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Learning and the persistence of appetite: Extinction and the motivation to eat and overeat☆

Mark E. Bouton *

Department of Psychology, University of Vermont, 2 Colchester Ave., Burlington, VT 05405-0134, United States

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ABSTRACT

The modern world is saturated with highly palatable and highly available food, providing many opportunities to associate food with environmental cues and actions (through Pavlovian and operant or instrumental learning, respectively). Basic learning processes can often increase the tendency to approach and consume food, whereas extinction, in which Pavlovian and operant behaviors decline when the reinforcer is withheld, weakens but does not erase those tendencies. Contemporary research suggests that extinction involves an inhibitory form of new learning that appears fragile because it is highly dependent on the context for expression. These ideas are supported by the phenomena of renewal, spontaneous recovery, resurgence, reinstatement, and rapid reacquisition in appetitive learning, which together may help explain why overeating may be difficult to suppress permanently, and why appetitive behavior may seem so persistent.

Human food intake is influenced by a large and very complex set of factors (e.g., [1]). However, there is little doubt that learning and conditioning processes are important among them. As Stephen Woods and others have emphasized, conditioning can play a very important role in determining the onset or timing of meals, preferences and aversions for different foods, and other aspects of eating and appetite (e.g., [2–4]; see also [5–7]). The purpose of this article is to selectively review some basic research on learning with an emphasis on extinction, a major inhibitory process in conditioning, and discuss some of the possible implications for understanding the persistence of appetite, difficulties in losing weight and maintaining weight loss, and the contemporary obesity epidemic.

The modern world is saturated with food and with opportunities to consume it. As noted by Kessler [8], we are constantly exposed to highly palatable, high-calorie foods that have been engineered with multiple layers of sugar, salt, and fat. From the perspective of learning theory, the high abundance of such tasty foods means that the world is full of very effective conditioning trials, i.e., opportunities to associate the food with cues in the environment (through Pavlovian conditioning) or with voluntary actions that lead to it (through operant or instrumental learning). Table 1 illustrates some of the many cues and operant behaviors that are available for association with food. In the Pavlovian case, it seems hard to avoid exposure to colorful food packaging, advertising logos, and the sight, smell and taste of foods. Any or all such stimuli can serve as Pavlovian conditional stimuli (CSs), and as CSs, they would be expected to engage approach behavior (e.g., [9]) and any of a number of conditioned responses that function to get the system ready for the meal (e.g., [10]). They might also trigger eating, even when the individual is full or satiated (e.g., [11–15]). Table 1 also illustrates some voluntary, operant behaviors available for reinforcement by the pleasures of eating—choosing a restaurant at the mall, purchasing food, opening the packaging to get at the food, and of course handling and eating it. Presentation of a Pavlovian CS would further excite or motivate these behaviors through Pavlovian-instrumental transfer (e.g., [16,17]), for example, by eliciting the "wanting" of food (e.g., [18,19]). Given the abundance and high palatability of the food in the environment today, basic learning processes could easily support strong appetite and food-motivated behavior.

Table 1 also lists a few examples of the kinds of "contexts" in which food consumption occurs. Contexts are usually "background" cues in which Pavlovian CSs are presented and operant behaviors are emitted. Thus, as illustrated in Table 1, CSs and operant behaviors never occur in a vacuum; they always occur in a context like a shopping mall, an airport, the couch in front of the television, or a social event such as a Superbowl party. Contexts like these may be directly associated with food, and have all the behavioral consequences of CSs noted above. Contexts can also provide a kind of hierarchical control over behavior that occurs in them (e.g., [20]), as I will illustrate below. In that case, they can engage behavior not by directly eliciting it, but by signaling whether or not the CS or the operant behavior will be associated with food.

Research in my laboratory and in others has discovered that contexts play an especially important role in *extinction*. In extinction, the reinforcer (food) is withdrawn, and the Pavlovian CS or the

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* Tel.: +1 802 656 4164; fax: +1 802 656 8783.
E-mail address: mark.bouton@uvm.edu.

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Table 1
Some natural conditioning events available for association with food.

Conditional stimuli (CSs)
Advertising logos
Food packaging
Sight of food
Smell of food
Taste of food
Operant (instrumental) actions
Approaching food court or restaurant
Purchasing food
Handling food
Contexts:
Airports
Shopping malls
Sporting events
Superbowl parties
Couch in front of the television

operant response consequently occurs without it. The strength of Pavlovian or operant behavior therefore declines. An important fact about extinction is that it does not erase the original learning; a great deal of research suggests that the CS or behavior's original meaning is still available in the brain, even after extensive exposure occasions in which the CS or the behavior has occurred without the reinforcer (e.g., [21,22]). This means that an individual may find it hard to unlearn behaviors and habits that have accumulated over years of drinking soda and eating junk food. Instead, research suggests that extinction depends at least partly on the organism actively learning something new that inhibits performance based on the original learning. As I illustrate below, the organism seems to learn that the CS or the behavior is no longer paired with the reinforcer *in the present context*. Behavior can thus return in other contexts, and this fact (among others) makes extinguished behavior seem persistent and vulnerable to relapse. I will illustrate the idea by reviewing several phenomena in extinction. The phenomena and their implications have been discussed elsewhere (e.g., [23,24]); what follows emphasizes recent research with food reinforcers and attempts to develop some specific implications for appetite and overeating.

