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Potentiation of Latent Inhibition

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Rats were given exposure either to an odor (almond) or a compound of odor plus taste (almond plus saline), prior to training in which the odor served as the conditioned stimulus. It was found, for both appetitive and aversive procedures, that conditioning was retarded by preexposure (a latent inhibition effect), and the extent of the retardation was greater in rats preexposed to the compound (i.e., latent inhibition to the odor was potentiated by the presence of the taste). In contrast, the presence of the taste during conditioning itself overshadowed learning about the odor. We argue that the presence of the salient taste in compound with the odor enhances the rate of associative learning, producing a rapid loss in the associability of the odor. This loss of associability will generate both overshadowing and the potentiation of latent inhibition that is observed after preexposure to the compound.

Keywords: rat, latent inhibition, potentiation, overshadowing, associability, aversion conditioning

According to the model for conditioning proposed by Pearce and Hall (1980), the associability (or conditionability) of a stimulus can be modified by experience. Specifically, it was suggested that the associability of a conditioned stimulus (CS) will decline as the consequence of that event (i.e., the occurrence of the unconditioned stimulus, US) comes to be predicted. In the formalization used by the model, associability is equated with a CS-specific learning rate parameter, α, which varies between zero and one. The associability of a novel stimulus is assumed to be high (its value being determined, perhaps, by the physical intensity of the stimulus). Once conditioning begins, the value of α is determined by the size of the discrepancy between growing associative strength (V) and the asymptote (λ) for conditioning set by the magnitude of the unconditioned stimulus (US; i.e., by $\lambda - V$). When compound stimuli are used in conditioning the summed associative strength of all of them enters into this expression.

One source of evidence for this account came from the observation that further conditioning was retarded when a CS had previously been trained to asymptote with a given US (e.g., Hall & Pearce, 1979). This effect was referred to as latent inhibition during CS–US pairings, the implication being that the effect produced by exposure to the CS alone (i.e., latent inhibition proper) was a consequence of an equivalent decline in α. However, although the formal model predicts such a decline (with λ at zero, α becomes set to zero) it does not predict the gradual, incremental nature of the effect—in its basic form the model predicts that α will go to zero after a single trial. A modification of the model (Pearce, Kaye, & Hall, 1982) was put forward in an attempt to deal with this issue, but this modification was somewhat ad hoc and did not succeed in capturing the proposed parallel between the loss of associability suffered by a CS during conditioning and that suffered by a stimulus during preexposure in the latent inhibition procedure.

This matter was addressed by Hall (1991) who argued that a true parallel required that the latent inhibition procedure be conceptualized as involving a learning process in which, over the course of preexposure, the organism learns about the consequences of the stimulus. As with orthodox conditioning, the decline in α would be a consequence of this learning. Hall described this learning as involving the formation of a stimulus-no event association. Possible ways in which this notion might be formalized within the context of the Pearce–Hall (Pearce & Hall, 1980) model of conditioning will be taken up in the General Discussion section; but even this informal version allows us to make certain interesting predictions. We focus here on the implications for the case in which preexposure is given to a compound stimulus.

The Pearce–Hall model predicts that conditioning with a compound stimulus will produce overshadowing for the following reason. Each element of the compound will acquire associative strength on each reinforced trial with the result that their summed associative strength will approach λ rapidly. At this point the outcome of the trial will be fully predicted, and the α value of each element will fall to zero. Further increases in associative strength will not then be possible, and the associative strength of each element will be less than what would be achieved if the element had been trained on its own. The same principle will apply to nonreinforced preexposure. In this case the outcome of the trial (the occurrence of no event) will come to be predicted more rapidly when the target stimulus is compounded with another (especially if that other is high in salience) and the α value of each will fall to zero after fewer trials than would be required if the stimulus was presented on its own. To the extent that the latent inhibition effect is determined by the α value of the CS, we may predict that the effect will be enhanced by preexposure in which the to-be-CS is presented as part of a compound. The mechanism that produces overshadowing of conditioning means that compound preexposure may actually potentiate latent inhibition.

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Experimental tests of this suggestion have been conducted several times before, using a range of conditioning procedures—conditioned suppression with auditory and visual cues (Honey & Hall, 1989; Mercier & Baker, 1985; Rudy, Krauter, & Gaffuri, 1976); appetitive conditioning (food-cup approach), again with auditory and visual cues (Reed, Anderson, & Foster, 1999; Reed & Tsakanikos, 2002); taste-aversion learning (Honey & Hall, 1988). The results of these studies are not, at first sight, encouraging. In many of them the presence of an added cue during preexposure to the target cue had no effect on the latent inhibition subsequently observed; and in some (Honey & Hall, 1988, 1989, Experiment 1; Reed et al., 1999, Experiment 4; Rudy et al., 1976, Experiment 2) the magnitude of the latent inhibition effect was reduced. These results, however, may not be decisive. As the authors of several of these studies pointed out, the stimuli used in them may have been susceptible to generalization decrement effects. Interactions at a peripheral level might mean that the target cue when presented alone on the test would not be perceived as being the same as that presented in the preexposure phase. If so, transfer of latent inhibition from preexposure to conditioning could not be expected, and any advantage produced by compound preexposure would not be able to show itself. This analysis is particular pertinent when the cues are drawn from the same modality (e.g., the two tastes used in the experiment by Honey & Hall, 1988), but it is likely apply in other cases too (e.g., orienting to a light could modify how a tone is perceived or vice versa). It follows that, to test the proposal under consideration here, it is necessary to choose cues that are unlikely to suffer from generalization decrement effects.

