Extinction of Conditioned Flavor Preferences

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Abstract

Although noted as a proponent of associative learning theory, Rescorla acknowledged that other mechanisms might be responsible for the within-event learning produced when two stimuli co-occur. To investigate this possibility, he conducted experiments in which rats experienced a compound of a novel flavor and a palatable nutrient, and demonstrated that a preference for the flavor established by this training did not show the pattern of extinction that might be expected of a preference based on a flavor-nutrient association. A review is presented of subsequent work on the extinction of such conditioned flavor preferences in rats. The results are found to depend on the motivational state of the rat in training and on test, on the match between the procedures on training and test, and on the details of the test procedure (the nature of the choice offered to the rat). When conditions are arranged appropriately, the extinction effect (a loss of the conditioned response) expected by standard associative theory can be obtained. What remains a problem for this theory is the observation (made originally by Rescorla himself) is that the effects of extinguishing a conditioned flavor preference are remarkably persistent. The failure to obtain recovery from the effects of the extinction procedure remains as a signal that this form of learning may involve processes other than the association formation used to explain many other forms of learning.

Keywords: Rescorla, extinction, flavor preference conditioning, configural learning

Extinction of Conditioned Flavor Preferences

Bob Rescorla will long be celebrated for his contribution to the study of conditioning and associative learning. He championed the view (e.g., Rescorla, 2003) that the role of such learning was to allow the animal to develop accurate knowledge of the environment, knowledge that can be changed as conditions in the world change. An important feature of such knowledge it that it allows the animal to predict with some accuracy, on the basis of current stimulus conditions, what will come next. Rescorla's first major publication, "Pavlovian conditioning and its proper control procedures" (Rescorla, 1967), established the basis for this view of conditioning. But although this view was maintained and developed over the next 50 or so years, he was well aware that there was more to it than that.

From time to time, when he turned his attention to what he termed "within-event" learning, Rescorla acknowledged that a theoretical framework that focused on the way in which one event *predicts* the occurrence of another might not be appropriate for the learning that goes on about complex, compound events, in which stimuli co-occur. The experimenter may think of a particular stimulus as a compound of A and B, and then apply standard theorizing in which the animal forms a link (or links) between the components. But Rescorla expressed doubts about the "attempt to force within-event learning into the conventional Pavlovian mold" (Rescorla & Durlach, 1982, p. 107). He went on to suggest (e.g., Higgins & Rescorla, 2004; Rescorla & Durlach, 1981; Rescorla, 1981, 1983), that the animal may come to perceive AB as a unitary event -- learning about this event could then influence the behavior shown to its supposed “components” not by way of associative links but because there will be generalization between AB and A (or B).

The notion that a complex event may be perceived as, and represented as, “a unit” has a long history in work on perception (Rescorla cites James, 1890; Köhler, 1941; Robinson, 1932; among others). In the world of conditioning research, it came to prominence with work on the procedure known as “evaluative conditioning”.

Evaluative Conditioning and Extinction

When Martin and Levey (1978) introduced the notion of evaluative conditioning they were concerned principally with effects demonstrated in human subjects, whose liking for, or disliking of, a particular picture could be changed by experience of this picture in conjunction with some other (see Levey & Martin, 1975). They attributed this effect, taken to reflect the modulation of an “evaluative response”, to a process of (a form of) Pavlovian conditioning.

At about the same time, experiments with animal subjects began to appear, showing formally similar effects in which the liking for a particular flavor could be modified by pairing it some other. Thus, Holman (1975) gave rats experience of flavors (almond and banana) mixed with saccharin and found that the preference could be shifted toward the flavor that had been paired with a stronger (and sweeter) concentration of saccharin. This effect was confirmed by Fanselow and Birk (1982), who also showed that a preference could be shifted in the opposite direction by pairing the flavor with the bitter taste of quinine. Similar effects were demonstrated when the target flavor was paired with a substance having nutritive properties: Bolles, Hayward, and Crandall (1981), using vanilla and anise as the target flavors, showed a shift in preference to the flavor that had been mixed with a high calorie diet. With this procedure, in which the added flavor is paired with a substance having metabolic consequences, we cannot know whether the shift in preference depends on these, rather than on the intrinsic flavor of the diet, although Bolles et al. veered in favor of the latter possibility. Parallel demonstrations of conditioned flavor preferences have been obtained for human subjects. Zellner, Rozin, Aron, and Kulish (1983) gave people a range of different flavors (varieties of tea), some sweetened with sucrose, and demonstrated, using a rating scale, that liking for these was enhanced. Baeyens, Eelen, Van den Bergh, and Crombez (1990) demonstrated equivalent effects using nonnutritive saccharin, and also the reverse, a reduction in the score for liking, by pairing the flavor with a bitter substance (Tween20, a form of detergent).

