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Learning what to expect and when to expect it involves dissociable neural systems

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ABSTRACT

Two experiments with Long-Evans rats examined the potential independence of learning about different features of food reward, namely, "what" reward is to be expected and "when" it will occur. This was examined by investigating the effects of selective reward devaluation upon responding in an instrumental peak timing task in Experiment 1 and by exploring the effects of pre-training lesions targeting the basolateral amygdala (BLA) upon the selective reward devaluation effect and interval timing in a Pavlovian peak timing task in Experiment 2. In both tasks, two stimuli, each 60 s long, signaled that qualitatively distinct rewards (different flavored food pellets) could occur after 20 s. Responding on non-rewarded probe trials displayed the characteristic peak timing function with mean responding gradually increasing and peaking at approximately 20 s before more gradually declining thereafter. One of the rewards was then independently paired repeatedly with LiCl injections in order to devalue it whereas the other reward was unpaired with these injections. In a final set of test sessions in which both stimuli were presented without rewards, it was observed that responding was selectively reduced in the presence of the stimulus signaling the devalued reward compared to the stimulus signaling the still valued reward. Moreover, the timing function was mostly unaltered by this devaluation manipulation. Experiment 2 showed that pre-training BLA lesions abolished this selective reward devaluation effect, but it had no impact on peak timing functions shown by the two stimuli. It appears from these data that learning about "what" and "when" features of reward may entail separate underlying neural systems.

1. Introduction

One important problem in the study of associative learning has been specifying the nature of the systems responsible for learning about and encoding different aspects of reward. For instance, Konorski (1967; also Wagner & Brandon, 1989) speculated that in Pavlovian learning a predictive stimulus can enter into separate associations with sensory and emotional aspects of reward. More recent work has established that separate neural systems underlies these two forms of learning (e.g., Balleine & Killcross, 2006). However, there are other aspects of reward that an organism can encode that can factor into learning (Delamater, 2012; Delamater & Oakeshott, 2007). Since Pavlov (1927) we have known that conditioned responding is temporally organized, and, indeed, there has been a considerable amount of research examining processes involved in interval timing (e.g., Addyman, French, & Thomas, 2016; Buhusi & Oprisan, 2013; De Corte & Matell, 2016; Kirkpatrick, 2014; Matell & Meck, 2004). We have, elsewhere, suggested that learning about the specific sensory properties of a reward, i.e., learning "what" it is, and learning to time its arrival, i.e., learning "when" it will occur, could entail two separate underlying learning systems with distinct, though overlapping, neural processes governing them (Delamater, Desouza, Rivkin, & Derman, 2014). However, recent research has also suggested that the occurrence of rewards in time are fundamentally encoded and that responding is a decision-based process based on various computations performed on the raw data stored within a temporal memory structure (e.g., Balsam & Gallistel, 2009; Gallistel & Balsam, 2014). Such an approach may predict that learning about "what" the reward is and "when" it will occur may recruit similar underlying psychological and neural processes that are not so distinct.

Research devoted to examining this issue has been scarce. If learning what a reward is and when it will occur entail separate systems, then variables affecting one should have little effect on the other. Balsam and his colleagues (Drew, Zupan, Cooke, Couvillon, & Balsam, 2005; Ohyama, Gibbon, Deich, & Balsam, 1999) showed that animals learn to time the arrival of reward from the onset of conditioning and retain this information throughout extinction as the conditioned response dissipates. These results suggest independence of the motivation to respond and learning to time the arrival of reward. However, a

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somewhat different conclusion comes from studies that have asked if interval timing effects are impacted by various manipulations of reward value. One popular method for assessing interval timing is known as the "peak procedure" (Roberts, 1981). In this task, animals are trained to press a lever for food reward after a specific amount of time has elapsed since the onset of a stimulus. Critically, responding is also assessed on non-rewarded probe trials in which the duration of the stimulus is usually 2–3 times that of rewarded trials. Responding averaged over these test trials gradually increases and peaks at a point centered close to the actual reward time before then falling off somewhat more gradually. This distribution of responding is taken as a strong indication that the animal has encoded when the reward is expected to occur.

There have been several reports suggesting that variables affecting reward value may have some impact on peak timing functions in this task, a result that would suggest the two processes to be interdependent (see Kirkpatrick, 2014 for a review). For instance, Roberts (1981) demonstrated that tests conducted while the animal is satiated can shift the entire peak response function to the right compared to when the animal is tested food deprived (also Galtress & Kirkpatrick, 2009; Galtress, Marshall, & Kirkpatrick, 2012). Interpretation of this result is complicated, though, by the additional observation that training the rat while sated and testing hungry also shifts the distribution to the right, as opposed to having the symmetrically opposite effect as would be expected if reward value interacts with reward timing in any straightforward way (Galtress et al., 2012).