To this end, the experiments reported here (which used the flavor-aversion conditioning paradigm) made use, not of two tastes (as in Honey & Hall, 1988), but of an odor as the target cue, compounded (in the critical experimental condition) with a taste during preexposure. It is quite possible, of course, that these two cues might still interact at a sensory or perceptual level and produce a generalization decrement effect that could obscure the effect we are seeking. However the likelihood of such an interaction seems less than for the case in which both cues are tastes; further, to show that the presence of a taste can potentiate the acquisition of latent inhibition by an odor, despite the potential role of generalization decrement, might be thought to provide a particularly convincing demonstration of the effect under investigation.

The use of these cues raises a further issue that must be addressed before turning to the procedure of central interest. The argument presented above, that led to the prediction that the presence of a more salient cue during preexposure would enhance latent inhibition, was based on drawing a parallel between the latent inhibition procedure and the overshadowing effect. The explanation offered for both effects relied on the assumption that the associability of the target stimulus will fall to zero more rapidly when it is trained in compound with another. Procedures that produce overshadowing when cues are conditioned in compound should produce potentiation of latent inhibition when the cues are preexposed in compound. Now it has sometimes been found, for the cues of the sort we intend to use, that the presence of a taste during conditioning can potentiate rather than overshadow acquisition by the odor (e.g., Rusiniak, Hankins, Garcia, & Brett, 1979). Our predictions about latent inhibition would not apply if the stimuli involved were not susceptible to the orthodox overshadowing effect.

We made efforts, therefore, to adopt a procedure likely to produce overshadowing. The precise conditions that determine when overshadowing rather than potentiation will occur are not fully resolved (see LoLordo & Droungas, 1989, for a review); but the work of Bouton, Jones, McPhillips, and Swartzentruber (1986) showed that overshadowing of odor by taste is the normal outcome when the odorant is mixed in with a flavored drink (unless the concentration of the odorant is very low). Accordingly we made use of parameters similar to those used by Bouton et al. and conducted a preliminary experiment to confirm that they did indeed generate the overshadowing effect.

Experiment 1

In this experiment, two groups of rats received flavor aversion conditioning, one group with an odor as the CS, the other with a compound of a taste plus an odor as the CS. The aversion acquired to the odor was then tested. Overshadowing would be demonstrated if the group trained with the compound showed a lesser aversion than that trained with just the odor.

Method

Subjects and apparatus. The subjects were 16 experimentally naive male hooded Lister rats with a mean ad lib weight of 324g at the start of the experiment. The rats were singly housed with continuous access to food in a colony room that was artificially lit from 8:00 a.m. to 8:00 p.m. each day. Access to water was restricted as detailed below.

The solutions used as experimental stimuli were administered in the rats' home cages at room temperature in 50-ml plastic centrifuge tubes, each equipped with a rubber stopper to which was fitted a stainless steel, ball-bearing tipped spout. The following flavored solutions were used: a solution of almond (2% vol/vol; almond flavoring supplied by Supercook, Leeds, U.K.) and a compound of 0.16 molar (M) saline and almond. Consumption was measured by weighing the tubes before and after trials, to the nearest 0.1g. The unconditioned stimulus for the conditioning trials was an intraperitoneal injection of 0.15 M lithium chloride (LiCl) at 10 ml/kg of body weight.

Procedure. A schedule of water deprivation was initiated by removing the standard water bottles overnight. On each of the following 10 days, access to water was restricted to two daily sessions of 30 min, at 11:00 a.m. and 5:00 p.m. (This 10-day period was chosen to match the procedure used in subsequent experiments, in which a 10-day period of preexposure, given under conditions of water deprivation, preceded the conditioning phase of the experiment.) The subjects were then randomly assigned to one of two groups for conditioning, one having the compound of saline and almond as the CS, the other having almond. On the first conditioning trial the rats received access to 10 ml of the flavored solution for 30 min in the morning drinking session, followed by an injection of LiCl. They were given free access to water in the afternoon session. The next day was a recovery day on which the rats had unrestricted access to water for 30 min during both morning and afternoon sessions. The second conditioning trial was given in the morning session of the next day. It was identical to the first except that the animals were given free access to the flavored solution for 30 min prior to the injection. Water was available for

the rats in the afternoon session next to this conditioning trial. The test sessions followed after a further recovery day. In three consecutive morning sessions, the rats were given free access to the almond solution for 30 min. Water was made available for 30 min in the afternoon sessions of these days.

