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BRIEF REPORT

Analysis of US-Preexposure Effects in Appetitive Conditioning

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In two experiments, rats received preexposure to one type of food followed by autoshaping in which presentation of one lever was associated with the preexposed food, and presentation of another lever with a novel type of food pellet. In both it was found that acquisition of the leverpress response occurred more readily on the lever associated with the novel food. This example of the US (unconditioned stimulus) preexposure effect is not to be explained in terms of the development of competing responses during preexposure. Explanations in terms of blocking by contextual cues and of habituation to the US are considered.

Keywords: US preexposure, autoshaping, habituation, appetitive conditioning, rats

It is well established that exposure to the event to be used as the unconditioned stimulus (US) in Pavlovian conditioning retards subsequent learning—the US preexposure effect. The effect is particularly well documented in studies of aversive conditioning—for the conditioned suppression procedure with shock as the US (e.g., Randich & LoLordo, 1979); for flavor-aversion conditioning, with nausea as the US (e.g., Riley & Simpson, 2001). The experiments to be reported here investigate the effects of US preexposure on appetitive conditioning. Previous work with appetitive procedures has produced an effect that, unlike that found with aversive procedures, is susceptible to explanation in terms of response competition at a peripheral level (see below). Our first aim was to provide a demonstration of the effect that could not be explained in this way; we then went on to use this appetitive version of the effect to assess the validity of explanations that have been devised for the aversive case, but which should have wider applicability.

The US-preexposure effect has been successfully obtained in several experiments using appetitive autoshaping procedures, both with rats and with pigeons as the subjects. It has been repeatedly demonstrated for pigeons that prior experience of unsignaled presentations of food will result in retarded conditioning when the food is subsequently used as the US in autoshaping, with key illumination as the conditioned stimulus (e.g., Balsam & Schwartz, 1981; Engberg, Hansen, Welker, & Thomas, 1972; Tomie, 1976). In experiments with rats, Timberlake (1986) used an autoshaping procedure in which the CS was a ball bearing that rolled across a channel in the floor of the chamber; as it left the chamber, food was delivered. The tendency of the rats to make contact with the ball bearing increased over training trials, but the rate of acquisition of this CR was retarded in rats given prior exposure to unsignaled presentations of food. Costa and Boakes (2009) used a more orthodox procedure in which the insertion of a response lever served as the CS signaling delivery of a sucrose US. When lever insertion immediately preceded sucrose the rats acquired the CR of lever pressing, but the rate of response was low in rats that had received prior exposure to unsignaled presentations of sucrose.

A possible explanation of these results is that the preexposure procedure establishes a response pattern, such as persistent approach to the site of food delivery, that competes with the CR being assessed during conditioning. There is some evidence from the experiments with rats to support this view. Timberlake (1986) reported that his rats showed a high level of responding directed toward the food tray during the conditioning trials, allowing the possibility that the lowered level of conditioned responding was a consequence of this competing response. In a further study, Timberlake gave two groups of rats preexposure in which the food delivery was contingent on their behavior, one group receiving food when they were close to the food tray, the other when they were distant from it. Conditioning of the response to the ball bearing was slower in the former group, perhaps indicating that approach to the food tray is a particularly effective competing response. Costa and Boakes (2009) also noted that rats given preexposure to the US showed a higher rate of magazine entry in the presence of the CS than nonpreexposeed subjects (although the difference fell short if statistical significance). In a study that parallels that reported by Timberlake (1986); van Hest, van Haaren, and van de Poll (1989) compared the effects of two forms of US preexposure on autoshaped leverpress responding in rats. For one group of rats, food delivery during preexposure was contingent on their approaching the food tray; for a second group it was delivered only when they did not approach the food tray. Subsequent autoshaping proceeded particularly slowly in the for-

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mer group. One interpretation is that leverpress responding is less likely to occur when the rat has its nose in the food tray, and more likely when it is elsewhere in the chamber.

