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A fundamental role for context in instrumental learning and extinction

Mark E. Bouton*, Travis P. Todd

University of Vermont, United States

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ABSTRACT

The purpose of this article is to review recent research that has investigated the effects of context change on instrumental (operant) learning. The first part of the article discusses instrumental extinction, in which the strength of a reinforced instrumental behavior declines when reinforcers are withdrawn. The results suggest that extinction of either simple or discriminated operant behavior is relatively specific to the context in which it is learned: As in prior studies of Pavlovian extinction, ABA, ABC, and AAB renewal effects can all be observed. Further analysis supports the idea that the organism learns to refrain from making a specific response in a specific context, or in more formal terms, an inhibitory context-response association. The second part of the article then discusses research suggesting that the context also controls instrumental behavior before it is extinguished. Several experiments demonstrate that a context switch after either simple or discriminated operant training causes a decrement in the strength of the response. Over a range of conditions, the animal appears to learn a direct association between the context and the response. Under some conditions, it can also learn a hierarchical representation of context and the response–reinforcer relation. Extinction is still more context-specific than conditioning, as indicated by ABC and AAB renewal. Overall, the results establish that the context can play a significant role in both the acquisition and extinction of operant behavior.

Contents

The issue of the contextual control of behavior has been a focus of research in learning theory for many years (e.g., Balsam and Tomie, 1985). One reason is that contextual cues are thought to be essential in supporting memory retrieval, which predicts that if retention is tested in a context that is different from the context in which information is learned, there should be a decline in performance (e.g., Spear, 1978; Tulving and Thomson, 1973). A second reason is that a number of influential models of associative learning have given context a central role (e.g., Rescorla and Wagner, 1972; Pearce, 1994; Pearce and Hall, 1980; Wagner, 1978, 2003). For many years, our laboratory has therefore studied the role of context in Pavlovian conditioning, where organisms learn to associate a conditioned stimulus (CS) with a reinforcer or unconditioned stimulus (US). In recent years, however, we have begun to extend our analysis to the role of context in operant or instrumental learning, where organisms learn to associate their behavior with reinforcers or outcomes. The purpose of the present article is to review some of the work we have done to date on the latter problem, i.e., the contextual control of operant learning.

For some time, our laboratory has also been interested in *extinction*, an especially fundamental process of behavior change. Extinction learning is essential for the survival of organisms, because it allows them to adapt to changes in their environment. During extinction, responding declines when the contingencies in

* Corresponding author at: Psychology Department, University of Vermont, Burlington, VT 05405-0134, United States. Tel.: +1 802 656 4164; fax: +1 802 656 8783.
E-mail address: mark.bouton@uvm.edu (M.E. Bouton).

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the environment change such that the US or reinforcer is no longer presented. In Pavlovian conditioning, the CS is repeatedly presented in the absence of the US, and the original conditioned response (CR) decreases. Although it has always been tempting to view extinction as a weakening or erasure of the original learning (e.g., Rescorla and Wagner, 1972), there is strong evidence that this is not the case. Instead, extinction results in new learning that is at least partly dependent on the context for expression (e.g., Bouton, 2002, 2004).

As suggested by our comments above, we have recently become interested in the extinction of instrumental, or operant, behavior. In operant extinction, responding declines when the reinforcer is no longer presented. Operant extinction learning might be a relevant model for understanding the suppression or inhibition of problematic voluntary behaviors in humans, such as overeating, gambling, and drug addiction. Further, operant extinction has become a powerful tool in studies of the neurobiology of drug addiction (for a review see Marchant et al., 2014). In order to have a complete neurobiological theory of addiction, it is important to understand the behavioral principles of operant extinction (e.g., Todd et al., 2014a). Thus, the study of operant extinction learning can have implications for understanding the elimination of problem behaviors in humans as well as the neural mechanisms that underlie it.

In what follows, we summarize recent research from our laboratory that has examined the contextual control of operant behavior. The first section of the paper focuses on operant extinction, which began as an investigation of its possible parallels with Pavlovian learning. Although the research has uncovered similarities between Pavlovian and operant extinction, it has uncovered some important differences as well. The second part of the paper then reviews research that has examined the contextual control of operant behavior before it has been extinguished. As a whole, the research has uncovered a rather central role of the context in controlling both acquisition and extinction. It also tentatively suggests something specific about the mechanism of contextual control: In conditioning, the animal seems to learn to make a specific response in a specific context, and in extinction, it seems to learn to inhibit a specific response in a specific context.

