Repeated extinction and reversal learning of an approach response supports an arousal-mediated learning model

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ARTICLE INFO

ABSTRACT

We assessed the effects of repeated extinction and reversals of two conditional stimuli (CS+/CS−) on an appetitive conditioned approach response in rats. Three results were observed that could not be accounted for by a simple linear operator model such as the one proposed by Rescorla and Wagner (1972): (1) responding to a CS− declined faster when a CS+ was simultaneously extinguished; (2) reacquisition of pre-extinction performance recovered rapidly within one session; and (3) reversal of CS+/CS− contingencies resulted in a more rapid recovery to the current CS− (former CS+) than the current CS+, accompanied by a slower acquisition of performance to the current CS+. An arousal parameter that mediates learning was introduced to a linear operator model to account for these effects. The arousal-mediated learning model adequately fit the data and predicted data from a second experiment with different rats in which only repeated reversals of CS+/CS− were assessed. According to this arousal-mediated learning model, learning is accelerated by US-elicited arousal and it slows down in the absence of US. Because arousal varies faster than conditioning, the model accounts for the decline in responding during extinction mainly through a reduction in arousal, not a change in learning. By preserving learning during extinction, the model is able to account for relapse effects like rapid reacquisition, renewal, and reinstatement.

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1. Introduction

Eliminating the correlation between a conditional stimulus (CS) and an unconditional stimulus (US) results in a progressive decline in responding to the CS. Extinction of the conditional stimulus is a learning process, critical to the organism's adaptation to a changing environment. There has been much conceptual and theoretical development devoted toward elucidating processes mediating declines in conditioned performance during extinction (e.g., Bouton, 2004; Gallistel and Gibbon, 2000; Killeen et al., 2009; Mackintosh, 1975; Pearce and Hall, 1980; Rescorla, 2001; Rescorla and Wagner, 1972; Wagner, 1981). One development that has become almost universally accepted is that declines in responding are not a result of extinction eliminating prior excitatory learning (e.g., Rescorla, 1993). Instead, at least two distinct processes emerge in extinction when US presentations are eliminated: (1) the sudden absence of the US results in a discriminable change in stimulus conditions, i.e., a generalization decrement develops,

and (2) the organism's expectancy that a CS signals a forthcoming US is violated, initiating new inhibitory learning (Mackintosh, 1974). Bouton (2004) further argues that this new inhibitory learning occurs in what becomes a novel stimulus context introduced by removal of the US with the extinction contingency (i.e., the generalization decrement). Thus, conditioning and extinction are learned and expressed conditionally as a function of the prevailing context.

Evidence that extinction results in context-mediated learning comes from situations in which, following extinction, reestablishing the original conditioning context restores responding (see Bouton, 2004, for a review). For instance, first training a CS-US association in one context (Context A), followed by extinguishing the CS in a different context (Context B), and finally reintroducing the original Context A produces a marked increase in responding to the CS, even in the absence of the US (Bouton and King, 1983; Bouton and Peck, 1989). These findings suggest that learning about the CS-US relation is preserved throughout extinction despite elimination of conditioned performance; re-exposure to the original conditioning context reveals this preserved learning. Related phenomena in which responding readily recovers following extinction, such as spontaneous recovery and rapid reacquisition, are attributed to a failure to retrieve the extinction memory when testing occurs outside of the temporal or stimulus context mediating extinction.

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Bouton (1993, 2004) suggested that extinction is just one example of a set of phenomena in which new learning temporarily interferes with performance, but not with the integrity, of an initially trained association. One such situation, the reversal of Pavlovian contingencies, has received relatively little attention with regard to exploring the behavioral processes mediating its effect. In reversal learning experiments, training begins with one CS paired with a US (i.e., CS+) while a different CS is paired with nonreinforcement (i.e., CS−). Following training, the CS+ and CS− are reversed. Consistent with Bouton's (1993) interference hypothesis, reversing Pavlovian contingencies results in effects similar to standard extinction (e.g., Spear et al., 1980; Thomas et al., 1985). The originally trained CS-US association survives subsequent reversals of CS+ and CS−.

The persistence of prior associations following CS+/CS− reversal was clearly shown by rats spontaneously recovering an initially trained magazine approach response that was conditional to a CS+/CS− discrimination, following five reversals of the original discrimination (Rescorla, 2007). During acquisition, eight 30-s diffuse light and white noise presentations were arranged per session as conditional stimuli, with one stimulus preceding the presentation of a food pellet (i.e., CS+) and the other preceding nonreinforcement (i.e., CS−). Next, CS+ and CS− assignments were reversed five times across eight-session blocks. One additional reversal was arranged to equate levels of responding to CS+ and CS− before rats were given six days without experimental sessions. Finally, the rats were placed back in their experimental chambers for a single session in which the light and tone were presented without reinforcement. Large elevations in responding were observed only to the most recently extinguished CS, as is observed with spontaneous recovery following simple extinction of a CS (e.g., Brooks and Bouton, 1993; Pavlov, 1927). Such effects suggest that similar processes mediate the learning underlying both extinction and reversal learning.