These observations do not constitute proof that the appetitive US-preexposure effect is to be explained solely in terms of peripheral response competition; but they do serve to show that this explanation cannot be ruled out when comparison is made between subjects given extensive as opposed to minimal prior exposure to food delivery in the conditioning situation. To show that the appetitive US-preexposure effect involves processes beyond simple response competition requires a different experimental design. In the experiments to be reported here we continued to use lever insertion as the CS for autoshaping with rats, but in our design, all subjects were given preexposure to the delivery of food pellets; all subjects should, therefore, develop a tendency to approach the site of food delivery in the training context. But what will happen if the nature of the food US is changed for the conditioning phase? Competing responses established during preexposure may still occur, but any effect of US preexposure that is specific to the particular food offered during preexposure might be expected to be abolished. More rapid acquisition when the nature of the US is changed for the conditioning phase would thus indicate that there is a component of the US-preexposure effect that is not to be explained in terms of competing responses. We will postpone a consideration of how such an effect might arise until the General Discussion. We will now report experiments designed to determine if the retarding effects of US preexposure in appetitive conditioning are specific to the particular type of food presented in the preexposure phase.

Experiment 1

The design of this experiment allowed a within-subject comparison. In the first, preexposure, phase, all subjects received unsignaled presentations of food. For half the subjects standard (cereal-based) food pellets were presented; for the remainder sucrose pellets were used. The test phase consisted of autoshaping in which the introduction of a lever into the experimental chamber signaled food delivery. Two different levers were used on separate trials, one being followed by a food pellet, the other by a sucrose pellet. We recorded the development of responding to these levers. The question of interest was whether responding would develop less readily to the lever that signaled the preexposed pellet than to the lever signaling the novel pellet.

Method

Subjects. The subjects were 16, experimentally naive, male hooded Lister rats with a mean free-feeding weight of 400 g at the start of the experiment. They were maintained at 85% of their free-feeding weights throughout the experiment. Experimental procedures were carried out during the lit hours of a 12-hr light: dark cycle, which commenced at 8:00 a.m.

Apparatus. The apparatus consisted of four operant chambers (supplied by Med Associates, St Albans, VT), measuring 30 × 24 × 21 cm. The front wall of each chamber contained two retractable response levers, 11.5 cm apart, center to center. Midway between the levers, at floor level, was a 5 × 5 cm opening in which was set a food tray to which 45-mg food pellets and 45-mg sucrose pellets (supplied by TestDiet, Richmond, IN) could be delivered. An infrared beam allowed entries to the food tray to be detected. The box was illuminated by a houselight set high on the rear wall of the chamber.

Procedure. Training consisted of daily 40-min sessions. During the 10 days of the preexposure phase all animals received 40 pellets per session, delivered according to a variable time (VT) 60-s schedule. For eight rats these were food pellets and for eight they were sucrose pellets. The levers were withdrawn from the chambers during this phase. A single session of lever autoshaping followed, during which the rat experienced 20 10-s insertions of a lever, presented according to a VT 120-s schedule, and responses to the lever were recorded. On 10 trials the left lever was presented, and on 10, the right; the schedule of presentation was random with the constraint that the same lever could not be presented consecutively more than twice. Upon withdrawal of the lever a pellet was presented; for half the rats the left lever was followed by food pellets and the right by sucrose pellets; for the remainder the arrangement was reversed. For half the rats the novel food type was associated with the left lever, and for half it was associated with the right lever.

