individually housed inside light and sound-attenuating isolation boxes equipped with fans providing ventilation and a background noise level of approximately 65 dB. The floor of the operant chamber consisted of stainless steel rods spaced 15 mm apart. A food trough (5 cm \times 5 cm) was centered in the right wall of the chamber, 2 cm above the floor. Head entries to the trough were detected by an infrared photocell. A response lever, not used in this experiment, was located to the left of the food trough. The chambers were dimly illuminated throughout the session by a red stimulus light located above and to the left of the food trough, 8 cm above the floor and 2 cm from the back wall. A speaker (6 cm \times 7 cm) was mounted in the top rear corner of the left wall and a clicker module (Med Associates, ENV-135 M) was mounted in the top front corner of the left wall.

2.1.3. Procedure

2.1.3.1. Pretraining. All animals were trained during one daily session occurring at approximately the same time each day. Subjects were first trained to retrieve pellets from the food trough over three daily sessions during which twenty 45 mg food pellets (Dustless Precision Pellets, BioServ, Frenchtown, NJ) were delivered on a variable time (VT-45 s) schedule. Rats were subsequently trained to make a head poke into the trough during the presentation of a cue. Pilot studies indicated that the response rates of the rats increased

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