All these early reports set their work in the context of Pavlovian conditioning, although not in the form favored by standard associative theories. Such theories, as exemplified by the work of Konorski (1967) and Wagner (e.g., 1981), postulate the formation of connections between entities representing the conditioned stimulus (CS) and the unconditioned stimulus (US) of the Pavlovian procedure. In these formulations, stress was laid on the ability of one stimulus to predict the occurrence of another. From the outset, Martin and Levey (1978) took a different approach. They proposed that the evaluative conditioning effect depended on the concurrent presentation of CS and US establishing what they referred to as a “CS/US complex” (perhaps equivalent to what later authors have called a “configural” cue). This form of learning was thought to allow the CS to take on some of the properties of the US. Baeyens and his associates (e.g., Baeyens et al., 1990) initially interpreted their findings in terms of Pavlovian flavor-flavor associations, but as new information became available they developed a distinct concept of evaluative conditioning that was procedurally the same as Pavlov's version but which depended on a different process for its effects (see, e.g., De Houwer, Thomas, & Baeyens, 2001). The special features of this form of learning, said to distinguish it from orthodox conditioning, were three: (1) it was not sensitive to what has been called "contingency" – specifically it was little affected by reduction in the correlation between CS and US; (2) the magnitude of the evaluative conditioning effect was poorly correlated with the extent to which the subjects showed awareness of the relation between the CS and US; (3) it was resistant to extinction, the preference being substantially maintained over repeated presentations of the CS alone.

As we have noted, the notion of evaluative conditioning arose from studies of human learning, and indeed Levey and Martin (1975) described the evaluative response as "characteristically human … [allowing] the plasticity of responding which is characteristic of human behaviour" (Levey & Martin, 1975, p. 225). Subsequent experimental work and theorizing (e.g., De Houwer et al., 2001; Hughes, De Houwer, & Perugini, 2019) has followed this lead. But the demonstration of conditioned flavor preferences in animals prompts the question of whether this phenomenon is properly to be regarded as involving a form of learning different from that described by standard associative learning theory. Do conditioned flavor preferences in animals show the special features identified by De Houwer et al. (2001) as characteristic of evaluative conditioning? Clearly there is no scope for assessing the second in the list (the presence or absence of subjective awareness), and there is little work on contingency effects in this context (but see Delamater, 2011). There is, however, a substantial body of work on the effects (or lack of them) of the extinction procedure on conditioned flavor preferences in rats. This work forms the substance of this review. To demonstrate that flavor preferences are immune or resistant to the effects of the extinction procedure would support the proposition that it would be a mistake “to force within-event learning into the conventional Pavlovian mold”.

Resistance to Extinction of Conditioned Flavor Preference: Preliminaries

Most of the work to be reviewed uses rats as the subjects and conditioning procedures in which a target flavor (the CS) is presented in compound with another (the US), chosen to enhance the preference for the target flavor. The terminology of traditional Pavlovian conditioning, CS and US, is used for convenience, and should not be taken to imply any theoretical position on the nature of the learning obtained. Our central concern is with the case in which CS and US are presented together. The typical CS is an aqueous solution of a novel, neutral (or slightly disliked) flavor, such as vanilla or almond.[1] As the rats are usually on a schedule of restricted access to water, they will drink even the less-preferred flavors. The US is provided by a substance that has a sweet taste, usually sucrose in the experiments to be considered.

Sucrose is a sweet, palatable substance, readily consumed by rats; and it also, as a carbohydrate, has nutritive, post-ingestive consequences. Both these properties are likely to play a role in establishing a flavor preference. The role of the sweet flavor is demonstrated by the effectiveness of saccharin as a US in establishing a flavor preference. We have already noted that Holman (1975) found that rats would develop a preference for a flavor paired with a stronger saccharin solution; and Albertella and Boakes (2006, Experiment 4) have demonstrated a persistent preference for a flavor that had been paired with saccharin in rats given a choice between that and plain water. That the post-ingestive consequences of consuming a carbohydrate can establish a preference for a flavor, independently of taste, is well established from studies in which consumption of the CS flavor is paired with an intragastric infusion of a carbohydrate (see Sclafani, 1995, for a review). For example, Sclafani and Nissenbaum (1988) found that rats developed a strong preference for cherry- or grape-flavored water consumed along with an intragastric infusion of the starch-derived polysaccharide polycose, over a flavor paired with an infusion of water.

We may assume that when rats are trained with an orally consumed, flavored sucrose solution, the learning that results is likely to involve both its sweet taste and its nutritive consequences. It may be that the motivational state of the animal could bias one form of learning over another. It is known that intragastric infusion functions can support conditioning even when the animals are not food deprived (e.g., Drucker, Ackroff, & Sclafani, 1994) but it remains possible that the nutritive qualities of a substance like sucrose will be more important when a rat is hungry than when it is well fed. (See Harris, Gorissen, Bailey & Westbrook, 2000, for analysis of this issue.) Whether or not this will be a relevant factor when saccharin is the US is difficult to say – after all, the sweet taste of saccharin might generate an expectation of nutritive consequences, the absence of which could be particularly salient if the animal is hungry. There are experimental results from studies using these USs to suggest that, at least under appropriate motivational conditions, both can generate preferences that seem immune to the effects of an extinction procedure.