Results and Discussion

On the first conditioning trial, all the subjects drank almost all the fluid presented. Group mean consumption scores were 9.2 ml for the group given the compound and 9.3 ml for the group given the element (almond) alone. Consumption was suppressed in both groups on the second conditioning trial, the scores being 5.1 ml for the compound group and 6.2 ml for the element group. These scores did not differ reliably; a one-way analysis of variance (ANOVA) yielded $F(1, 14) = 1.17$ (here, and throughout, a significance level of $p < .05$ was adopted). Group mean consumption scores for the three test trials are shown in Figure 1. Consumption was suppressed in both groups on the first test trial, but thereafter a difference emerged, with the compound group drinking more (showing less of an aversion) than the group trained with just the odor. An ANOVA showed there to be significant effects of group, $F(1, 14) = 5.22$; of trial, $F(2, 28) = 45.86$; and of the interaction between these two variables, $F(2, 28) = 3.96$. A simple main effects analysis confirmed that the groups did not differ on Trial 1, $F < 1$; but differed reliably on Trial 2, $F(1, 42) = 3.75$; and Trial 3, $F(1, 42) = 10.46$. These results confirm that overshadowing can be obtained with the odor-taste compound used here. They do not speak to the issue of when overshadowing rather than potentiation will occur; nor do they, in themselves, say anything about the process responsible for overshadowing (but see the Discussion of Experiment 2, where this issue will be considered further). They do, however, demonstrate that the particular cues and training procedures used here are suitable for the purposes of the experiments that will be described next.

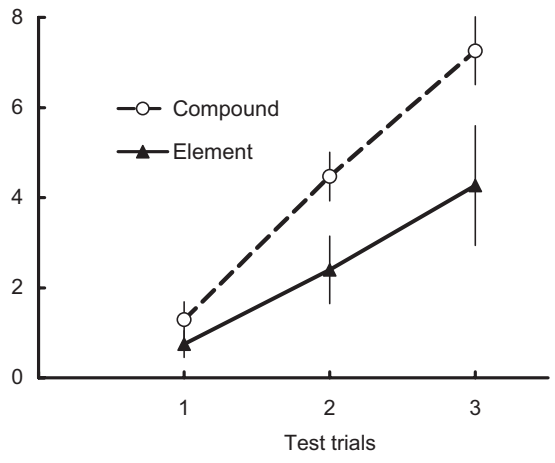

Figure 1. Experiment 1: Mean scores (plus and minus SEMs) for consumption of water with an almond odor. The element group had received aversion conditioning with this odor; the compound group had received conditioning with a compound of almond and saline.

Experiment 2

In this experiment we investigated the effects of preexposure in which the target cue was presented either alone or in compound. There were three groups of rats, all of them given conditioning with the odor (almond) as the CS as described in Experiment 1. The groups differed in the treatment they received prior to conditioning. One received preexposure to the compound of almond and saline, one received preexposure to almond alone, and the third received preexposure to neither of these cues. We can expect acquisition of the aversion to be retarded in the almond-preexposed group in comparison to the nonpreexposed group (i.e., we expect a latent inhibition effect). The question of interest was whether the presence of the taste (saline) during preexposure for the compound group would enhance the size of the latent inhibition effect.

Method

The subjects were 24 male hooded Lister rats with a mean ad lib weight of 348g at the start of the experiment. The rats had previously been used in another experiment in which they had experienced food deprivation, but they were naive to all aspects of the current procedure. Housing and maintenance conditions were as described for Experiment 1.

Water deprivation was initiated by removing the standard water bottles overnight; on each of the following 4 days, access to water was restricted to two daily 30-min sessions at 11:00 a.m. and 5:00 p.m. The subjects were then randomly assigned to one of three equal-sized groups. On the morning session of each of the next 6 days (the preexposure phase), subjects in the compound group received access to 10 ml of the mixture of saline and almond. The element group received access to 10 ml of almond, and the control group access to 10 ml of water on these sessions. All subjects received free access to water in the afternoon sessions of this phase. Three conditioning trials followed in which consumption of the almond solution was followed by an injection of LiCl. After the final postconditioning recovery day, the rats were given a test session that consisted of a 30-min presentation of almond. In details not described here, the procedure followed that of Experiment 1.

Results and Discussion

The rats drank all of the solutions made available to them during the morning sessions of the preexposure phase, and on the first trial of the conditioning phase. The results for the next two conditioning trials and the nonreinforced test trial are shown in Figure 2. It shows that all three groups acquired an aversion, but differed in the ease with which they did so, with the control group learning more readily than the group preexposed just to almond (the element group), which in turn learned more readily that the group preexposed to the compound. An ANOVA with group and trial as the variables was conducted on the data summarized in the figure. There were significant effects of group, $F(2, 2\ 1) = 11.91$; and of trial, $F(2, 42) = 124.67$; and a significant interaction between these variables, $F(4, 42) = 3.24$. An analysis of simple main effects showed there to be differences among the groups on all trials shown in the figure: For the second conditioning trial, $F(2,$

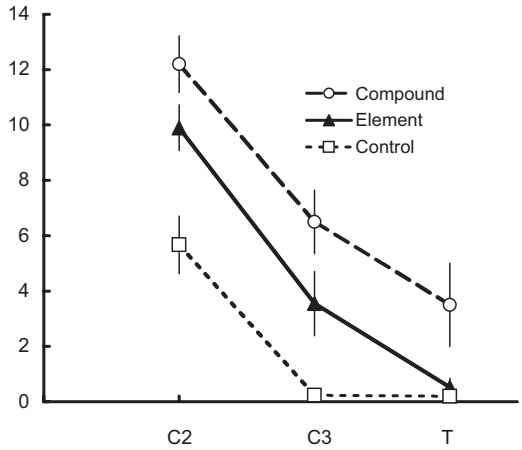

Figure 2. Experiment 2: Mean scores (plus and minus SEMs) for consumption of almond, during aversion conditioning (C2 and C3 are the second and third conditioning trials) and a nonreinforced test (T) trial. The element group had experienced prior exposure to almond; the compound group prior exposure to a compound of almond and saline; the control had received preexposure to neither the odor nor the taste.

