Analysis of the US-preexposure effect in flavor acceptance conditioning

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ABSTRACT
In three experiments, rats received exposure to a sucrose solution followed by conditioning with a neutral flavor as the conditioned stimulus (CS) and sucrose as the unconditioned stimulus (US). In Experiments 1 and 2, some rats were given both the preexposure and the conditioning phases in a highly familiar context (the homecage), whereas other animals received both phases in a novel and distinctive context. In both cases the magnitude of the conditioning effect was reduced by preexposure to the US. Experiment 3 directly assessed the possible role of contextual cues by changing the context between the exposure phase and the conditioning phase but found no loss of the US-preexposure effect in these conditions. These results lend no support to the blocking-by-context account of the US-preexposure effect; alternative interpretations are considered.

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Prior exposure to the event to be used as the unconditioned stimulus (US) in subsequent classical conditioning retards the development of the conditioned response (CR) – the US preexposure effect (for reviews see Randich & Lolordo, 1979a; Riley & Simpson, 2001). The effect has been repeatedly demonstrated in a range of aversive conditioning paradigms, particularly in the conditioned emotional response (CER) preparation with shock as the US (e.g., Randich & Lolordo, 1979b), and in flavor aversion conditioning with an injection of lithium as the US (see Hall, 2009, for a review). Randich and Lolordo (1979a) suggested that both nonassociative and associative learning processes might play a role in producing the effect. The nonassociative process of interest here is that responsible for habituation. The US-preexposure involves repeated presentation of a given stimulus and might thus be expected to produce habituation, normally defined in terms of a reduction in the magnitude of the unconditioned response (UR). It is possible that the change in the effectiveness of the US evidenced by the behavioral change might also show itself as a reduction in the ability of the US to serve as a reinforcer in subsequent conditioning. The associative process of interest is that responsible for blocking (e.g., Kamin, 1969). Exposure to a US will occur in a certain context, and associations will form between the US and cues that are present when it occurs (those that originate from the apparatus in which the US is presented and also, in the case of lithium injections, those provided by the injection procedure – see De Brugada, Hall, & Symonds, 2004). These cues will come to predict the occurrence of the US and thus could act to block acquisition by the conditioned stimulus (CS) introduced in the conditioning phase of the experiment.

The US-preexposure effect has also been demonstrated with appetitive conditioning procedures, chiefly in experiments using autoamphifying procedures with rats and pigeons as the subjects (e.g., Balsam & Schwartz, 1981; Costa & Boakes, 2009; Engberg, Welker, Thomas, & Hansen, 1972; Timberlake, 1986; Tomie, 1976a, 1976b; Tomie, Murphy, Fath, & Jackson, 1980; Van Hest, Van Haaren, & Van De Poll, 1989). As for the aversive case, blocking by contextual cues has been invoked as an explanation for the appetitive version of the effect (see Tomie, 1976a, 1976b); and although it may seem implausible that the habituation might reduce the reinforcing power of food for a hungry animal, this possibility cannot be ruled out. It is well established for our own species that preference for a given food declines when that food has been experienced repeatedly.
(e.g., Hetherington, Pirie, & Nabb, 2002; Meiselman, de Graaf, & Lesher, 2000). It seems possible then (although this has not been tested directly) that the reinforcing power of such a food would also suffer a decline.

Discussion of the role of these processes in producing the US-preexposure effect in appetitive conditioning may be premature, however, given that the autoshaping results are open to a simpler and more parsimonious explanation. As has been pointed out a number of times (e.g., Costa & Boakes, 2009; Van Hest et al., 1989), the preexposure procedure used in these experiments can establish persistent food-tray directed behavior which, when carried over to the autoshaping phase, could interfere with the acquisition and performance of signal-directed responding. The effect seen in these experiments could thus be a consequence of response competition at a peripheral level. Our first aim, therefore, in the work to be reported here, was to provide a demonstration of an appetitive US-preexposure effect that was not susceptible to explanation in terms of response competition. We then went on to explore the role of habitation and of blocking by context in generating the effect obtained.