Results and Discussion

During the preexposure phase, it was noted that all rats entered the food tray repeatedly from the first day, and that all consumed all of the pellets offered during this phase. Leverpress responding during the test session is shown in the top panel of Figure 1. Pilot work had shown that acquisition of leverpressing occurred rapidly in this procedure and accordingly we recorded responding on each individual trial. The figure thus shows the group mean number of leverpresses on each trial for the lever associated with the familiar (i.e., preexposed) food type and for the lever associated with the novel food. Responding increased over trials on both levers, but did so more rapidly on the lever associated with the novel food. The data summarized in the figure were subjected to a mixed-design analysis of variance (ANOVA), which confirmed this description of the results. The within-subject variables were trial and reinforcer type (preexposed or novel); the between-subjects variable was whether the pellet given during preexposure was of food or sucrose. This yielded significant effects of trial, $F(9, 126) = 3.31$, of food type, $F(1, 14) = 6.03$, and a significant interaction between these variables, $F(9, 126) = 2.11$. (A significance level of $p < .05$ was adopted.) No other effects or interaction were significant; all Fs < 1, apart for the main effect of food versus sucrose preexposure, $F(1, 14) = 2.82$, and the three-way interaction, $F(9, 126) = 1.26$. These results confirm autoshaping proceeded less well with the familiar food type, and demonstrate that this effect was independent of whether that was sucrose or the standard food pellet. It may be noted, however, that the latter was somewhat more effective than the former in generating responding: The group mean total responses recorded on the lever associated with food was 12.88; the score for sucrose was 8.44; $t(15) = 1.93$, $p < .1$.

These results show that autoshaping proceeds more slowly when the food type used as the US has been rendered familiar; they thus constitute a demonstration of an appetitive version of the US-preexposure effect. With the procedure used here, in which all animals acquired the potentially competing response of food-tray approach, the effect is not to be explained in terms of peripheral

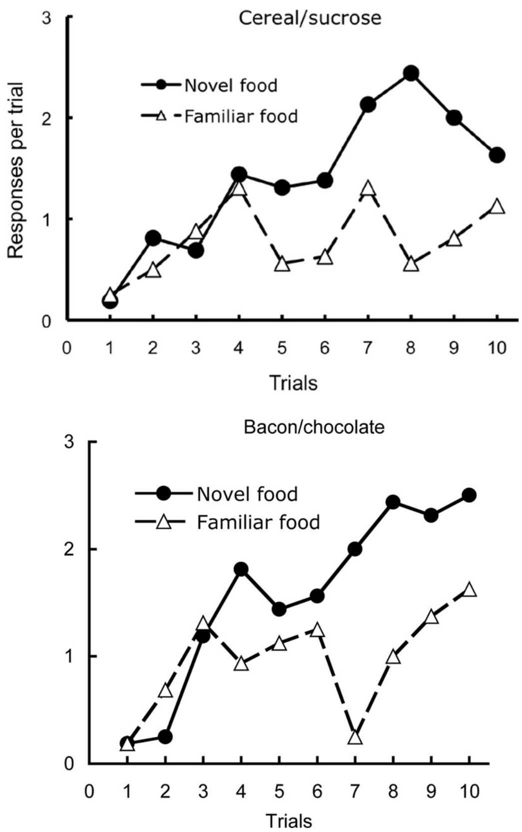

Figure 1. Group mean leverpress responses per trial on the lever associated with the preexposed (familiar) food type and the lever associated with a novel food type. Experiment 1: top panel; Experiment 2: lower panel.

response competition. We turn, therefore, to a consideration of possible explanations that parallel those offered for aversive instances of the US-preexposure effect. Attention has focused on two possibilities (Randich & LoLordo, 1979). The first is that preexposure to a US has its effect by way of habituation—that repeated presentations of a US not only reduce its ability to evoke its unconditioned response (UR), but also its effectiveness as a reinforcer. The second is the suggestion that effect depends on associative learning and blocking; that during preexposure an association is formed between the context and the US and that this acts to block acquisition of the measured CR during the test phase. At first sight, the results of Experiment 1 may seem to rule out this second explanation, given that all our subjects had experience of deliveries of food of some sort during preexposure, and thus all had the opportunity to form a context-food association. We next consider how the blocking-by-context account might be elaborated to deal with this issue, and provide a test of this elaboration as Experiment 2.