63) = 12.71; for the third conditioning trial, $F(2, 63) = 11.27$; for the test trial, $F(2, 63) = 3.69$. Pairwise comparisons using Tukey's test (with $p < .05$) showed that on conditioning Trial 2 the control group differed from the other two groups, which did not differ between themselves; on conditioning Trial 3 the compound and control groups differed from each other, but the element group differed from neither; and on the test trial, the compound group differed from each of the other groups. The data for Trial 3 were examined further, by means of *t* tests, which revealed that each group differed significantly from each of the others.

The effect of preexposure to the CS in the element group of this experiment constitutes an example of the well-established phenomenon of latent inhibition. Our new result comes from the group given preexposure to the CS in compound with another cue. These animals appeared to learn even less readily than the element group; that is, latent inhibition appeared to be enhanced. The experiments that follow explore this potentiation effect, but before turning to them we should say something about the implications of the results presented so far for the analysis of overshadowing.

As we have already said, previous experiments have often found that preexposing the to-be-CS in compound with another cue reduces the size of the latent inhibition effect. We suggested that this outcome was a consequence of generalization decrement. If this argument is accepted, it implies that the cues used in the present experiment were free from generalization decrement effects. Now the phenomenon of overshadowing in conditioning has been of theoretical interest chiefly because it supports the notion of cue competition—the notion, central to several influential theoretical models (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972), that cues conditioned in compound compete for some limited information-processing resource. However the proponents of these theories would acknowledge that the overshadowing effect could just as easily be a consequence of generalization decrement; that responding to the CS tested on its own may be weak simply because the test stimulus is not perceived as being the same as that conditioned in compound. It has proved surprisingly difficult to disconfirm this possibility experimentally (but see Kaye, Gambini, & Mackintosh, 1988) and, indeed, generalization decrement has been adopted as the core explanation for overshadowing by some theorists (e.g., Pearce, 1987). However, the results reported here, in combination with those of Experiment 1, appear to provide such a disconfirmation. The present experiment provides evidence that the cues used are not susceptible to generalization decrement effects; and Experiment 1 shows that the standard overshadowing effect can be obtained with these same cues. This example of the overshadowing effect is readily explained by a range of cue-competition theories; but the potentiation of latent inhibition obtained in this experiment appears to be uniquely predicted by the Pearce–Hall model, and we now return to explicit examination of this potentiation effect.

Experiment 3

The results of Experiment 2 are potentially of substantial significance. Accordingly we thought it important to confirm their reliability (in particular to replicate the critical difference between the element and compound groups, which was significant only by way of an ad hoc *t* tests in that experiment). We also wanted to include further control conditions. In this experiment, therefore, we replicated (with only minor procedural changes) the treatment given to the compound and element groups of Experiment 2. We added two further groups (to be referred to as unpaired groups). These experienced the same preexposure and test procedures as the other two groups, but they did not receive the conditioning trials in which almond was followed by an injection of LiCl; rather the almond and the injection were experienced on separate occasions. We have assumed that the effect seen in Experiment 2, the difference between the element and compound groups in their consumption of almond on test, is a consequence of a difference between them in ease of conditioning. The unpaired groups of the present experiment allow us to confirm that this difference does indeed depend on conditioning.

Method

The subjects were 32 male hooded Lister rats with a mean ad lib weight of 354g at the start of the experiment. They were naive to all aspects of the current procedure. After water deprivation had been established, they were assigned at random to one of four equal-sized groups. For rats in the compound-paired and element-paired groups, the procedure was the same as that described for the compound and element groups of Experiment 2, except that in this experiment only two conditioning trials were given prior to the test trial. The compound-unpaired and element-unpaired groups differed from the paired groups in the treatment given during the conditioning phase. On the day in which the paired groups received their first conditioning trials, the unpaired groups were given access to 10 ml of almond in the morning session and an injection of LiCl in the afternoon session. On the next conditioning day, the unpaired groups were given access to water for 30 min followed by an injection of LiCl in the morning session, and a 30-min presentation of almond in the afternoon. Exposure to almond and to LiCl was thus matched in the paired and unpaired groups. After the recovery day that followed the last injection, all

subjects received a nonreinforced test trial with almond. On the day following the almond test, all subjects were given a test with saline, receiving free access to this solution for 30 min in the morning session. This test was included to allow an assessment of the strength of any within-compound, saline-almond, association that may have been formed during preexposure (see Discussion). Details not specified here the procedure were the same as those described for Experiment 1.