In the experiments to be reported in this article, we made use of a flavor conditioning procedure in which consumption of a previously neutral flavor is enhanced by prior experience of that flavor presented in compound with a sucrose solution. The effect seems to have two sources (see e.g., Fedorchak, 1997). One reflects a shift in the palatability of the neutral flavor, perhaps as a consequence of the formation of a flavor-flavor association; the second depends on the formation of an association between the target flavor and the nutritional consequences of consuming sucrose (a flavor-calories association). The effect of the latter form of learning is most clearly seen when the animals are hungry during the test (Fedorchak & Bolles, 1987; but see also Harris, Gorissen, Bailey, & Westbrook, 2000), and this procedure was adopted in the present experiments. If either (or both) of these forms of learning is susceptible to the US-preexposure effect, prior exposure to sucrose should restrict the development of a conditioned enhancement of consumption.

The advantage of using this form of conditioning is that it is possible to give prior exposure to the US simply by giving sucrose in the animal’s drinking water before the start of conditioning, a procedure that precludes the formation of any obvious potentially competing response. A further advantage is that the rat’s initial reaction to a strong sucrose solution is to show (slight) neophobia; monitoring consumption thus allows the possibility of assessing the degree to which this aspect of the response to the US shows habitation. And finally, contextual cues can be manipulated in this procedure by changing the cage in which the experimental fluids are presented.

An example of the US-preexposure effect in flavor-preference conditioning has been provided by Harris et al. (2000, e.g., Experiment 4); in the present Experiment 1 we sought to demonstrate the effect with our own training procedures. These differed from those used by Harris et al. chiefly in that we used a stronger concentration of sucrose (to allow the possibility of assessing habitation of neophobia during preexposure) and in our use of a single-bottle procedure in the test phase. (Harris et al. used a flavor-preference test involving a choice between the conditioned flavor and another: in our, flavor-acceptance, procedure, we measured absolute consumption.) In Experiment 2 we explored the role of context by comparing the size of the effect obtained when the experimental context was novel at the start of training or was very familiar. In Experiment 3, we directly manipulated contextual cues by switching contexts between the two stages of training. In all experiments we monitored the change in the neophobic UR evoked by the sucrose solution.

**Experiment 1**

The design of this experiment is summarised in Table 1. Two groups of rats received flavor-preference conditioning in which the novel flavor of mint (the CS) was paired with a sucrose solution (the US). This was followed by a test (referred to as the CR test in the table) in which the mint was presented alone. Rats in the preexposed group experienced presentations of the sucrose solution on eight occasions before the start of conditioning; those in the control group were given equivalent

<table>
<thead>
<tr>
<th>Group</th>
<th>Preexposure</th>
<th>UR Test</th>
<th>Conditioning</th>
<th>CR Test</th>
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<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
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<tr>
<td>Preexposed</td>
<td>8 Sucrose</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
<td>M</td>
</tr>
<tr>
<td>Control</td>
<td>8 Water</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
<td>M</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
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</tr>
<tr>
<td>Pre Home</td>
<td>8 Sucrose</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
<td>M</td>
</tr>
<tr>
<td>Pre Context</td>
<td>8 Sucrose</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
<td>M</td>
</tr>
<tr>
<td>Cont Home</td>
<td>8 Water</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
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<tr>
<td>Cont Context</td>
<td>8 Water</td>
<td>Sucrose</td>
<td>4 M + Sucrose</td>
<td>M</td>
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<tr>
<td><strong>Experiment 3</strong></td>
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<tr>
<td>Pre Same</td>
<td>8 Sucrose (A)</td>
<td>Sucrose (B)</td>
<td>4 M + Sucrose (A)</td>
<td>M</td>
</tr>
<tr>
<td>Pre Different</td>
<td>8 Sucrose (A)</td>
<td>Sucrose (B)</td>
<td>4 M + Sucrose (B)</td>
<td>M</td>
</tr>
<tr>
<td>Cont Same</td>
<td>8 Water (A)</td>
<td>Sucrose (B)</td>
<td>4 M + Sucrose (A)</td>
<td>M</td>
</tr>
<tr>
<td>Cont Different</td>
<td>8 Water (A)</td>
<td>Sucrose (B)</td>
<td>4 M + Sucrose (B)</td>
<td>M</td>
</tr>
</tbody>
</table>