1. Contextual control of operant extinction

As described above, it is now commonly understood that Pavlovian extinction results in new, context-dependent learning. One reason for this belief is that responding to an extinguished CS will return if the CS is tested outside the extinction context. This is known as the *renewal effect* (Bouton and Bolles, 1979). (In animal experiments, contexts are usually defined as the chambers in which conditioning occurs; they typically differ in visual, tactile, and olfactory characteristics.) For example, after CS–US pairings in Context A, and CS alone presentations (extinction) in Context B, responding will return (renew) when the CS is subsequently tested in the original Context A (ABA renewal; Bouton and Bolles, 1979; Bouton and King, 1983; Bouton and Peck, 1989) or in a third, relatively neutral context (ABC renewal; Bouton and Bolles, 1979; Harris et al., 2000; Thomas et al., 2003). Renewal is also observed when both conditioning and extinction occur in Context A, and the CS is then tested in Context B (AAB renewal; Bouton and Ricker, 1994; Laborda et al., 2011; Tamai and Nakajima, 2000). The AAB and ABC forms of renewal are especially important at the theoretical level because they indicate that mere removal from the context of extinction is sufficient for renewal to occur. Thus, the extinction context somehow inhibits behavior, so that removal of the CS from that context can turn on responding to the CS again.

Does operant extinction also result in context-dependent inhibitory learning? Until recently, the degree to which it did had been unclear. Although ABA renewal had been routinely demonstrated with either food or drug reinforcers (e.g., Bossert et al., 2004; Chaudri et al., 2009; Crombag and Shaham, 2002; Hamlin et al., 2007, 2008; Nakajima et al., 2000; Welker and McAuley, 1978; Zironi et al., 2006), several reports had failed to demonstrate AAB renewal (see Bossert et al., 2004; Crombag and Shaham, 2002; Nakajima et al., 2000) and the evidence for ABC renewal was mixed (e.g., Zironi et al., 2006). The lack of evidence of AAB and ABC renewal left unanswered the crucial question of whether mere removal from the extinction context was sufficient to cause response recovery.

Recent research from our laboratory, however, has demonstrated all three forms of renewal after instrumental extinction (e.g., Bouton et al., 2011). In a representative experiment (Bouton et al., 2011, Experiment 1), rats first learned to lever-press for food pellets on a variable-interval 30 s (VI 30 s) schedule (pellets were made available on average every 30 s at which point the next lever press resulted in their delivery). After initial training in Context A, they then underwent extinction (in which lever presses no longer resulted in pellet delivery) in either Context A or B. Over the course of extinction, lever pressing declined and reached a very low rate. Finally, using a within-subject test procedure, all rats received a test session in both Contexts A and B (order counterbalanced) in which they could lever press, but no pellets were delivered. Both ABA and AAB renewal were observed. For rats trained in Context A and extinguished in B, lever pressing renewed when it was tested back in the original training context (A). Importantly, for rats trained and extinguished in Context A, responding also renewed when they were tested in Context B (see also Todd et al., 2012a). In a separate experiment, renewal also occurred when training, extinction, and testing all occurred in different contexts (ABC renewal; see also Todd et al., 2012b). Thus, for the first time the experiments provided clear evidence that testing outside the context of extinction is sufficient to cause renewal of operant behavior.

We also began to examine the behavioral mechanisms that might contribute to the phenomenon. Although the ABC and AAB effects suggest a role for some form of inhibition provided by the extinction context, our initial study (Bouton et al., 2011; Experiment 1) also found that the ABA renewal effect was significantly stronger than the AAB effect. This may have occurred because in the ABA design subjects are returned to a context that has been directly associated with the reinforcer. Other research has indicated that operant responding can be modulated after extinction by direct context-reinforcer associations (Baker et al., 1991). However, we found that extensive extinction exposure to Context A without the lever present prior to renewal testing did not reduce the strength of the ABA renewal effect (Bouton et al., 2011, Experiment 4). Exposure to Context A should have weakened any context-reinforcer associations that might be present. The fact that renewal was not weakened by extensive exposure to the renewal context suggested that the responding observed in the renewal context was likely not a function of direct association between the context and the reinforcer. Instead, Context A could have enabled strong ABA renewal by setting the occasion for the response–reinforcer relation or by directly eliciting the response – two mechanisms we will return to in the second half of this paper.

In a subsequent set of experiments, Todd, 2013 examined possible mechanisms of how the extinction context controls extinction. Theoretically, there were at least three possibilities. Perhaps the simplest was that during extinction the context might acquire a direct inhibitory association with the representation of the reinforcer (Polack et al., 2011; but see Bouton and King, 1983; Bouton and Swartzentruber, 1986, 1989). Mechanistically, this might occur because a strong excitatory association might be formed between the response and the reinforcer during acquisition. Then, during extinction, the surprising omission of the expected reinforcer would cause inhibition to accrue between