Results and Discussion

Figure 3 shows group mean scores for consumption of the almond solution on the two conditioning trials and the test trial. On the first conditioning trial, all subjects drank almost all of the 10 ml made available. The effect of this trial was to produce an evident suppression of consumption in only one of the groups (the element-paired group); in the other groups consumption was maintained, or even increased when free access was given on the second conditioning trial. On the test trial (i.e., after two conditioning trials), suppression of consumption became evident in the compound paired group, but in neither of the unpaired groups. An ANOVA was conducted on the data for the second conditioning and test trials, with preexposure stimulus (element or compound) and conditioning procedure (paired or unpaired) as between-subjects variables. There was a significant main effect of conditioning procedure, $F(1, 28) = 127.15$; and of trial $F(1, 28) = 106.48$; but not of preexposure condition, $F(1, 28) = 2.47$. There was a significant interaction, $F(1, 28) = 46.71$, between trial and conditioning procedure, reflecting the fact that the difference between the paired and unpaired conditions was most marked on the test trial; and a significant interaction between preexposure condition and conditioning procedure, $F(1, 28) = 7.75$. No other interactions reached significance, Fs < 2.

A simple main effects analysis of the interaction between the preexposure and conditioning variables showed that the compound and element groups differed in the paired condition, $F(1, 28) = 28.84$, thus replicating the effect reported in Experiment 2 that conditioning is slower after preexposure to the compound than after exposure to just the CS. There was no difference between the element and compound groups in the unpaired condition, $F(1, 28) = 2.24$. We have interpreted the difference between the groups in the paired condition (and in Experiment 2) in terms of latent inhibition, but a possible alternative account is that the higher level of consumption shown by the compound group is the result of the formation of an association between the elements (almond and saline) during preexposure. Saline, at this concentration, is a preferred taste for rats (they choose it over water) and an association between almond and saline might increase the amount of the former that is consumed. The absence of a difference between the unpaired groups challenges this hypothesis, as the direct effects of the within-compound association should be evident on these groups too. It should be acknowledged that the null result seen in the unpaired condition may not be decisive; it is possible, for instance, that in this condition a ceiling effect on consumption might have obscured a difference between the compound and element groups. Accordingly we addressed the general issue again, using a different experimental design, in Experiment 4.

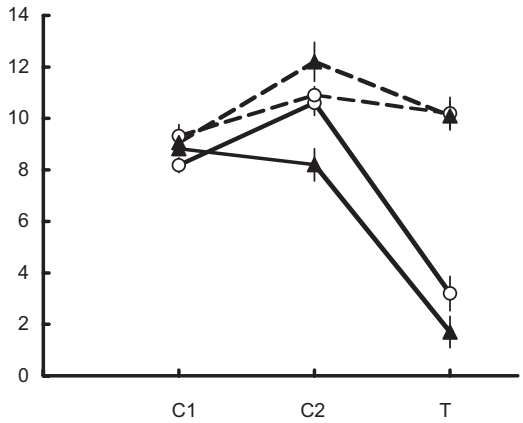

Figure 3. Experiment 3: Mean scores (plus and minus SEMs) for consumption of almond, during conditioning trials (C1 and C2) for the paired groups and a nonreinforced test (T) trial. The element groups had experienced prior exposure to almond; the compound groups prior exposure to a compound of almond and saline. The unpaired groups were given almond on trials C1 and C2, but experienced the event used as the US for the paired groups, on separate occasions.

The results for the test trial with saline are shown in Figure 4. Consumption appeared to be somewhat suppressed in the paired groups, but there was no clear effect of the type of preexposure given. An ANOVA confirmed this impression; there was a significant effect of the conditioning procedure, $F(1, 28) = 5.07$; but not of the preexposure procedure $F < 1$; or for the interaction, $F(1, 28) = 1.49$. That the paired groups drank less than the unpaired groups presumably reflects generalization to saline of the aversion established to almond. That the compound-paired group did not differ from the element-paired group shows that our procedure failed to generate any marked sensory-preconditioning effect—preeexposure to a compound, followed by conditioning to one element and a test with the other element (the training given to the compound paired group), is the essence of the sensory preconditioning procedure. We have no evidence therefore, that preexposure to the compound generated an effective within-compound association. The significance of this observation is that Reed and his collaborators (e.g., Reed, 1995a, 1995b; Reed et al., 1999; Reed & Tsakanikos, 2002) offered an explanation for the effects of compound preexposure that depends on the assumption that such exposure results in the formation of associations between the elements of the compound. No decisive conclusion can be derived from our null result but we note that our failure to find sensory preconditioning is inconsistent with attempt to apply this sort of explanation to the potentiation of latent inhibition effect reported here.

Experiment 4

In this experiment we attempted to establish the generality of the effect demonstrated in our previous experiments, by repeating the essential features of Experiment 2, but making use of an appetitive rather than an aversive conditioning procedure. The taste and odor used as the stimuli were the same as before, but conditioning consisted of pairing the odor with sugar. Although Experiment 3 produced no evidence for the formation of within-compound associations involving the odor and saline, we hoped that the specific

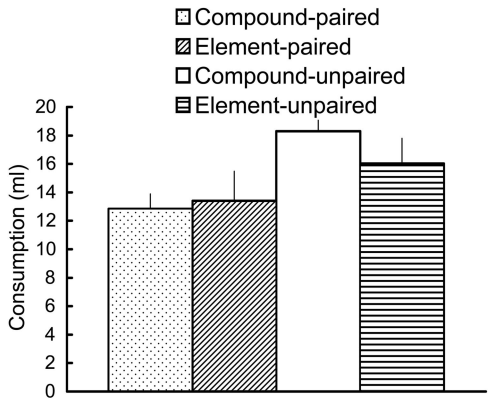

Figure 4. Experiment 4: Mean scores (plus SEMs) for consumption of saline. The element groups had experienced preexposure to almond; the compound groups preexposure to a compound of almond and saline. The paired groups then received aversion conditioning with almond as the CS; the unpaired groups experienced and the event used as the US for the paired groups, on separate occasions.