Note. Sucrose refers to a 20% sucrose solution; M refers to a 2% mint solution; Pre: preexposed; Cont: non-preexposed control. Both groups in Experiment 1 and the context groups of Experiment 2 experienced experimental treatments in a novel context. A and B (Experiment 3) refer to different experimental contexts.
access to water. Lesser consumption of mint on the CR test in the preexposed than in the control group would indicate the occurrence of the US-preexposure effect. Following the procedure used by Harris et al. (2000), experimental treatments were given in a novel and distinctive context (which might be expected to maximise the likelihood that effects depending on context conditioning would be obtained). In order to assess the extent to which preexposure reduced the neophobic response to sucrose, all subjects were given a single trial prior to conditioning (referred to as the UR test in the table) on which consumption of sucrose was measured.

Method

Subjects and apparatus

The subjects were 16, experimentally naïve, male hooded Lister rats, obtained from Charles River Laboratories (mean weight of 345 g). They were housed individually in home cages measuring 35 cm × 22 cm × 19 cm and made of translucent white plastic with wood shavings as bedding. The rats were maintained on a 12-h light/12-h dark cycle (lights on at 8.00 a.m.).

Experimental procedures were conducted in a distinctive experimental context. This context was a room located in a separate part of the laboratory, dimly lit by a 30-W red lamp; a background of continuous white noise (70 db) was provided by a speaker close to a rack of cages measuring 33 cm × 20 cm × 19 cm. They differed from the home cages in that the walls were made of clear plastic and the floor was covered in commercially obtained cat litter. The unconditioned stimulus (US) was a 20% (w/v) sucrose solution, and the conditioned stimulus (CS) was a 2% (v/v) mint solution (peppermint flavoring supplied by Supercrock; Leeds, UK). The compound of sucrose and mint presented during conditioning was made up so as to preserve these concentrations. All the solutions were made with tap water and given to the animals in 50-ml graduated tubes fitted with rubber stoppers and stainless steel ball-bearing tipped spouts. Fluid intake was measured by weighing tubes before and after sessions.

Procedure

The rats were assigned to two equal-sized groups at the beginning of the experiment. To initiate a schedule of water deprivation, the standard water bottles were removed overnight; over the next 2 days, access to water was restricted to two 30-min sessions per day (starting at 10:30 a.m. and 4:30 p.m.). Water continued to be made available in the home cage during the afternoon drinking session throughout the experiment. The next 8 days constituted the preexposure phase. All rats were transferred to the experimental context for the morning session where they were given access for 30 min to 15 ml of the sucrose solution (the preexposed group) or 15 ml of water (the control group). On the next day, all animals received access to 30 ml of sucrose for 30 min (the UR test). The next 4 days constituted the conditioning phase, in which all subjects were given 10 ml of the mint-sucrose compound in each morning session. After the last conditioning session, the rats were deprived of food; on the next day, they received access to water for 30 min in the home cage in both morning and afternoon drinking sessions, and also had access to 10 g of food during the afternoon session. On the morning of the following day, the rats were given access to the mint solution for 30-min in the training context (the CR test).

The conditioning parameters used here were chosen on the basis of a pilot experiment in which eight rats received conditioning trials as described above, and a further eight received unpaired presentations of mint and sucrose. (Mint was presented in the morning sessions and sucrose in the afternoon sessions.) On the test, those in the paired condition drank 5.06 ml of the mint solution, and those in the unpaired group drank 2.81 ml, $F(1, 14) = 5.59$, thus demonstrating the efficacy of this procedure in producing conditioning.