Experiment 2

The two types of food used in Experiment 1 differed not only in their sensory qualities (texture and taste) but also, possibly, in their motivational properties, given that the food pellet supported higher rates of autoshaped responding than did the sucrose pellet. This observation prompts consideration of a possible explanation of the results obtained in terms of blocking by contextual cues. Assume that the preexposure phase establishes an association between the context and a reinforcer of a given magnitude (a magnitude that will be different for food and for sucrose pellets). On conditioning trials on which the preexposed US is presented, its value will be accurately predicted by the context, and blocking of new learning can be expected. But on trials with the novel US, the size of the reinforcer will be different—greater for some and less for others, depending on which pellet was given during preexposure. Changes in reinforcer magnitude of either type have been shown to be capable of producing unblocking (e.g., Dickinson, Hall, & Mackintosh, 1976; Holland, 1984). If unblocking occurs in our procedure then it is possible that the lever associated with a novel food will acquire greater associative strength than the lever associated with the food previously experienced in the context. In the latter case the context will accurately predict the value of the food that is presented and blocking might occur.

To address this issue we changed the type of food pellet used in the present experiment. Instead of using food and sucrose, both food types were standard cereal-based food pellets, equivalent in their nutritional value. They differed only in their sensory qualities, one having (allegedly) a bacon flavor, the other a chocolate flavor. (Human observers agreed that these pellets differed in flavor, but there was debate as to the accuracy of the labels.) The question to be answered was whether prior exposure to a given food type would retard subsequent autoshaping with this food as the US, when comparison was made with acquisition supported by a novel US that differed only in its sensory properties.

Method

The subjects were 16 experimentally naive hooded Lister rats with a mean free-feeding weight of 390 g. The apparatus was the same as that used in Experiment 1. The pellets used (supplied by TestDiet of Richmond, IN) were 45-mg flavored food pellets, chocolate and bacon. The preexposure phase was reduced to 5 days, with 80 pellets being delivered in each session, according to a VT 30-s schedule. In other respects the procedure was identical to that used in Experiment 1—that is, half the rats received preexposure to bacon-flavored pellets and half to chocolate-flavored pellets; all then received autoshaping with two levers, one associated with pellets having a novel flavor and one with the preexposed pellets.

Results and Discussion

The results for the autoshaping session are shown in the lower panel of Figure 1. As for Experiment 1, data are shown for each of the 20 trials on each session, separately for the lever that signaled the novel food and for the lever that signaled the preexposed food. It was found that leverpressing developed more readily on the lever associated with the novel food type. An ANOVA was conducted on the data summarized in the figure, with pellet flavor (bacon or chocolate) during preexposure as a between-subjects factor, and the within-subject factors of reinforcer type (novel or familiar), and trial. There was a significant effect of trial, $F(9, 126) = 3.59$, and a significant effect of reinforcer novelty $F(1, 14) = 16.34$. No other effects or interactions achieved significance; all other Fs < 2, the largest being for the interaction between trial and reinforcer novelty where $F(9, 126) = 1.41$. There was no indication that the two pellet flavors differed in their ability to support autoshaping. The group mean total responses recorded on the lever associated with bacon was 14.00, and the score for the lever associated with chocolate was 12.44; these did not differ reliably, $t(15) = 0.74$, $p = .47$.

This experiment confirms the results of Experiment 1, showing that conditioning is retarded when rats have been given prior exposure to the particular type of food used as the US. As before, all animals received preexposure to food pellets on one type or the other, and there is thus no reason to think that this result is an outcome of interference from response patterns acquired during the preexposure phase. It is possible that a context–US association established during preexposure influenced the rate of acquisition during conditioning, but this context-blocking effect might be expected to operate equally on both levers. That is, acquisition of the leverpress response might well occur more readily if the outcome of lever presentation is not predicted by the contextual cues; but given that the two food types were chosen to be equivalent in their motivational properties, the contextual cues would predict the magnitude of the novel reinforcer as accurately as they predict that of the preexposed reinforcer. Blocking (in so far as this depends on the ability of the blocking cue to predict the size of the US) would thus occur with respect to both levers, and could not produce a difference between them.