procedures used in this experiment (specifically the use of a strong, 20%, sucrose solution) would establish an association between the odor and sugar that would become evident as a conditioned preference for the odor. (Balleine, Espinet, & Gonzalez, 2005, whose procedure we adopted, found evidence for preference conditioning with a 20% sucrose solution as the reinforcer.) The question of interest was whether latent inhibition produced by prior experience of the odor could be enhanced by presenting the odor in compound with a taste during the preexposure phase.

Method

The subjects were 24 experimentally naive male hooded Lister rats with a mean ad lib weight of 450g at the start of the experiment. Three flavored solutions were used; two of these (almond, almond + saline) were the same as those used in the previous experiments; the third, used in the conditioning phase was a compound consisting, in the final mixture, of 2% almond and 20% sucrose. The rats were maintained in the same way as was described for Experiment 2. After the water deprivation schedule had been established they were divided into three groups (the compound, element, and control groups, with 8 rats per group) for the preexposure phase. The procedure used in this phase was the same as described for Experiment 2.

The next 3 days constituted the conditioning phase. On the morning session of each of these days, all rats were given access to 10 ml of the almond + sucrose mixture for 30 min. During the afternoon sessions on the first 2 of these days, the rats were given access to water for 30 min. After the third trial the rats were allowed free access to water but food was removed so that they were 23-hr food-deprived when it came to the test on the following morning. The rats were deprived of water 3 hr before the test which consisted of access to the almond solution for 30 min. After this test the rats were given free access to water and 12g of food. A second test identical to the first was given in the next morning session. In details not specified here the procedure was the same as that described for the previous experiments.

Results and Discussion

Group mean scores (consumption of the almond solution) for the two test trials are presented as the upper panel of Figure 5. Consumption declined slightly from Trial 1 to Trial 2, consistent with the extinction of a conditioned preference. To our surprise, there was no evidence of latent inhibition in the element group; these animals drank the almond as readily as the control subjects that had not been given preexposure. It is not clear what parameters would need to be modified to produce this, normally robust, effect in this training procedure. However, the absence of an effect is not a problem for our present purposes—indeed, an enhancement of latent inhibition might be best detected when the standard effect is rather weak. The results for the compound group are consistent with the enhancement hypothesis; these subjects drank less of the almond (showed less sign of a conditioned preference) than the other groups. An ANOVA conducted on the data shown in Figure 5 revealed there to be a significant effect of group, $F(2, 21) = 3.50$; the effect of trial fell short of significance, $F(1, 21) = 2.55$, as did the interaction between these variables, $F < 1$. Pairwise comparison among the groups (t tests) showed that the compound group differed significantly from each of the other two groups, which did not differ one from another.

The result shown at the top of Figure 5 is potentially of substantial theoretical significance; but the numerical difference be-

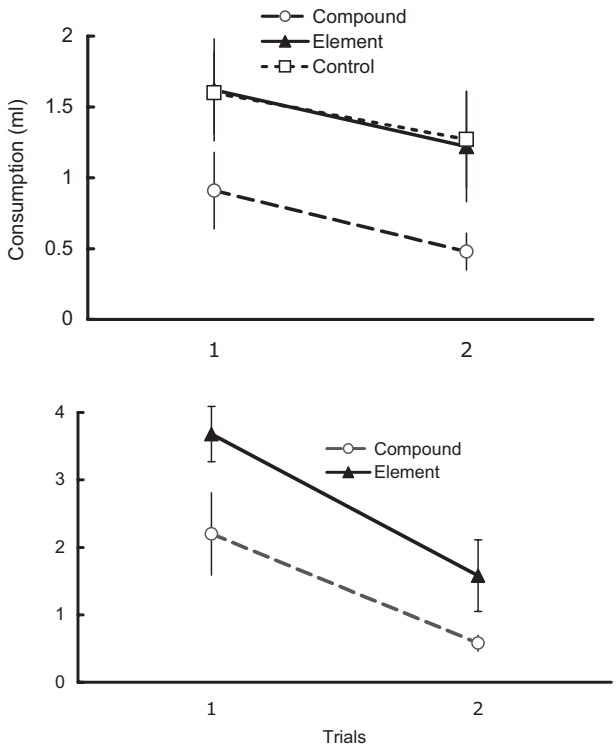

Figure 5. Experiment 5: Mean scores (plus and minus SEMs) for consumption of almond, after conditioning on which almond had been paired with sucrose. Before conditioning, the element group had experienced exposure to almond, and the compound group exposure to a compound of almond and saline; the control (top panel only) had received preexposure to neither the odor nor the taste.

tween the critical groups was small, and the conditioning procedure is, perhaps, less well-established than the aversive procedure used in our other experiments. Accordingly we thought it worthwhile to confirm the reliability of the result. A further 16 rats were given training identical to that described above for the element and compound groups. The results of the test trials are shown in the lower panel of Figure 5. Absolute levels of consumption were a little higher than those of our original experiment, but the pattern of results was the same, with the compound group drinking less than the element group. An ANOVA showed there to be significant effects of group, $F(1, 14) = 13.59$; and of trial, $F(1, 14) = 11.47$. The interaction between these variables was not significant, $F < 1$.