Results and discussion

Consumption of fluid during the preexposure phase (of sucrose for the preexposed group; of water for the control group) is shown in Fig. 1. The amount consumed increased gradually over trials in both groups, perhaps as a consequence of habituation of an exploratory response to the context (a response that could interfere with drinking). In addition, consumption was particularly suppressed on Trial 1 in the group given sucrose, indicating a neophobic response to this substance. An analysis of variance (ANOVA) was conducted on the data summarized in the figure, with group and trial as the variables. There was a significant main effect of trial, $F(7, 98) = 19.77$, but not of group ($F < 1$). The interaction between the variables was significant, $F(7, 98) = 2.72$. Analysis of this interaction showed the difference between groups to be significant only on Trial 1, $F(1, 14) = 8.30$; the next biggest difference, on Trial 3, yielded $F(1, 14) = 2.34$ ($p = .15$). A difference between the groups was also observed on the UR test, the results of which are summarized in Table 2; this difference fell short of statistical significance, however, $F(1, 14) = 1.74$. The groups differed in their consumption of the mint-sucrose compound when it was first presented. On the first conditioning trial, rats in the control group drank only 5.17 ml of the compound; thereafter, they drank all that was available. Preexposed rats drank all that was available on all the trials. The difference between the groups on the first trial was statistically reliable, $F(1, 14) = 17.94$. The source of this effect is not clear – possibly a neophobic reaction to mint interacted with a similar response to the, still novel sucrose, to produce particularly marked suppression of drinking in the control group.

The critical results for the final CR test with mint are shown in Table 2. In spite of the fact that the control subjects consumed somewhat less of the mint-sucrose compound during conditioning, these subjects drank more of the mint solution on test.
than did the preexposed subjects, $F(1, 14) = 30.65$. That is, conditioning proceeded less readily in subjects given preexposure to sucrose, a demonstration of the US-preexposure effect, confirming that previously reported by Harris et al. (2000).

The experiments that follow investigate possible sources of this effect. There is evidence from this experiment that the initial response to sucrose habituates with repeated presentation, and it is possible (but by no means necessary) that the reinforcing power of this substance changes along with the observed UR. Harris et al. (2000) offered blocking by contextual cues as the explanation, and this seems a real possibility, given that the use of a novel context for the preexposure phase will presumably increase the likelihood that contextual cues will form an association with events that occur in their presence. This issue is taken up in the next experiment.

**Experiment 2**

The aim of this experiment was to confirm the reliability of the US-preexposure effect obtained in Experiment 1 and to begin an analysis of the possible role of contextual cues. There were four groups of subjects (see Table 1). The two preexposed-context and control-context groups matched the groups of Experiment 1. The other two groups, preexposed-home and control-home, were treated identically except that they remained in their home cages throughout the experiment, and all experimental treatments were given there. Given the well-established latent inhibition effect, we assume that the contextual cues of the very familiar home environment will be less likely to form associations with events that occur in their presence than will the cues provided by a novel context. If the US-preexposure effect depends on blocking by context, the effect should be attenuated or abolished in the groups trained in the home cage.

**Method**

The subjects were 32 experimentally naïve male Wistar rats (from Harlan Laboratories, Italy), with a mean weight of 299 g at the start of the experiment. They were housed and maintained under the same conditions as those described for Experiment 1, with the following exceptions. The home cages measured 50 cm × 56 cm × 14.5 cm and were made of trans-