Additional findings have shown a dissociation between manipulations affecting overall response rate and response timing. For instance, Meck (2006) found that caudate putamen lesions undermined response timing in a dual-peak procedure without undermining differences in overall levels of responding, whereas nucleus accumbens shell lesions eliminated peak rate response differences in this task without impacting temporal control. These data support the view that factors affecting response rate and timing are dissociable. Similarly, Ohyama et al. (2000) also showed that systemic injection of a dopamine antagonist immediately suppressed the overall rate of responding without immediately affecting temporal control in a peak timing task. Together these data suggest dissociations between the processes mediating response rate and temporal control in this task.

Another approach has been to examine the role of reward magnitude on interval timing in the peak procedure. It has been observed that peak distributions produced with small rewards are right-shifted to those produced with large rewards (Galtress & Kirkpatrick, 2009), though sometimes other aspects of the peak distribution such as initiation times are more sensitive than the actual peak of the distribution (Balci et al., 2010; Ludvig, Balci, & Spetch, 2011). The result suggests that timing itself may depend upon the magnitude of the anticipated reward.

Perhaps the most relevant type of experiment for the question of whether reward identity ("what") and temporal encoding ("when") involve dissociable or interactive systems uses the reward devaluation task. In this task, it is determined if devaluing a reward following a conditioning phase affects stimulus control when the stimulus is tested under extinction conditions. The logic of this test is that if a stimulus has associated with some specific feature of the reward and that feature has then independently been devalued (in the absence of the stimulus), subsequent testing under extinction conditions should reveal a decrement in performance. The effect is assumed to reflect the fact that the stimulus is capable of activating a specific representation of the now-devalued outcome (e.g., Delamater & LoLordo, 1991; Rozeboom, 1958). To date, there have only been two studies using this task in connection with a peak timing procedure in order to separately assess reward identity and timing, and the results have not been entirely consistent with one another. Galtress and Kirkpatrick (2009) observed that compared to a baseline training phase, the peak function was shifted to the right when testing occurred following reward devaluation training (where food intake was independently paired with a LiCl injection designed to establish an aversion to the food). Delamater et al. (2014), however, reported that following devaluation the motivation to respond was reduced, but the timing of the peak function was not affected.

There were several procedural differences between the tasks used by Galtress and Kirkpatrick (2009) and Delamater et al. (2014) that could be crucial. Delamater et al. (2014) trained their animals in a Pavlovian task with two separate stimuli each paired with a qualitatively different reward, and then devalued one of these rewards through extensive selective devaluation training (one reward was paired repeatedly, and the other unpaired, with LiCl). Finally, the two stimuli were tested at the same time under extinction conditions. In contrast, Galtress and Kirkpatrick (2009) trained their rats in an instrumental task with a single stimulus and reward pair. They then tested their animals under extinction conditions after a limited amount of reward devaluation training (one or two food-LiCl pairings). Peak functions shifted to the right in the Galtress and Kirkpatrick (2009) study, but this assessment depended upon a comparison of responding following devaluation to baseline responding during training sessions that also included rewarded trials. In the Delamater et al. (2014) study, responding following reward devaluation was assessed in the same extinction session to one stimulus whose associated outcome had been devalued to another whose outcome had not been devalued. Under those conditions we did not find any evidence to suggest that reward devaluation impacted the peak timing function.

In order to further investigate the potential independence or interdependence of reward identity and timing the present studies extended these studies in two ways. First, because we think it is important to assess timing functions at the same time following a selective reward devaluation manipulation, we assessed the generality of our findings in a Pavlovian task to an instrumental peak timing task. Second, we assessed, perhaps more directly, the independence of "what" and "when" learning by assessing the effects of region-specific brain lesions on reward timing and selective devaluation effects. Other research has shown, convincingly, that the basolateral amygdala (BLA) is necessary for rats to encode sensory aspects of reward in Pavlovian devaluation (and other) tasks (e.g., Blundell, Hall, & Killcross, 2001; Corbit & Balleine, 2005; Hatfield, Han, Conley, Gallagher, & Holland, 1996; Johnson, Gallagher, & Holland, 2009). Here, we ask whether pretraining BLA lesions might affect selective reward devaluation and reward timing performance differentially. If learning to encode the "what" and "when" of reward entails distinct systems, and "what" learning depends upon a functioning BLA, then such lesions should disrupt the selective reward devaluation effect but leave peak timing functions intact.

2. Methods

2.1. Experiment 1

2.1.1. Subjects

Subjects were 32 experimentally naïve Long-Evans rats, male (n = 16) and female (n = 16), that were bred at Brooklyn College and derived from Charles River laboratories. The study was run in two identical replications (n = 16 per replication). Males' free-feeding weights ranged between 338–376 g in replication 1 and 489–608 g in replication 2, and females' weights ranged between 223–256 g in replication 1 and 240–305 g in replication 2. They were maintained at 85% of their free feeding weights in a colony room on a 14 h: 10th LD cycle and housed in groups of 3–4 animals per cage in standard transparent plastic tub cages (17 × 8.5 × 8 in) with wood chip bedding. All experimental procedures were performed during the light phase of their light/dark cycle at the same time of day. All procedures were performed in accordance with the approved guidelines of the IACUC of Brooklyn College.

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