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Assessments of Changes in the Effective Salience of Stimulus Elements as a Result of Stimulus Preexposure

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Rats received exposure to 3 flavor compounds, AX and BX, presented in alternation, and CX, presented on a separate block of trials. The hypothesis that this treatment would leave B effectively more salient than C was tested in 3 ways. Experiment 1 showed that the unconditioned response evoked by B was stronger than that evoked by C. Experiment 2 showed that B was more effective than C when used as a reinforcer in a sensory preconditioning procedure. Experiment 3 showed that B was learned about more readily than C as a conditioned stimulus in flavor aversion conditioning. Alternating preexposure to 2 similar stimuli may protect their distinctive features from the loss of salience normally produced by nonreinforced exposure to a stimulus.

Certain schedules of preexposure to two similar stimuli (call them AX and BX, where A and B represent the unique features of the stimuli and X features that, being similar, they hold in common) can facilitate subsequent discrimination between them. This perceptual learning effect has frequently been demonstrated with rats in flavor aversion conditioning (e.g., Bennett & Mackintosh, 1999; Blair & Hall, 2003b; Mondragón & Hall, 2002). For example, in the procedure used by Blair and Hall (2003b) rats received preexposure consisting of alternating trials with the flavor compounds AX and BX and a separate block of trials with the compound CX. (A, B, and C were saline, sucrose, and lemon, and X included an explicitly added common element, quinine.) An aversion was then established to the AX compound and generalization to BX and CX was tested. It was found that the aversion generalized less readily to BX than to CX; that is, discrimination between AX and BX appeared to be enhanced.

Blair and Hall (2003b; see also Blair & Hall, 2003a; Hall, 2003) explained their results in terms of the suggestion that the preexposure procedure engages a learning process that modifies the perceptual effectiveness (the effective salience) of the various stimulus elements. They suggested that repeated presentation of a stimulus will result in a decline in its effective salience and that such was the fate of the C and X elements in their experiment. But they also suggested that presenting the AX and BX in alternation attenuates or reverses this process for the unique features that distinguish these similar stimuli. It was proposed that this form of exposure enhances the salience of A and B (or at least, results in a less dramatic decline than that suffered by C). The test performance shown to BX and CX was explained in terms of these changes. Blair and Hall argued that the aversion shown to these compounds on the generalization test will be largely a consequence of the associative strength acquired by the X element as a result of aversive conditioning with AX as the conditioned stimulus (CS). But the ability of X to evoke its conditioned response (CR) will be modulated by the other stimuli that are present on the test—the more salient B element will be more likely to interfere with the CR to X than will the less salient C element, so that generalized responding will be less vigorous to BX than to CX.

The central feature of this interpretation is the suggestion that the preexposure procedure used by Blair and Hall (2003b) results in B having a greater effective salience than C. We have shown how the results of the generalization test with BX and CX can be interpreted in these terms. But if this characterization is correct, the difference between B and C should be evident on a range of other measures. The experiments reported in this article investigate three such measures.

Perhaps the most obvious difference between two stimuli that differ in salience (that differ, e.g., in their physical intensity) is that the more salient stimulus will evoke a more vigorous unconditioned response (UR) than will the less salient—a loud tone will evoke a more pronounced startle response than will a soft tone; a strong solution of quinine will evoke more neophobia than will a weak solution. It follows from the hypothesis under consideration that, after preexposure of the sort used by Blair and Hall (2003b), the UR evoked by stimulus B should be greater than that evoked by C. This prediction was investigated in Experiment 1. A further property of the salience of an unconditioned stimulus (US) is evident when the stimulus is used as a reinforcer in classical conditioning—the acquisition of the CR to a given CS will proceed more rapidly the more salient the US. In Experiment 2 we paired a novel stimulus with B or with C to test the implication that the association between this novel CS and B would be better formed than that between this CS and C. Finally, in Experiment 3, we looked at the effects of using B or C as the CS in a standard conditioning procedure. Because, for a given US, conditioning proceeds more readily the more salient the CS, we predicted that the CR would be better acquired when B rather than C was used as the CS.

Experiments 1A and 1B

Rats (even when thirsty) show a reluctance to drink a quinine solution and will drink less of it than they will of plain water. The

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size of this aversive response is determined by the concentration of the quinine solution; pilot experiments conducted in our laboratory have confirmed that rats drink less of a strong solution than of a weak solution. Because the intensity of a stimulus is accepted to be a major determinant of its salience we may say that the aversive response to quinine is dependent on stimulus salience. In Experiment 1A we made use of this observation to evaluate the proposal that salience can be modified by stimulus exposure. As in the experiments of Blair and Hall (2003b) all subjects received exposure to the flavor compounds AX and BX, presented in alternation, and to a block of CX trials. For one group of rats (the intermixed group) it was arranged that stimulus B would be quinine; for a second group (the blocked group) it was arranged for C to be quinine. If the preexposure procedure leaves B effectively more salient than C, then the two groups should respond differently when presented with the same quinine solution on test. The solution will be effectively stronger for rats in the intermixed group than for rats in the blocked group and accordingly those in the former group should be less willing to consume it.

Experiment 1B used the same logic as Experiment 1A except that in this case the target solution was of sucrose. Within broad limits (Spector & Smith, 1984) rats will consume more of a strong than of a weak sucrose solution. Rats given preexposure with B as sucrose might therefore be expected, on test, to consume more of a given sucrose solution than rats given preexposure with C as sucrose. In Experiment 1B, therefore, our hypothesis predicts that the intermixed group should drink more on the test than the blocked group.