<table>
<thead>
<tr>
<th>Group</th>
<th>UR Test</th>
<th>CR Test</th>
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<tbody>
<tr>
<td>Experiment 1 Preexposed</td>
<td>15.47 (1.05)</td>
<td>1.76 (0.19)</td>
</tr>
<tr>
<td>Control</td>
<td>13.33 (1.23)</td>
<td>4.35 (0.42)</td>
</tr>
<tr>
<td>Experiment 2 Pre Home</td>
<td>16.62 (1.92)</td>
<td>3.51 (0.90)</td>
</tr>
<tr>
<td>Pre Context</td>
<td>16.22 (0.78)</td>
<td>5.42 (0.74)</td>
</tr>
<tr>
<td>Cont Home</td>
<td>10.76 (0.70)</td>
<td>6.71 (0.94)</td>
</tr>
<tr>
<td>Cont Context</td>
<td>9.17 (0.59)</td>
<td>6.43 (1.07)</td>
</tr>
<tr>
<td>Experiment 3 Pre Same</td>
<td>16.54 (1.65)</td>
<td>3.46 (0.46)</td>
</tr>
<tr>
<td>Pre Different</td>
<td>3.89 (0.37)</td>
<td>4.67 (0.42)</td>
</tr>
<tr>
<td>Cont Same</td>
<td>10.87 (1.05)</td>
<td>5.22 (0.45)</td>
</tr>
<tr>
<td>Cont Different</td>
<td>5.22 (0.45)</td>
<td></td>
</tr>
</tbody>
</table>

*Note: Scores given are group means (with SEMs in parentheses) for consumption of sucrose on the UR test and of mint on the CR test. Pre: preexposed; Cont: non-preexposed control.*
parent plastic. The cages used in the experimental context measured 32 cm × 21 cm × 12 cm and were made of translucent plastic. The rats were assigned to one of four equal-sized groups. The treatment given to the preexposed-context and control-context groups exactly matched that given to the preexposed and control groups of Experiment 1. The preexposed-home and control-home groups differed only in that they remained in their home cages throughout the experiment.

Results and discussion

As in Experiment 1, rats given preexposure to sucrose drank less on the initial trials of preexposure than on later trials (see Fig. 2); consumption of water in the control subjects remained fairly constant so that by the end of the phase, the rats given sucrose were drinking more than those given water. There was no difference between animals that remained in the home cage and those that were transferred to the experimental context. An ANOVA with preexposure condition, context, and trial as the variables yielded significant main effects of trial, $F(1, 28) = 15.67$, and of preexposure condition, $F(1, 28) = 10.91$, and a significant interaction between these variables, $F(1, 28) = 8.84$ (all other $F$s < 1). Analysis of simple effects showed there to be a difference between Trials 1 and 8 in the preexposed subjects, $F(1, 15) = 22.32$, but not in the control subjects ($F < 1$).

There was a clear effect of preexposure on the UR test (see Table 2), with rats in the preexposed groups drinking more than those in the control groups, who experienced sucrose for the first time on this test. An ANOVA conducted on the data presented in the table, with preexposure condition and home vs. context as the variables, revealed a significant effect of preexposure, $(1, 28) = 32.31$; there was no effect of the type of context and no significant interaction between these variables ($F$s < 1). There were no differences among the groups in the amount of the mint-sucrose compound they consumed during conditioning. Group mean scores per session were 8.52 ml for preexposed-context, 8.22 ml for preexposed-home, 8.23 ml for control-context, and 8.99 ml for the control-home group. An ANOVA with preexposure condition and context condition as the variables revealed no significant effects: for the preexposure variable, $F(1, 28) = 1.38$; other $F$s < 1.

The results of the CR test are shown in Table 2. A US-preexposure effect was evident in that preexposed subjects drank less than control subjects. This was true both for the groups trained in the context and those trained in the home cage. There was no sign that the size of the effect was reduced in the home cage groups (in fact, the effect was numerically larger in the latter groups). An ANOVA showed there to be a significant effect of the preexposure variable, $F(1, 28) = 5.21$; there was no significant effect of the home cage vs. context variable ($F < 1$), and no significant interaction between these variables, $F(1, 28) = 1.41$.