The results shown in Figure 5 parallel those of Experiments 2 and 3 in showing that conditioning proceeded less readily after preexposure in which the CS was presented in compound with another than after preexposure in which the CS was presented alone. In the earlier experiments, with their aversive conditioning procedure, this showed on test as greater consumption of the test solution the compound group. The appetitive procedure used in this experiment meant that the effect showed as a lower level of consumption in the compound group. This difference helps rule out certain possible trivial interpretations of the effect. It cannot be said, for instance, that there is some feature of compound exposure (perhaps to do with habituation of neophobia) that makes rats drink more (or less) of one of the elements when it is presented alone. Both outcomes can be observed and, which is obtained depends on the nature of the conditioning given before the test. These results also confirm that the effect seen Experiments 2 and 3 was not the direct consequence of the formation of a within-compound association during compound preexposure. Such an association, it was suggested might act to boost consumption of the odor on test. It cannot therefore be responsible for the outcome of the present experiment in which the compound group drank less than the element group.

Experiment 5

In this experiment we reverted to the aversive conditioning procedures of Experiments 2 and 3. We modified the preexposure arrangements so that all subjects experienced two odors, one presented on its own, the other in compound with the taste. One group of subjects then received conditioning with the odor that had been presented alone as the CS; a second group received conditioning with the odor experienced previously in compound. Our previous results would be confirmed if the conditioning occurred more slowly in the latter group; the result to be expected if preexposure in compound with a taste potentiates latent inhibition to the odor.

The advantage of this design is that the two groups are fully matched in their preexposure experience—they differ only in which of the preexposed odors is used in the conditioning phase. This allows us to rule out certain possible explanations for the effects previously obtained. For example, it might be pointed out that the preexposure procedure used in Experiments 2 to 4 means that for one group (the compound group) both the odor and the taste undergo latent inhibition, whereas for the other (element group) only the odor does so. It might further be argued that if there is a degree of similarity between the taste and the odor, the latent inhibition suffered by the taste might generalize to the odor in the test phase, resulting in slowed learning in the compound group. (This would be potentiation of latent inhibition of a sort, but it would not involve the associability-change process of chief interest to us.)

Method

The subjects were 16 male hooded Lister rats with a mean ad lib weight of 525g at the start of the experiment. They had previously been used in another experiment but were naive to all aspect of the current procedure. Four flavored solutions were used. Two of these (almond, almond + saline) were the same as those used in previous experiments; in addition a solution of vanilla (2% vol/vol vanilla flavoring from Supercook, Leeds, U.K.) and a compound (of 0.16 M saline and 2% vanilla) were used. After the water deprivation schedule had been established, the rats received 12 days of preexposure consisting of six presentations of one odor (O1) alternating with six presentations of the other (O2) in compound with saline (i.e., of O2 + saline). Half the rats received 10 ml of O1 on odd-numbered days and 10 ml of O2 + saline on even days; the rest received the solutions in the opposite order. O1 and O2 were counterbalanced, with half the rats receiving almond as O1 and vanilla as O2, and half the reverse arrangement.

The rats were assigned to two equal-sized groups for the conditioning phase. All received two conditioning trials with LiCl as the US and a nonreinforced test trial. The procedure was the same as that described for Experiment 3. For the element group, O1 was used as the CS; for the compound group, O2 was used as the CS. Details not specified here were the same as those described for Experiments 2 and 3.

Results and Discussion

Figure 6 shows the group mean amounts consumed on the conditioning and test trials. As before, the rats consumed almost all

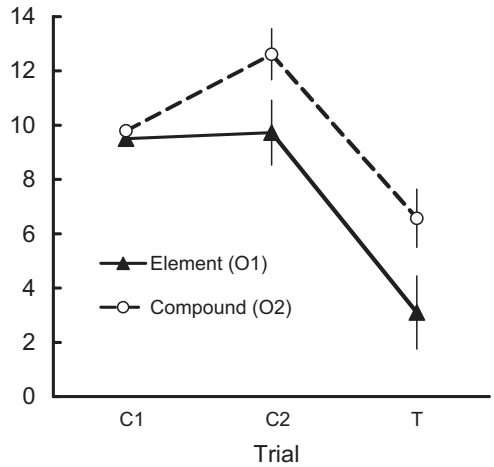

Figure 6. Experiment 6: Mean scores (plus and minus SEMs) for consumption of a solution having an odor, during aversion conditioning trials (C1 and C2) and a nonreinforced test (T) trial. Prior to conditioning all animal had received preexposure to one odor presented alone (O1), and another (O2) presented in compound with saline. For the element group, O1 was the CS; for the compound group, O2 was the CS.

the fluid made available on the first conditioning trial, and the groups did not differ in this, $F(1, 14) = 1.32$. When given free access on Trial 2, the element group drank less than the compound group. Consumption was suppressed in both groups as a result of this second conditioning trial, but the difference between them was maintained on the test trial. An ANOVA with group and trial (second of conditioning and test) as the variables produce significant effects group, $F(1, 14) = 4.99$; and of trial, $F(1, 14) = 81.60$. The interaction was not significant, $F < 1$. In this experiment, therefore, we have successfully replicated the effect seen in Experiments 2 to 4 (slower conditioning after compound than after element preexposure) using a procedure in which the groups were equated in their experience of tastes and odors in preexposure.