Key Experiments

The phrase "resistance to extinction" is taken to refer to the empirical observation that a CR may be maintained in spite of the fact that the CS is presented alone, in the absence of the supposed US. An indication that conditioned flavor preferences might show unusual resistance to the effects of the extinction procedure came initially from studies using the gastric infusion technique. After pairing one fruit flavor (the CS+) with a polycose infusion and another (the CS-) with water, Sclafani and Nissenbaum (1988) gave extensive testing in which the rats were allowed a choice between the CS+ and CS- in the absence of any infusion. A clear preference for CS+ was maintained throughout. (See also Drucker et al., 1994; Elizalde & Sclafani, 1990.) But, as Harris, Shand, Carroll, and Westbrook (2004) have pointed out, the interpretation that this effect reflects a failure of extinction of the response to the CS+ is insecure. The initial training given to the rats may be expected to establish not only a positive reaction to the CS+ but also a negative reaction to the CS-. Since the inhibitory properties of a CS are known to be maintained in spite of exposure to the stimulus in the absence of a reinforcer (e.g., Zimmer-Hart & Rescorla, 1974), a tendency to avoid the CS- could maintain some preference for the CS+ even if the latter was suffering from the effects of the extinction procedure. Support for this interpretation comes from the observation (Drucker et al., 1994) that loss of preference for the CS+ flavor could be obtained when the extinction procedure consisted a choice between that flavor and unflavored water (rather than a CS-).

This problem (at least) was avoided in the series of experiments reported by Harris et al. (2004) that have been taken to confirm that, under certain conditions, a conditioned flavor preference governed by the CS+ might be immune to the effects of the extinction procedure. An example is provided by their Experiment 2A. In this study, thirsty rats were given twice-daily 10-min sessions of access to an 8% solution of sucrose flavored with almond. Half the subjects were on a schedule of restricted access to food during this phase of training; the remainder were allowed free access to food. The subjects were then tested, twice daily, for seven days, with 10-min presentations of access to two bottles, one containing water the other the unsweetened almond solution. All animals were allowed free access to food during this phase. Initially all subjects showed a marked preference for the almond solution. This preference was maintained at high level (with the preference ratio, intake of almond over total amount consumed, staying at about 0.9, over all 7 days of the test) in the subjects that had been hungry during training. The results for the subjects that were sated during training were ambiguous. They maintained a preference for the flavor over water during the test, but an increase in consumption of the latter resulted in a marked decline in their preference ratio. The change in this latter measure could be taken to represent an extinction effect.

This failure to obtain the extinction effect, at least under certain motivational conditions, has been confirmed in a number of later experiments, using the same general experimental designs and procedures. Thus, Harris et al. (2004), in their Experiment 2B, again found that rats allowed free access to food throughout maintained their conditioned preference over the course of a test of flavor versus water. (The preference ratio for animals given a change of motivational state, in this case being sated during training but made hungry for the test phase, showed a substantial decline, again largely as a consequence of a nonspecific increase in consumption of both water and almond.)

Albertella and Boakes (2006) reported three experiments using essentially the same procedures as those of Harris et al. (2004), except that all subjects had free access to food prior to each training and test trial in all phases of the study. They found no evidence of extinction in choice tests of flavor vs. water. One of their studies included an extinction test in which the rats were given access to a single bottle containing the trained flavor over six days. Consumption remained steady over these trials (unsurprisingly, as the rats were water-deprived throughout the experiment); but in spite of this forced exposure to the flavor, there was no sign of loss of the preference for it when, in a subsequent test, the rats were given a choice between the flavor and water. (See also Boakes, Albertella, & Harris, 2007, Experiment 2, for confirmation of this result.)

Finally, we should note the effects obtained with a nonnutritive sweetener. Albertella and Boakes (2006) conducted a study (their Experiment 4) that was essentially identical to those done with sucrose, but include a condition in which saccharin was the US. Training with a 0.4% (wt/vol) saccharin solution produced a preference closely similar to that produced by 8% sucrose. For neither US was there any effect of six sessions of exposure to the flavor alone on the size of the preference. These results were taken to indicate that a preference established by the immediate sensory properties of the US, rather than its metabolic consequences, can show marked resistance to extinction. The effect of motivational state has not been investigated for this US.

Implications

The acquisition of a flavor preference in the experiments just described is readily explained in standard associative terms, that is, in terms of the development of excitatory links between central representations of the CS and aspects of the US. For a US like sucrose these are likely to be multiple. The studies using the gastric infusion technique (e.g., Sclafani, 1995) indicate that the nutritive properties alone are capable of supporting learning. But the sweet taste itself can be effective (as studies with saccharin show). It has been commonly assumed (see, e.g., Harris et al., 2000) that the critical association in this case is between two stimuli (that is, between the CS flavor and sweet taste of a sugar or saccharin), but a stimulus-response link, between the flavor and the hedonic response to sweetness, has also been postulated (see, e.g., Harris et al., 2004: Dwyer, Pincham, Thein, & Harris, 2009).