These results confirm the reliability of the effects demonstrated in Experiment 1. The results of the UR test were consistent with the proposal that exposure to sucrose results in habituation of neophobia; the CR test produces a clear US-preexposure effect. They lend no support, however, to the hypothesis that the US-preexposure effect depends on blocking by contextual cues, given that the effect was observed as readily when these cues were familiar as when they were novel. But this result cannot be taken as decisive evidence against the context-blocking interpretation of the effect – the notion that latent inhibition will restrict acquisition of associative strength by home-cage cues, however plausible, is no more than an assumption for which there is no direct evidence. In Experiment 3, therefore, we adopted a different procedure for assessing the role of context.

Experiment 3

Evidence that blocking by context plays a role in generating the US-preexposure effect obtained in the CER procedure has come from experiments in which exposure to the shock is given in one context and conditioning is given in a different context. In these circumstances, the effect is attenuated (Randich & Ross, 1984). We adopted this strategy in the present experiment. We made use of two experimental contexts, both different from the home cage. All subjects experienced sessions in both contexts during the preexposure phase, but, for the preexposed groups, sucrose was presented in just one of them.
Rats in the preexposed-same group then received conditioning trials in the context in which the sucrose had previously been presented; rats in the preexposed different group received conditioning in the other context. If the US-preexposure effect depends on blocking by contextual cues, we might expect the effect to be attenuated in the latter group.

The contexts used were the same as those described by Symonds and Hall (1997, Experiment 2) in a study of context-aversion conditioning in which rats received a lithium injection in one context but not in the other. This experiment showed that an aversion was established just to the context associated with injection, demonstrating that the rats could discriminate between these contexts, that the contextual cues are capable of supporting conditioning, and that the CR established to one context does not generalize substantially to the other. In the experiment by Symonds and Hall, the strength of the context aversion was assessed by means of a blocking test, acquisition of a nausea-based aversion to a novel flavor being blocked when conditioning was given in the context in which the US had previously been presented. Their result thus constitutes, for the aversive case, a demonstration of the US-preexposure effect, and provides evidence that blocking by contextual cues is (at least in part) responsible for that effect. The present experiment allows a parallel investigation of the appetitive case.

Method

The subjects were 32 male hooded Lister rats (from Charles River Laboratories) with a mean-feeding weight of 457 g (380–500 g) at the start of the experiment. They were assigned to one of four equal-sized groups (see Table 1). Two sets of cages, both distinct from the home cage, served as the experimental contexts. One set consisted of the small dark cages used as the experimental context in Experiment 1. Those in the second set were larger, measuring 42 cm × 35 cm × 16 cm, and were located in a fully lit colony room situated in a separate part of the laboratory. The walls and floor of the cage were made of translucent white plastic, and the wire mesh roof included a section through which a drinking spout could be inserted. There was no bedding in this cage.

Throughout the experiment, all subjects received two 30-min sessions per day, one in each context. For half the rats in each group, the small dark cage was experienced in the morning session during preexposure and the large bright cage in the afternoon session; for the remainder, the arrangement was reversed. Rats in the preexposed groups received access to 15 ml of the sucrose solution in the morning sessions of each of the 8 days of the preexposure phase; in the afternoon sessions, 15 ml of water was made available. Control subjects received equivalent treatment except that water was presented in both sessions. The UR test was conducted on the day following the end of the preexposure phase. On this session, all animals received access in the morning session to 30 ml of sucrose for 30 min in the context that they had previously experienced in the afternoon sessions; this allowed the response to sucrose to be assessed for all subjects in a context in which it had not previously been experienced. Water was given in the other context in the afternoon session.

Over the next 4 days (the conditioning phase), all animals received the mint-sucrose compound in the morning session with water being presented in the afternoon session. This was followed by a test trial on which mint was presented in the morning session. For rats in the preexposed-same and control-same groups, the contexts were arranged as during preexposure. For rats in the preexposed-different and control-different groups, the context experienced in the afternoon session was now presented in the morning session, and vice versa. In details not specified here, the procedure followed that described for Experiment 1.