1. Renewal of extinguished appetitive behavior

One phenomenon that is especially central to the contemporary understanding of extinction is the renewal effect. Renewal has been studied most extensively in Pavlovian learning. In its simplest form, if a CS is associated with a reinforcer in one context (e.g., Context A), and then extinguished in a second one (Context B), the CS elicits behavior again when it is returned to the original context (Context A). This is called ABA renewal. Renewal can also be observed if conditioning, extinction, and testing respectively occur in Contexts A, B, and C (ABC renewal) and A, A, and B (AAB renewal). Although the latter forms of renewal are often somewhat weaker than the classic ABA form, they are interesting because the final return of the behavior occurs in a context other than the original conditioning context. ABC and AAB renewals thus indicate that simple removal from the context of extinction can be sufficient to cause a return of conditioned responding. Something learned in, and specific to, the extinction context inhibits or suppresses the conditioned response. Hence, extinction is at least partly a context-dependent form of learning.

Many well-known studies of renewal used fear conditioning techniques, where a tone is first paired with footshock and then consequently evokes fear (e.g., [25,26]). The renewal of fear has implications for the treatment and understanding of anxiety disorders (e.g., [23,27]). However, we have also demonstrated various forms of renewal in appetitive conditioning, where a CS like a tone is paired with food pellets (e.g., [28–30]). In this case, food responding is elicited by the CS again when it is removed from the extinction context. The parallel between aversive and appetitive conditioning is strong. In either case, there is often surprisingly little effect on the strength of the response to the CS when the CS is switched from Context A to Context B at the beginning of extinction. That is, the first context switch has little influence on conditioned responding. Like the ABC and AAB renewal phenomena themselves, this feature of behavior suggests that conditioned responding can transfer surprisingly well to new contexts, while extinction is more context-specific. The asymmetry or imbalance may be fundamental to the persistence of motivated behavior and appetite.

Weight loss is notoriously difficult to maintain after clinical treatment, and Wilfley et al. [31] have recently noted how renewal effects might contribute to making maintenance difficult. The renewal effect might also work in more natural settings, outside the domain of clinical treatment. For example, a friend of mine was able to eat sensibly and extinguish a number of habitual appetitive behaviors while she was at school for several months, away from a home environment in which the family often gathered socially with great quantities of food. At school, she stopped shopping for (and cooking) large amounts of food when she was expecting guests, and refrained from over-indulging at potlucks and dinner parties. On return home to the family over the holidays, however, all the original behaviors returned. In a similar way, those of us who feel cravings in the presence of the odor of cinnamon buns may learn to suppress the urge to eat in their presence when we visit the shopping mall. But the odor may trigger the desire again when we encounter it at the airport.

The renewal effect is clearly evident in operant as well as Pavlovian conditioning. Interestingly, its importance in operant learning has been a focus of several behavioral pharmacology laboratories investigating drug self-administration. The “compulsion” that some individuals have to take drugs might bear some resemblance to the “compulsion” that others have to eat food. ABA renewal effects have now been documented after extinction when rats have been reinforced for lever pressing with injections of heroin (e.g., [32]), cocaine (e.g., [33]), a mixture of heroin and cocaine (e.g., [34]), or oral delivery of ethanol (e.g., [35,36]). Specifically, when the rat learns to take the drug via lever pressing in one context and then is extinguished in another, drug seeking returns when the animal is simply returned to the original context. ABA renewal has also been demonstrated in operant experiments in which rats have learned to lever press for food pellets instead of drugs (e.g., [37,38,76]). Nakajima et al. [37] also found the renewal effect in discriminated operant conditioning, where rats first learned to perform the operant response in the presence of a light discriminative stimulus. In this case, renewal took the form of increased responding in the presence of the light in Context A after it had been fully extinguished in Context B. The context thus controlled the tendency of the light to instigate food-seeking behavior.

Most of the initial operant work focused on ABA renewal, ignoring the ABC and AAB forms. In fact, there were a number of failures to produce the AAB renewal effect [32,34,37]. This created a puzzle, because as noted above, ABC and AAB renewals are important in suggesting that removal from the extinction context is sufficient to renew behavior. However, my colleagues and I have recently produced good evidence of each of the renewal effects in free operant learning [39]. For example, in one experiment rats were first trained to lever press in Context A on a variable-interval (VI) 30-s schedule of food-pellet reinforcement. After several daily sessions, they received four sessions of extinction training in either Context A, the same context, or Context B, a second context. After extinction was complete, the rats were tested in extinction in both Contexts A and B (counterbalanced). As shown in Fig. 1, when the rats extinguished in Context B were tested in Context A (the ABA renewal condition), there was a robust return of extinguished lever pressing. And when the rats extinguished in Context A were tested in Context B (the AAB renewal condition), there was also an increase in responding. Although the AAB effect was significantly weaker than the ABA effect,