The problem for this associative interpretation is the failure of these preferences to show the extinction effect that would be expected of a classically conditioned excitatory link. There is some indication that extinction can be obtained, provided the animals are hungry, or have been hungry during training, which could accord with a standard Pavlovian conditioning analysis in which the CS (the flavor) precedes the occurrence of the effective US (ingestion of a nutrient). But when animals are not food-deprived, or are trained with saccharin, an extinction effect can be elusive. It is this finding that prompts the suggestion that the associations formed in these conditions have special properties (e.g., Harris et al., 2004, postulated that a change in the hedonic response might be especially long-lasting). Alternatively (following, among others, Rescorla, 1983) we may want to adopt an account that regards the configural cue of flavor + sweet as a single entity and rejects the notion that an association is formed between them. According to some accounts (e.g., Pearce, 2002) this form of learning would not be susceptible to influence by an extinction process that operates on associations. Whichever line is taken, the implication is that the failure to find a standard extinction effect in some types of flavor-preference learning requires us to contemplate the possibility that there is a form of conditioning that is importantly different from the traditional Pavlovian version.

Before taking this theoretical step it will be worthwhile to look in more detail at the experimental evidence on extinction in flavor preference learning that has been thought to make it necessary. The work is described under two main headings. The first deals with experiments in which the rats are given restricted access to food during training and/or testing. At issue here is whether the trained preference does indeed show the features of extinction that would be expected of a standard CS-US association. The second deals with studies in which the animals are not food-deprived. At issue here is whether the apparent failure of the extinction to produce a loss of preference indicates that the original source of the preference was something other than a standard CS-US association.

Extinction Effects in Hungry Rats

Problems in Demonstrating an Effect

Given the results of the “key experiments”, described previously, it is no surprise that much of the subsequent work would focus on mechanisms of extinction (or the lack of it) in flavor-preference learning shown by non-hungry rats. There are however, some studies raising the possibility that mechanisms other than the formation of a standard CS-US association may be at work even for subjects that are trained when hungry and with a nutritive US. The most obvious (although, it will be argued, least problematic) come from studies showing that it can be difficult to demonstrate extinction even in hungry animals.

The experiments by Harris et al. (2004), described above, form the basis for the proposal that a standard extinction effect can be obtained if the rats are hungry. It should be noted, however, that their procedure was unusual in that in their experiments the motivational state of the rats was changed between training and the extinction test phase. (In one study the rats were hungry during training and food-deprived for the test; in another this arrangement was reversed.) An animal's motivational state can be regarded as constituting part of the context in which learning occurs and performance is tested, and in that case, the subjects in these experiments experienced a context change from training to test. There is some evidence (e.g., Archer, Sjödén, & Nilsson, 1985) that a conditioned response to a flavor will fail to transfer across contexts. If so, the loss of preference in the experiments by Harris et al. would not necessarily reflect an extinction process.

Whether conditioned responding does show this form of context specificity has been disputed (e.g., Bouton, 1990; see also Hall, 1991), but it it has been widely accepted that extinction learning is sensitive to a change of context (Bouton, 2004). Contextual factors can then provide a viable explanation for the results reported by Badolato, Hall, and Boakes (2021) in which the extinction procedure appeared to be ineffective. In their experiments, the rats were explicitly food-deprived throughout, but in spite of using procedures that otherwise were closely similar to those of Harris et al. (2004), they failed to detect extinction. These procedures were successful in establishing a clear preference for the flavor (almond or vanilla) paired with sucrose as measured by a two-bottle choice test of flavor versus water. And although this preference was less strong on a second test given up to 12 days later, the decline was no greater in subjects given the extinction treatment (daily presentations of a bottle containing the CS flavor) than in control subjects given only water over the interval.

Although these findings may seem to undermine the proposal that a standard CS-US association underlies the preference acquired by hungry rats, Badolato et al. (2021) offered a different interpretation. They pointed out that their procedure involved a (seemingly minor) change between the extinction and testing procedures in one aspect of the context. Specifically, their rats were given a single bottle containing the flavor during the extinction phase, but were given two bottles (flavor vs. water) in the test; Harris et al. (2004) used two bottles throughout. Evidence that a small change of context of this sort can be critical came from a further experiment by Badolato et al. This confirmed that an extinction effect could be obtained simply by making two bottles available throughout the procedure.

The observation that flavor preference learning in rats may be surprisingly sensitive to changes of aspects of the context that seem trivial to the experimenter, makes it prudent to examine closely cases in which extinction apparently fails to occur. This will not be an issue in the experiments to be discussed next -- experiments in which an extinction effect has been obtained -- but will need to be borne in mind when it comes to consideration of experiments that failed to obtain an effect.

Experimental Analysis of the Extinction Effect

In spite of the constraints implied by the results of Badolato et al. (2021) an extinction effect in hungry rats has been obtained in a range of experiments in which the rats were hungry throughout the procedure, or, following Harris et al.