Although Bouton's (1993) interference hypothesis accounts for a wide range of phenomena, its implementation as a dynamic learning model is rather challenging. It is unclear, for instance, whether new learning needs to be encoded in a unique storage module to maintain the integrity of old learning. Various solutions have been proposed in which old learning is encoded in the hidden layers of a neural network (Burgos and Murillo-Rodriguez, 2007; Kehoe, 1988; Larrauri and Schmajuk, 2008). The importance of specific components of these networks is not assessed explicitly, and thus it is difficult to determine the merit of these models beyond the proximity of predicted to obtained data. Relative to neural networks, simple learning rules such as those articulated by classic dynamic learning models (Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972) have the advantage of simplicity and tractability but, as with Bouton's model, they do not specify a solution to the problem of how previously acquired associations endure under extinction. Miller et al. (1995) suggest that interference may stem from the asymmetry and simultaneity of excitatory and inhibitory conditioning, but no satisfactory quantitative implementation of this solution has been advanced.

This paper introduces a dynamic learning model that accounts for the persistence of learned associations over repeated extinction, reacquisition, and reversal training. The model is based on Killeen et al.'s (2009) notion that the probability of responding to a CS on any given trial is a function of past CS-US pairings – much in line with classic dynamic learning models and even earlier stimulus sampling models (Estes, 1950) – and the momentum of response and no-response states. The new model explains the persistence of learning using just one additional assumption, that learning and performance are conditional to US-elicited arousal (Killeen et al., 1978).

To collect behavioral data, we took advantage of the fact that organisms approach discrete visual stimuli that predict the delivery of appetitive rewards (Brown and Jenkins, 1968; Hearst and Jenkins, 1974; Peterson et al., 1972). The discovery of conditioned approach responses was important because the realm of Pavlovian conditioning broadened from relatively simple reflexes to larger skeletal movements (Hearst, 1977). Approach responses show all signs of being instances of Pavlovian conditioning (Farwell and Ayres, 1979), and can be measured conveniently and automatically to assess responding to CSs differentially associated with a US.

2. Experiment 1

Extinction and reversal learning data were collected under varying training conditions using two CSs. Conditioned responding was alternately acquired for one CS and extinguished for both CSs in blocks of multiple sessions. We propose an arousal-mediated learning model to account for conditioned response probabilities across all training conditions. Model parameters were estimated and possible variations of the model are considered. Finally, the model is extended to account for latencies—intervals between CS onset and conditioned response.

2.1. Methods

2.1.1. Subjects

Five male Sprague–Dawley rats originally were obtained from Harlan (Indianapolis, IN) and were maintained in a temperature- and humidity-controlled environment on a 12-h light/12-h dark cycle with lights on at 7:00 am. Rats weighed approximately 300 g and were maintained at approximately 80% of their adult weights (±20 g) by postsession feeding of rat chow. Prior to the present study, all rats participated in a study examining the effects of systemic injections of dopaminergic compounds on conditioned approach responses. Given the previous conditioning history, no additional preliminary training was necessary. All studies were carried out in accordance with the Guide for Care and Use of Laboratory Animals as adopted by the National Institutes of Health. University of Michigan's Committee on the Use and Care of Animals approved all experimental protocols.

2.1.2. Apparatus

Six Med Associates® (St. Albans, VT, USA) operant conditioning chambers were used. Each chamber was approximately 30 cm long, 24 cm wide, and 21 cm high, and housed in a sound-attenuating cubicle with a ventilation fan. A dipper (0.1-ml reservoir) that could deliver liquid food (Vanilla Ensure®) was centered on the front panel within an approximately 4.1 cm (h) × 3.5 cm (w) aperture with its bottom edge 2 cm above a grid floor. An LED recessed in the roof of the aperture could be turned on to illuminate the aperture and was used as the conditional stimuli. An infrared photobeam located immediately above the dipper receptacle recorded head entries into the aperture and were the primary dependent measure in the present study. Control of experimental events and data recording were conducted with Med Associates interfacing and programming. Sessions occurred 5 days per week at approximately the same time.

2.1.3. Procedures

All sessions consisted of 16 Pavlovian conditioned approach trials with two different visual conditional stimuli and were approximately 40 min in duration. During the first Acquisition condition for three rats, 8 trials per session consisted of illuminating the aperture with a steady light for 15 s prior to a 7-s presentation of the dipper (hereafter CS+ trials). Another 8 trials per session consisted of flashing the aperture light on and off every 0.1 s for 15 s prior to 7 s of no dipper presentation (hereafter CS− trials). The CS+ and CS− stimuli were reversed for the other two rats. Prior to all CS+