Results and discussion

Group mean scores for the amount of fluid consumed during the preexposure phase are presented in Fig. 3, which collapses the same and different groups in each preexposure condition (these groups receiving identical experience in this phase of training). Consumption increased over trials in both groups, but much more markedly in the subjects preexposed to sucrose than in the control subjects. Initial neophobia meant that the former drank rather less than the latter group on the first trial;
thereafter the rats given sucrose drank more than those given water. An ANOVA conducted on the data summarized in the figure showed a significant effect of preexposure condition, $F(1, 28) = 35.77$, a significant effect of trial, $F(7, 196) = 21.59$, and a significant interaction between these variables, $F(7, 196) = 11.47$. Analysis of simple effects showed that the groups differed on each trial; for the smallest difference (on Trial 7), $F(1, 28) = 7.83$.

The results of the UR test are presented in Table 2. As in previous experiments, there was evidence of neophobia in the control subjects who drank less on this test than did the preexposed subjects. An ANOVA with preexposure condition and context condition as the variables revealed a significant effect of preexposure, $F(1, 28) = 17.54$. The different context groups drank somewhat more on this test than did the same context groups, but the difference was not statistically significant, $F(1, 28) = 3.34$. The interaction between the variables was not significant ($F < 1$). Neophobia was also evident on the first conditioning trial. On this trial, subjects in the control groups drank rather less of the mint-sucrose compound than did subjects in the preexposed groups; thereafter, all drank the full amount made available. The group mean scores for the first trial were 7.35 ml for the preexposed-different group, 8.36 ml for the preexposed–same group, 5.88 ml for the control–different group, and 5.56 ml for the control–same group. An ANOVA, with preexposure condition and context condition as the variables, revealed only a significant effect of preexposure, $F(1, 28) = 8.35$ (other $Fs < 1$).

The results of the final CR test are shown in Table 2. The general level of consumption shown by these, rather large, rats was higher than that seen in the preceding experiments, but the pattern of results was the same, with the preexposed subjects consuming less than the control subjects. This US-preexposure effect was not influenced by the change of context. An ANOVA with preexposure condition and context condition as the variables showed a significant effect of preexposure, $F(1, 28) = 8.68$, but no significant effect of context, $F(1, 28) = 1.31$, and no significant interaction ($F < 1$). We conclude that, in this preparation, the US-preexposure effect is quite immune to a change in context between preexposure and conditioning.

**General discussion**

Presenting a neutral flavor in compound with a sucrose solution will establish a preference for that flavor and will enhance consumption of the flavor on a conditioned acceptance test. In all three of the experiments described here, it was found that prior experience of sucrose reduced the magnitude of this effect. This constitutes a demonstration of the US-preexposure effect in an appetitive conditioning paradigm. Unlike previous appetitive experiments that have used an autoshaping procedure, this effect is not readily susceptible to an explanation in terms of the interfering effects of competing responses established during preexposure. It provides, rather, a parallel to instances of the effect that have been obtained in aversive procedures (such as CER). In seeking an explanation, therefore, it seems sensible to examine the applicability of the mechanisms that have been proposed for the aversive case, specifically of blocking by context, and of habituation.

As we have already noted, the CER version of the US-preexposure effect can be attenuated by a change of context between preexposure and conditioning. This observation has been taken to indicate that the effect depends (at least in part) on blocking by context — that the contextual cues come to signal the US during preexposure and thus block conditioning to the CS introduced in the conditioning phase. This was the explanation favored by Harris et al. (2000) for their demonstration of the appetitive US-preexposure effect. The experiments reported here provide no support, however, for the view that blocking by context plays any significant role in this version of the US-preexposure effect. The effect was readily obtained when procedures were carried out in the home cage, that is, in a context unlikely to form a strong association with the US during preexposure; and a change from one context to another between preexposure and conditioning had no influence on the size of the effect.