(2004), food-deprived just for the test phase. It should be noted, with respect to the latter arrangement, that since the subjects in these experiments are on a schedule of limited access to water they will reduce their intake of dry food, even when this is freely available, and will thus impose a degree of food deprivation on themselves. (Harris et al., 2004, have described rats given this treatment as being in a state of "latent hunger".) A practical advantage of using this arrangement is that rats that are not explicitly food-deprived during the initial phase of training drink more readily than food-deprived animals and thus receive greater exposure to the flavors of experimental importance. Demonstrations of the reduction in or loss of a conditioned preference under these motivational conditions are readily available (e.g., Delamater, 2007, Experiment 3; Garcia-Burgos & González, 2012; Higgins & Rescorla, 2004; Harris et al., 2004, Experiments 2A and 2B; González, Morillas, & Hall, 2016, Experiment 1A).

This outcome is to be expected on the assumption that the acquired preference is based on an associative link, whether between the CS flavor and the nutritive qualities of the US or between the flavor and the immediate sensory properties of the US (or both of these). Although the suggestion that an association established by Pavlovian conditioning might be "unlearned" or erased by the extinction procedure cannot be totally discarded (Delamater & Westbrook, 2014), the primary source of the extinction effect is taken to be some form of inhibitory learning (e.g., Delamater, 2004) that negates the (substantially intact) excitatory association. In the formulation proposed by Konorski (1967), initial training will establish a CS-US link, whereas extinction training will establish a CS-no US link that inhibits the first. This notion has been widely adopted (see, e.g., Hall, 2002; Bouton, 2004). A feature of this account is that the basic extinction procedure will not turn the extinguished CS into a net inhibitor (informally, a stimulus that signals that the US will not occur). Rather the extinction procedure will strengthen the CS-no US link up to the point at which it matches the strength of the CS-US link, and, at that point of neutrality, no further learning will occur. Further experimental analysis, however, raises doubts about the validity of this interpretation.

Higgins and Rescorla (2004, Experiments 1 and 3) gave rats that were food-deprived throughout the experiment, daily access to a mixture of polycose and almond, sufficient to establish ready consumption of almond alone. (Polycose is a polysaccharide that is palatable to rats and, at appropriate concentrations will be preferred over sucrose and glucose; see Sclafani & Clyne, 1987). Following this acquisition phase the rats were allowed repeated access to almond alone. This experience produced a decline in consumption, an extinction effect. Strikingly, however, retraining these rats, by giving further experience of the polycose-almond compound, was ineffective in reestablishing the positive response to almond. This is not what would be expected of a standard Pavlovian association. This phenomenon of resistance to retraining after extinction was confirmed in a study by Garcia-Burgos and González (2012, Experiment 4). Their procedures differed in that the US used was sucrose and the rats were explicitly food-deprived only after the conditioning phase had been completed.[2] But again, after the preference for almond had been extinguished, further presentations of the almond - sucrose compound failed to reestablish the preference.

Garcia-Burgos and González (2012) presented a set of further tests, using the same general procedures, confirming that the posttraining presentations of the flavor in their experimental preparation produced a stimulus with properties other than those expected on the basis of simple extinction. It has been known since Pavlov (1927) that an extinguished conditioned response (CR) will show spontaneous recovery when an interval is inserted between the end of the extinction procedure and a further presentation of the CS. But Garcia-Burgos and González (in their Experiment 1) found no sign of the recovery of a flavor preference when an interval of 10 days was inserted between the end of the extinction procedure and the test. In their Experiment 2 they went on to look for another, commonly observed, extinction-related phenomenon -- the reinstatement effect; that is, recovery of an extinguished CR produced by giving the subject reexposure to the US (e.g., Bouton, 1984; Bouton & Bolles, 1979). In their case, however, no such recovery was obtained. Rats given access to the sucrose solution after the extinction procedure showed no enhancement of the response to the almond on a subsequent test.

Role of Conditioned Inhibition

In discussing these findings, Garcia-Burgos and González (2012) suggested that the extinction procedure (or "posttraining flavor exposure" as they termed it) did not simply negate the effects of initial conditioning, but rather established the flavor as a conditioned inhibitor. A net inhibitor might be able to resist the effects of the passage of time and of the reinstatement procedure, and it would certainly be expected to show resistance to retraining. A direct test of the possible inhibitory properties of a flavor given posttraining exposure was presented in Experiment 5 of Garcia-Burgos and González. Their Experiment 4, on resistance to retraining (along with that of Higgins and Rescorla, 2004), constitutes an example of a retardation test for conditioned inhibition. Their Experiment 5 provided the other required test – the summation test. In this, rats received initial training with two flavors each paired with sucrose; one flavor then received the extinction procedure prior to a test with the two flavors presented together. The flavor given extinction was found to reduce the conditioned preference controlled by the other, an outcome that, combined with the retardation effect previously demonstrated, supports the interpretation that this training procedure is capable of generating conditioned inhibition.