Although the food pellets used in this experiment were chosen to be matched in their motivational properties they differed, of course, in their sensory properties. The results obtained could thus still be explained in terms of blocking by contextual cues if it were the case that a change in just the sensory properties of the US was capable of producing unblocking. The experimental evidence on this matter allows no simple conclusion. Some studies (e.g., Bakal, Johnson, & Rescorla, 1974; Ganesan & Pearce, 1988; Williams, 1994) have found that, provided the affective value of the US is maintained, blocking persists in spite of a change in qualitative aspects of the US. Others (e.g., Blaisdell, Denniston, & Miller, 1997) have found that unblocking occurs when the US is changed in this way. Two hypotheses (not necessarily alternative) have been put forward to explain these divergent results. First, Blaisdell et al. have suggested that unblocking will occur only when the sensory properties of the USs (including in this the cues associated with the URs they evoke) are radically different. Blaisdell et al. found unblocking when the USs were very different—electric shock and immersion in cold water; Williams, by contrast changed simply from a food pellet to a sucrose pellet (or vice versa) and found that blocking was maintained. Second, it has been suggested that whether or not unblocking is found will depend on the nature of the response being measured. Betts, Brandon, and Wagner (1996) found that a conditioned emotional response, dependent on the affective properties of the US, showed blocking whereas a consummatory response, specific to the particular US did not.

These considerations support the conclusion that is unlikely that unblocking occurred in our experiment. The CR measured, contact with a lever signaling food, was not a consummatory CR dependent on the specific sensory properties of the food; rather, we assume, it was an appetitive response produced by the general expectation that an affectively positive event of some sort would follow. And the two reinforcers used were not radically different, being as similar to one another as those used by Williams (1994) in his study, which failed to find any sign of unblocking (indeed, in Experiment 1, they were identical to those used by Williams). What follows is that the more rapid acquisition of the response to the lever associated with the novel food is not to be interpreted in terms of an unblocking effect. Blocking by contextual cues (if it operates at all in this procedure; see below) will influence performance on both levers and cannot explain the difference between them.

General Discussion

. Previous studies of the US-preexposure effect in appetitive conditioning have compared groups given extensive as opposed to no (or little) preexposure to the US, and their results have thus been explicable in terms of the direct effects of responses established in the preexposed subjects during the preexposure phase. In the experiments reported here, all subjects received extensive preexposure to food deliveries in the training apparatus, and thus all had the opportunity to acquire potentially competing responses. Nonetheless, acquisition of an autoshaped CR occurred less readily with the preexposed food as the US than when a novel type of food was used as the US. We take this to be an instance of a US-preexposure effect akin to that often demonstrated for aversive conditioning procedures.

One explanation offered for the aversive version of the US preexposure effect emphasizes the role of context conditioning, suggesting that an association formed between context and US during preexposure acts to block acquisition of the association between the target CS and the US during the test phase. There is plentiful evidence that this mechanism plays an important role in the aversive case (see, e.g., De Brugada, Hall, & Symonds, 2004). This explanation is not readily applicable to the present results, however, given that all subjects received context–food pairings during preexposure and thus all, presumably, acquired the context–food association. We have considered the possibility that this association might fail to produce blocking when the taste of the food is changed, but have presented evidence that argues against this. More generally, the view that a strong context–food association hinders subsequent conditioning is hard to support. Standard laboratory practice assumes that thorough "magazine training" (i.e., extensive exposure to free food in the context) promotes rather than retards subsequent conditioning, and unpublished work from our own laboratory has confirmed this. (The rapid acquisition seen in the present experiments may be a further example of the effect.) Formal experiments (e.g., Pearce & Hall, 1979; Baker, Steinwald, & Bouton, 1991) support the view that conditioned responding for food tends to be more vigorous in a context that is strongly associated with food. These observations all point toward the conclusion that a context–food association tends to summate with, rather than compete with the association responsible for the emission of a given CR for a food reinforcer.

If blocking by contextual cues is not responsible for the appetitive US-preexposure effect, we need to consider again the other explanation that has been offered for the aversive case. This is that preexposure allows habituation to occur, the implication being that the learning process engaged by this procedure produces not only a reduction in the ability of the preexposed stimulus to evoke its UR (the hallmark of habituation) but also a reduction in its ability to serve as a reinforcer. Could such a process operate with food as the US?