If we define habituation empirically, as a decline in the magnitude of the UR as a result of repeated presentation of the US, then our experiments produced evidence of the phenomenon, with consumption of the sucrose solution being less on early trials than on later ones. It is not obvious, however, why a substance that appears to become increasingly acceptable with experience, should then function less well as a reinforcer. This observation prompts consideration of a quite different interpretation of the results reported here. It is well established that a consummatory response can show successive negative contrast — specifically consumption of a weak sucrose solution is much reduced in rats that have had previous experience of a strong solution (see Flaherty, 1996, for a review). If rats given preexposure to sucrose come to perceive it increasingly positively (a possible interpretation of their increasing consumption over the course of preexposure) then its omission on the test trial might evoke a particularly large contrast effect. The difference between the preexposed and control subjects would then be a consequence of their differing reactions on the test trial, rather than an example of the US-preexposure effect as it is usually understood. Although admittedly speculative, there is little in our data to argue against such an account. It may be noted, however, that the increase in consumption during preexposure occurs over just the first few trials, in which case the four conditioning trials given to the control subjects might be expected to generate the same change in palatability in these animals.

An alternative possibility (equally speculative) is that the apparent increase in palatability seen during preexposure, is accompanied by a decline in the effective salience of the stimulus. How this would influence subsequent conditioning depends on the source of the conditioned response. One interpretation of the enhanced consumption of the CS flavor is that it reflects an increase in the palatability of that flavor that is a consequence either of the formation of a direct flavor–flavor association (i.e., an association between the CS flavor and the taste of sucrose) or of the formation of a configurational representation of the two (Pearce, 2002). A reduction in the effective salience of the sucrose would make this stimulus less capable of entering into the relevant associations, and in the absence of such learning, the palatability of the sucrose would
be unable to influence the response to the CS. A second interpretation of the nature of the CR is that consumption on test is enhanced because the flavor of the CS becomes established as a cue that signals the nutritional properties of the sucrose solution. In this case a reduction in the effective salience of the sensory properties of the sucrose might seem to be irrelevant. It should be acknowledged, however, that the link between the CS and the motivational properties of the US may not be direct but may be mediated by a chain of associations (flavor of CS – sensory properties of US – motivational properties of US). If so, a reduction in the salience of the central link of the chain might again be expected to result in a reduction of the magnitude of the CR that is observed.

This latter interpretation suggests a further possible account of the appetitive US-preexposure based, not on habituation, but on a revised version of the blocking hypothesis. If experience of sucrose allows the formation of an association between its flavor and its nutritional consequences, then our preexposure procedure should ensure that this association is well established in the preexposed subjects prior to the conditioning phase. The presence of this association might be expected to block the formation of a direct association between the flavor of the CS and the consequences of ingesting sucrose. If the CR to the CS on test is a reflection of the strength of this direct association, then it is to be expected that prior exposure to sucrose will attenuate the CR.

Our present results do not allow a choice among these possibilities. They do, however, serve to demonstrate the reality of the appetitive US-preexposure effect, demonstrate the inadequacy of the context-blocking interpretation in this case, and lend some support to an account that assumes that preexposure to a US results in a reduction in its effective salience (and thus in its effectiveness as a reinforcer). If this latter possibility is accepted, there is no reason why it should be applied just to appetitive examples of the US-preexposure effect. Admittedly, the evidence that the effect obtained in flavor-aversion learning depends on blocking by contextual cues is strong (De Brugada et al., 2004) and there is little sign of habituation when nausea is used as the US (but see De Brugada, González, & Hall, 2005); but things may be different for the CER procedure. Blocking by contextual cues may play some role in this procedure, but there is evidence that an effect can be found even when contextual blocking appears to be ineffective (e.g., Baker, Mercier, Gabel, & Baker, 1981). Given the evidence that repeated exposure to a shock can reduce the ability of the shock to evoke its UR (e.g., Hall & Rodriguez, 2010), the proposal that habituation-induced reduction in the effective salience of the US contributes to the US-preexposure effect in CER seems viable.

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References