As Garcia-Burgos and González (2012) acknowledge, standard theories of associative learning (e.g., Pearce & Hall, 1980; Rescorla & Wagner, 1972) do not expect simple extinction training to generate conditioned inhibition (and such training does not routinely do so). It has been suggested that conditioned flavor aversion might constitute an exception (Calton, Mitchell, & Schachtman, 1996; Hart, Bourne, & Schachtman, 1995), but more extensive work has failed to support this suggestion (Aguado, de Brugada, & Hall, 2001; Brooks, Bowker, Anderson, & Palmatier, 2003). It remains possible, however, that the effects demonstrated with conditioned flavor preference constitute evidence that this form of learning, at least, requires a different form of explanation.

Alternatives to Conditioned Inhibition

The proposal of Garcia-Burgos and González (2012), that the extinction procedure in this paradigm can turn a flavor into a net inhibitor, provides an explanation for some aspects of the experimental results just discussed. It is not, however, without problems. At the empirical level, it may be noted that the effects of their extinction procedure were surprisingly long-lasting, even seemingly, permanent. Reinforcing a stimulus that has previously acquired inhibitory properties can be expected (eventually) to render it excitatory. It is possible, of course, that had more extensive retraining been given in their Experiment 4, a conditioned response might have been reestablished, but the absence of any effect is striking.

A more compelling argument comes from an effect obtained when the initial conditioning phase makes use of a serial procedure in which presentation of the CS flavor precedes that of the sweet US. This procedure sometimes fails to establish a reliable preference for the CS flavor. Garcia-Burgos and González (2012) failed to find an effect in three of their experiments, possibly because the rats were not hungry during the initial phase of training (although a preference was obtained in a further experiment using the same general training procedures). The procedures used by Higgins and Rescorla (2004), however, in their Experiment 2, were perfectly effective in establishing a sizeable preference in subjects given access to the CS followed by access to the US solution. Subsequent exposure to the CS alone produced an extinction effect of the sort seen in animals trained with a simultaneous presentations of CS and US. But when it came to the reconditioning, with the flavor again paired with polycose, a different outcome was obtained – in this case reacquisition occurred readily.

The significance of this result lies in the extent to which it undermines the account, just outlined, that attempts to explain the results obtained with simultaneous presentations of CS flavor and sweet US in terms of the acquisition of net inhibitory strength by the CS. On the face of things, the associative learning processes at work to generate inhibition in the simultaneous case should also operate when the CS and US are presented sequentially. Perhaps they are, and the reacquisition obtained by Higgins and Rescorla (2004) in their experiment simply reflects the power of reinforcement to overcome an initial deficit. The question that remains, however, is why the equivalent procedure was so poor at overcoming any inhibitory strength acquired as a consequence of simultaneous presentations of CS and US.

A possible answer is that the preference established by simultaneous presentation of a flavor CS and a sweet US depends (at least in part) on a form of learning that is not to be explained in terms of standard associative processes. To this extent these experiment with hungry rats lend support to the proposal that some aspects of flavor preference learning require a different form of explanation. This proposal was based on, and derived its chief support from, experiments in which the rats were not food deprived. These are considered next.

Extinction Effects in Non-Hungry Rats

By non-hungry is meant: not explicitly food-deprived. As has been noted already, rats on a schedule of water-deprivation will eat less than otherwise and may thus experience “latent hunger” (Harris et al., 2004). This may be enough to allow learning about the nutritive consequences of sucrose consumption (to the extent that such learning depends on motivational state), and Harris et al, have suggested that the learning generated in this state will show an extinction effect when the animals are food-deprived for the test phase. Our primary concern in this section, however, is with the case in which access to food is maintained throughout. In this case latent hunger may be present both during training and during extinction. But, as shown by the experiments already described, this is not in itself enough to guarantee an extinction effect; that is, there are a number of demonstrations of the failure to find a clear effect of the extinction procedure in non-hungry rats (e.g., Harris et al., 2004).

Before turning to these experiments, the issue of the context-specificity of extinction should be considered. Given the sensitivity of extinction to a change of context (as demonstrated by Badolato et al., 2021) it is possible that some cases of the failure to find an effect are a consequence of this sensitivity. This could apply, for instance, to the procedure used in several of the experiments reported by Albertella and Boakes (2006) in which the extinction procedure consisted of presentation of a single bottle containing the flavor CS, whereas the test involved a choice between two bottles (flavor vs. water). There is room for doubt, therefore, about the failure of Albertella and Boakes to obtain extinction, particularly in their experiment that used saccharin as the US. An extinction effect with this US effect was obtained by Díaz and De la Casa (2011) using a procedure that differed from that of Albertella and Boakes in that it presented the rats with two bottles, both during training and during the extinction phase. It remains the case, however, that a failure to find an extinction effect with sucrose as the US (as was observed by Albertella & Boakes) has been confirmed in other studies in which this sort of context change was not introduced. Experiments using this US are thus our central concern.