In order to explain the present results it would be necessary to assume that the habituation effect is specific to a particular type of food (defined in terms of its sensory properties). It is well established that repeated exposure to food of a given type can produce what may be thought of as a short-term habituation effect (known as sensory-specific satiety) specific to the preexposed food—subjects satiated for one type of food will none the less eat another type (e.g., Rolls, Rolls, Rowe, & Sweeney, 1981). Sensory-specific satiety can influence conditioned responding. Balleine and Dickinson (1998) trained rats to perform two different instrumental responses, each for a given type of food (the foods differing only in their sensory attributes). Satiating the animals on one food type produced a selective effect, with responding being reduced on a subsequent test (conducted in extinction) on the lever associated with that food type. These results may seem encouraging, but there are important differences between the procedures used in such experiments and our own. First, the Balleine and Dickinson procedure is concerned with the motivational processes that sustain instrumental performance once it has been acquired; our experiments concern the power of the US to support initial acquisition. Second, sensory-specific satiety effects are short term (Balleine & Dickinson gave the satiation treatment immediately before the test session); our studies are concerned with a long-term effect generated over a series of sessions, spaced over days.

Evidence for long-term sensory-specific habituation to foodstuffs comes from studies with human subjects looking at the effect of variety (as opposed to monotony) in the diet. Rolls and de Waal (1985) observed that refugees constrained to subsist for long periods (up to 6 months) on a restricted set of foods evidenced a reduced liking for and willingness to eat these foods. This general effect has been confirmed several times in experimental studies. For example, Meiselman, deGraaf, and Lesher (2000) gave volunteer participants a free lunch each day for a week, one group receiving the same menu each time, another having a menu that changed from day to day. For those in the monotony condition, it was found that ratings of liking declined over the course of the week, as did actual intake of most of the food items presented.

These studies establish the reality of long-term habituation to certain aspects of foods, but they do not demonstrate is that the habituation process reduces the effectiveness of the foodstuff as a reinforcer in conditioning. Indeed, it is not immediately obvious why it should do so. These habituation effects are specific to a given food type, with other types being accepted readily (an organism that habituated to the caloric or nutritional content of food would not long survive). We must assume, therefore that the motivational aspect of a food is not subject to habituation in the way that its sensory properties are. But it is, of course, just these motivational properties that, we have argued, support the development of the CR in our conditioning procedure. One possible solution to this puzzle emerges if we assume that the association formed in our experiments between the CS (the lever) and the motivational properties of food is indirect, and goes by way of the food's sensory properties. Thus the autoshaping procedure could generate an association between the CS and the taste of the pellet that follows it; performance would depend on the fact that the taste signals certain positive motivational consequences. Preexposure to a novel food might be helpful in promoting conditioning, to the extent that the association between the sensory and motivational properties of a food pellet would be preestablished. But if preexposure to the taste produces habituation, and thus a reduction in the effective salience of that taste, the initial association between the CS and the taste would be difficult to form, and the overall result could be a low level of conditioned responding.

It has long been thought (see, e.g., Randich & LoLordo, 1979) that habituation to the US may be a source of the US-preexposure effect, but there has been little direct evidence to support this view. Many studies using shock as the US have produced results that accord with the hypothesis that the effect is a consequence of blocking by contextual cues (e.g., Randich, 1981; Randich & Ross, 1984; but see Baker, Mercier, Gabel, & Baker, 1981). And experiments using flavor aversion conditioning (see Hall, 2009, for a review) have found little sign of habituation to the effects of a nausea-inducing injection but good evidence that the US-preexposure effect in this procedure is a product of blocking by contextual (specifically, injection-related) cues (but see De Brugada, González, Gil, & Hall, 2005). None of this proves, of course, that habituation plays no part in the effects observed with aversive procedures. If it is accepted that our present experiments demonstrate a role for habituation with an appetitive US, this may encourage research seeking evidence for an equivalent process in the aversive case.

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