General Discussion

The experiments reported here have shown, for the stimuli used here, that the taste will overshadow the odor when conditioning is given with a compound of the two (Experiment 1). The stimuli were especially chosen (on the basis of the analysis offered by Bouton et al., 1986) as being likely to produce overshadowing rather than the potentiation of conditioning of odor by taste that is sometimes seen. According to the account of overshadowing offered by Pearce and Hall (1980), the effect occurs because the associability of both elements of the compound falls to zero as soon as the compound fully predicts it consequences, something that happens rapidly because of the presence of the more salient element (the taste in this case). In the Introduction we discussed the possibility that a process of this sort might operate during nonreinforced preexposure to stimuli (latent inhibition training). If animals are capable of learning, in some way, that a preexposed event has no consequence, they should learn this more quickly when trained with the compound, this being more salient than the element alone. This interpretation implies that the associability of the odor should fall to zero more rapidly when it is preexposed in compound than when preexposed alone; that is, the principle of overshadowing (paradoxically) predicts a potentiation of the latent inhibition effect. Experiments 2, 3, 4, and 5 demonstrated just such an effect.

This account, may seem unduly complex, involving, as it does, both association formation (the association between the cue and the absence of a consequence) and a change in an associability parameter. Because a stimulus-no event association might, in itself, be expected to interfere with subsequent conditioning (and thus produce latent inhibition) an appealing alternative might be to suggest that compound preexposure acts by directly potentiating the formation of the association—after all, the potentiation of conditioning to an odor by a taste has sometimes been observed with standard conditioning procedures. The problem for this analysis is that our Experiment 1 has clearly shown that, with our stimuli, the taste overshadows aversion conditioning to the odor when an orthodox US is presented. Assuming, as we have, that the principles that underlie associative learning about a no-event representation are the same as those that apply to learning about a US, leads to the conclusion that, with our stimuli and preexposure procedures, the stimulus-no event representation is likely to be overshadowed rather than potentiated. The potentiation of latent inhibition that we have observed must be assumed to occur despite, rather than because of, any associative interference effects.

In this context, it is appropriate to consider the implications of a series of experiments by Reed and his collaborators (e.g., Reed, 1995a, 1995b; Reed et al., 1999) that have been taken as supporting an associative interference account of latent inhibition. These experiments have usually involved preexposure consisting of two phases—presentations of A, followed by a phase of presentations of AB (where A and B represent different stimuli). Conditioning with B as the CS was found to be slow in comparison with the performance shown by a group that received A and then B alone in the preexposure phases. Reed's interpretation was that the initial phase of exposure to A allowed the formation of an A–no event association, and that the AB exposure trials allowed the formation not only of a B–no event association but also of a within-compound B–A association. Conditioning with B as the CS would be retarded because the interfering no event representation would be activated not only B itself but by way of the associative chain: B–A–no event. Our present results suggest an alternative interpretation—according to our analysis, prior exposure to A, by establishing the A–no event association, would mean that the AB compound would accurately predict its consequences on the very first presentation so that the associability of B would fall to zero immediately. The latent inhibition shown by B would therefore be expected to be particularly profound. It is also possible, of course, that both these processes operate and that both contribute to the latent inhibition seen under these training conditions,

Having said this, it should be acknowledged that the nature of the learning supposed to go on during nonreinforced preexposure is rather poorly specified by any of the relevant theories. We have referred, glibly, of the formation of a stimulus-no event association but no attempt has been made to formalize this notion or to clarify the (somewhat counterintuitive) concept of a no-event representation on which it depends. An alternative, and perhaps more satisfactory interpretation follows if we take, as a starting point, the assertion that the events used as the preexposed stimuli in the latent inhibition procedure, are probably not truly neutral. Rather, such stimuli are likely to evoke the expectation of some consequence (that is, in associative terms, to have an excitatory association with the representation of some other event). It is possible that this may be an intrinsic property of novel stimuli; but it is not necessary to make this assumption as there is likely to be some degree of generalization from different but related stimuli that the animal will have experienced outside the experimental context (e.g., all our rats have tasted food and experienced its effects).

What follows from this analysis is that the associative learning that will go on during nonreinforced preexposure will be inhibitory in nature (see Killcross & Balleine, 1996, for a slightly different but related approach). The preexisting excitatory association activated by presentation of the stimulus will excite the representation of some further event that does not then follow; standard learning rules (such as those incorporated in the Pearce–Hall model) predict the formation of an inhibitory link strong enough to negate the original excitation. At this point, according to the model, the net associative strength of the cue will be zero; as will its α value (leading to a latent inhibition effect should the cue be used as a CS in subsequent conditioning). Critically, the learning that occurs during nonreinforced preexposure will proceed more rapidly when a salient cue is present, leading to the prediction that latent inhibition will be potentiated by compound preexposure.

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