Extinction and US Devaluation

Having demonstrated the basic effect of interest (i.e., the apparent ineffectiveness of the extinction procedure in non-hungry subjects), Harris et al. (2004) went on to analyze it by means of a study of the effects of US devaluation, a procedure that has been used in several subsequent experiments, and has contributed importantly to theoretical analysis of the phenomena.

Initial observations. In their Experiment 3, Harris et al. (2004) looked at the effect of devaluing the nominal US by pairing sucrose consumption with a nausea-inducing injection of LiCl. All their subjects received flavor-preference conditioning with pairings of almond and sucrose; some then experienced the extinction procedure (presentations of almond alone), others not. Sucrose devaluation then followed. A final test of the almond preference showed that the extinction procedure was not without effect in that it appeared to “protect” the conditioned preference from the effects of devaluation of the sucrose. Such devaluation reduced the preferences in subjects not given extinction. Harris et al. proposed, in explanation, that devaluing sucrose might capable of reducing the preference that was produced by an initial association between almond and the sweet taste of sucrose, but the initial training could also produced another form of associative learning that could serve to maintain the preference in spite of extinction training. This other form they characterized as stimulus-response (S-R) learning, the stimulus being the flavor and the response the hedonic reaction to its sweet taste.

This account has a number of problems. Evidence that directly challenges the idea comes from a study by Dwyer et al. (2009). They used the pattern of licking shown by the rat as a measure of the palatability of a flavored solution and thus of the hedonic reaction to it. After conditioning, palatability was found to be high; but although consumption remained high over the course of extinction, the pattern of licking indicating high palatability declined. That is, a high level of consumption was maintained in spite of the fact that the hedonic response acquired by the flavor appeared to show extinction. The force of this argument has been weakened by more recent work challenging the reliability of the microstructure of licking as an indicator of the rat's hedonic response (Riordan & Dwyer, 2019). It remains the case, however, as Harris et al. (2004) themselves acknowledged, that the assumption that this S-R learning would resist the effects of the extinction procedure and thus maintain the preference, was itself quite arbitrary. Subsequent experimental work has generated less arbitrary alternatives.

Further experimental analysis. Delamater (2007) took up the issue in a series of experiments addressing the same questions as those of Harris et al. (2004), but using an experimental procedure intended to provide a more sensitive measure of the effects of interest. Delamater pointed out that the choice-test procedure used in the experiments by Harris et al. (2004), and in the related studies described above, was likely to be an insensitive measure of any loss of a conditioned preference for the trained flavor. Even if extensive extinction produces a marked reduction in the positive value of the flavor, so long as it remains better-liked than plain water, the rat will be likely to consume the former rather than the latter. Accordingly Delamater turned to a procedure in which two flavors received initial reinforced training, allowing assessment of the effects of the extinction procedure on one of them in a final test in which both were presented. If extinction is at all effective, a preference for the control, nonextinguished, flavor should be evident.

Delamater (2007) combined this choice-test procedure with an investigation of the effects of US devaluation, paralleling that of Harris et al. (2004). Thus, after initial flavor-preference training followed by extinction of one of the flavors, some rats received aversion training in which sucrose was associated with an injection of LiCl; control subjects received unpaired presentations of sucrose and LiCl. The results for those given flavor-aversion training align with those reported by Harris et al. These rats showed a marked preference for the flavor that had undergone the extinction treatment, a result taken to indicate that the extinction procedure had weakened the sensory-specific, flavor-sweet link, thus protecting the response controlled by this flavor from the effects of devaluation. Equally important, Delamater found an effect of the extinction procedure in the control subjects that received only the unpaired presentations of LiCl. These subjects showed a preference for the flavor that had not undergone the extinction procedure; that is, the use of a sensitive choice-test procedure successfully revealed what appears to be a standard extinction effect for a preference demonstrated to depend on a flavor-sweet link.

Devaluation effects in hungry rats. Delamater (2007) reported work paralleling that just considered, but in which the rats were hungry during training and testing. The effects obtained differed from those he obtained in non-hungry subjects, but in general they accord with conclusions reached in our preceding discussion of extinction effects in hungry subjects. Recall that for non-hungry subjects rats in Delamater's experiments the devaluation procedure resulted in a preference for the flavor that had undergone extinction. For hungry subjects, by contrast, although the size of the effect was attenuated, a preference for the non-extinguished flavor was maintained. Delamater's interpretation was that although the performance of non-hungry rats was controlled chiefly by the sensory properties of the US rather than its nutritive properties, the reverse was the case for the hungry rats. For the latter, devaluation of the flavor would act to remove the component of the preference maintained by its association with the sweet taste, but, being hungry, the link with the post-ingestive consequences would still be maintained and effective in generating a preference.

Conclusion. Following the lead of Harris et al. (2004), the focus of the work carried out with nonhungry rats has been on the effects consequent on devaluation of the sucrose US. But equally important is the demonstration, by Delamater (2007), of a standard extinction effect in control subjects given only unpaired presentations of the US and nausea, a result confirmed by González, Morillas, and Hall (2016) in their Experiment 3. González et al. raised the issue of whether this seemingly irrelevant aspect of the procedure played any role in generating the test result. Can evidence of extinction can be obtained, using the choice test procedure of Delamater (2007), when these trials with separate presentations of sucrose and LiCl are omitted: that is, in non-hungry rats given appropriate treatment -- a sensitive two-flavor test procedure -- in the absence of any aversion conditioning. The answer appears to be "yes". In two experiments using these procedures, González et al. (2016) found a distinct (if not statistically reliable) preference for the non-extinguished flavor. More recently Delamater, Tu, and Huang (2021) have reported three experiments using the same basic design that successfully generated significant extinction effects in all cases.

Spontaneous Recovery

The experiments just described focused directly on the ability of nonreinforced presentation of a flavor to reduce a conditioned preference. They produced no clear effects that would require us to adopt an explanation other than that supplied by some version of standard associative learning theory. The picture is somewhat different, however, when another post-extinction test, spontaneous recovery, is considered. A CR supported by a standard Pavlovian CS-US association would be expected to show recovery if an interval were allowed to elapse after extinction and before the test. As we have seen, this effect is not reliably obtained in hungry rats (García-Burgos & González, 2012), and there are similar doubts about the case in which the rats are not food-deprived. Diaz and De la Casa (2011) found a small recovery effect in non-hungry rats given an interval of 21 days between the end of an extinction phase and a further preference test. But no evidence of recovery was obtained in an extensive set of studies conducted by Delamater, Tu, and Huang (2021). Their experiments used a version of the two-flavor, choice procedure that had proved sensitive to the direct effect of extinction in non-hungry rats. In these experiments the rats were trained with two pairs of flavors, one of each pair being given 10 extinction trials (presentations in the absence of the US, which was either sucrose or polycose) prior to a final choice test. For one pair of flavors the test immediately followed the end of the extinction phase; for the other pair the interval between the end of extinction and the test was 21 days. There was no indication of a difference in performance between these two conditions.

In my earlier discussion of the parallel results obtained by García-Burgos and González (2012) it was suggested that their failure to obtain spontaneous recovery (and related post-extinction effects) might be explained in terms of inhibitory learning. The analysis that was offered relied on the suggestion that in their experiments, using hungry rats, there was the possibility that the extinction procedure would establish the CS flavor as conditioned inhibitor signaling the omission of a nutritive outcome, the calories offered by sucrose. This account fares less well with the present results; that is, if we accept that the preference shown by non-hungry rats is based principally on the sweet taste of sucrose rather than its nutritive properties then an analysis that depends on learning about the latter is hard to apply. In this case, therefore, there is good reason to turn to the alternative that the preference depends on the formation of a configural representation of flavor+sucrose that retains its effectiveness in spite of the formation of a separate flavor-alone representation on the extinction trials.

Brief Summing-Up

The notion that flavor-preference learning might supply an example of a form of learning that, although it depends on the direct pairing of two identifiable events, is not to be fully explained in terms of the formation of a direct association between them, was endorsed and developed by Rescorla (e.g., 1981). Much of the subsequent support for this idea was derived from a series of studies (prompted initially by those of Harris et al., 2004) that were taken to indicate that a conditioned flavor preference did not show extinction as an orthodox Pavlovian CS would be expected to do. The review of the studies offered here, at least those investigating the course of extinction itself, provides little support for this proposal. With appropriately sensitive training and testing procedures, an extinction effect can be reliably obtained. What remains, however, is the observation that other extinction-related phenomena (the reinstatement effect, resistance to retraining, spontaneous recovery, and so on) do not behave as would be expected from a simple associative account. It is these effects that indicate the possible need for a different account based, not on direct association, but on some form of configural learning.

It is worth noting, in this context, that it was just such a phenomenon (resistance to retraining) that Rescorla himself chose to investigate (Higgins & Rescorla, 2004) and to put forward as supporting a configural analysis. He made no claim that a conditioned flavor preference (even one established by concurrent presentations of the flavor and a sweet taste) would not decline with repeated presentations of the flavor alone. Such a decline can be expected, according to a configural account (e.g., Rescorla, 1981) as, over the course of the "extinction" procedure, the animal will come to discriminate the element from the compound, having first failed to do so. But other properties of the compound itself will remain untouched and be evident with appropriate tests of behavior.

Footnotes

[1] In many studies of flavor-preference conditioning, the flavorants used are likely to function primarily as odors; however, as they are consumed orally and may also have a taste component, I will refer to them as flavors.

[2] It should be noted that a change of motivational state from conditioning to the test can be construed as constituting a change of context. As was discussed with respect to the results of Badolato et al. (2021), flavor preferences can be very sensitive such change. It could be worthwhile to investigate the range of phenomena covered by García-Burgos and González (2012) using procedures that avoid this motivational shift.

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