Method

Subjects and apparatus. The subjects for Experiment 1A were 16 male hooded Lister rats (*Rattus norvegicus*) with a mean ad-lib weight of 425 g at the start of the experiment. These rats had previously been used in an unrelated experiment but were naive to all aspects of the current procedure. A further 16 rats (with a mean ad-lib weight of 455 g), from the same stock and with a similar history, were used in Experiment 1B. The rats were singly housed for the duration of the experiment 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 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 flavor compounds were used in Experiment 1A: a compound consisting of 0.16 M saline (NaCl) and 0.00006 M quinine sulphate, a compound of 0.16 M saline and vanilla (1% [vol/vol] vanilla flavoring supplied by Supercook, Leeds, United Kingdom), and a compound of 0.16 M saline and almond (2% [vol/vol] Supercook almond flavoring). The solution used on test contained 0.00006 M quinine sulphate. Consumption was measured by weighing the tubes before and after trials, to the nearest 0.1 g. Three flavor compounds were used in Experiment 1B. Two of these (vanilla + saline and almond + saline) were the same as those used in Experiment 1A. The third was a compound consisting of 0.16 M saline (NaCl) and 0.0825 M sucrose. The solution used on test was 0.0825 M sucrose.

Procedure. In both experiments, a schedule of water deprivation was initiated by removing the standard water bottles overnight. On each of the following 2 days access to water was restricted to two daily sessions of 30 min, at 11:00 a.m. and 5:00 p.m. Presentation of fluids continued to be given at these times throughout the experiment.

Over the next 6 days (the preexposure phase), all subjects received four presentations of each of the three flavors AX, BX, and CX. Half of the rats were first given 4 days intermixed access to flavors AX and BX, with 10 ml of one compound being presented during the first daily drinking session and 10 ml of the other during the second. For half of these rats, AX was the morning stimulus and BX was the afternoon stimulus, and for the remainder, the reverse was true. The next 2 days consisted of blocked presentations of CX in which 10 ml of this flavor was made available in both morning and afternoon drinking sessions. The remainder of the subjects received the blocked presentations of CX on the first 2 days of the phase followed by 4 days of AX and BX.

For all the rats in Experiment 1A, Stimulus X was saline. For 8 rats (to be referred to as the intermixed group), Stimulus B was quinine, and A and C were vanilla and almond (counterbalanced); for these subjects, therefore, the compound containing quinine was presented during the intermixed preexposure phase. For the remaining 8 rats (the blocked group), stimulus C was quinine, and A and B were vanilla and almond (counterbalanced); for these subjects, therefore, the compound containing quinine was presented in a blocked fashion. The rats in Experiment 1B received equivalent treatment except that sucrose took the place of quinine. Thus in this experiment, for the intermixed group, the compound containing sucrose formed either the morning or the afternoon stimulus during intermixed preexposure; for the blocked group, the sucrose compound was presented on a separate block of trials.

In Experiment 1A, a 2-day test phase directly followed the last day of preexposure. In two consecutive morning sessions, the rats were given free access to the quinine solution for 30 min. Water was made available for 30 min in the afternoon sessions on these days. In Experiment 1B a single test session with sucrose was given. Because we were concerned that the rats would drink this solution very readily, we attempted to increase the sensitivity of the test by weighing the drinking tubes at 10-min intervals during the 30-min session.

Results and Discussion

There was some evidence of neophobia on the first trial of the preexposure phase of Experiment 1A when 4 rats failed to drink the full amount offered. Only 1 of the rats drank less than 7 ml (a subject in the intermixed group given the quinine + saline compound drank 6.1 ml); thereafter, all drank the full amount. In Experiment 1B, all of the rats drank the full amount on all preexposure trials.

The results of the test trials of Experiment 1A are shown in Figure 1. As the figure shows, the intermixed group drank less of the quinine than the blocked group on both test trials. An analysis

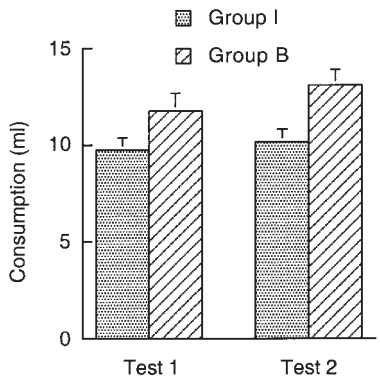

Figure 1. Experiment 1A: Consumption of a quinine solution on two test trials. Both groups had been preexposed to quinine (presented in compound with another flavor). For Group I (intermixed), these preexposure trials had alternated with presentations of another, similar, flavor. For Group B (blocked), the quinine compound was presented as a separate block of trials. Vertical bars represent standard errors of the means.

of variance (ANOVA), with group and trial as the variables, showed there to be a significant main effect of group, $F(1, 14) = 6.48$. (Here and elsewhere a significance level of $p < .05$ was adopted.) Neither the main effect of test, $F(1, 14) = 3.46$, nor the interaction between the variables was significant ($F < 1$). The data presented in the figure pool the results of two subgroups, one presented with CX on the first 2 days of the preexposure phase and one presented with CX on the last 2 days of preexposure phase. There was some suggestion that the effect of interest was marginally larger in the latter subgroup (rats in the intermixed condition drank a mean of 9.6 ml on test; those in the blocked condition drank a mean of 12.7 ml) than in the former subgroup (10.3 ml for the intermixed condition and 12.2 ml for the blocked condition). But with only 4 rats in each of these subgroups, it is not surprising that a statistical analysis with order of presentation as a variable revealed no significant effects ($F < 1$, both for the main effect of order and for the interaction of order and condition).

Cumulative scores for the three 10-min bins of the test of Experiment 1B are shown in Figure 2. All rats drank the sucrose readily during the first 10 min of the test and drank relatively little thereafter. Critically, however, the groups differed in the amount consumed in the first 10-min bin, with, in this case, the intermixed group drinking more than the blocked group. An ANOVA, with group and bin as the variables, produced no significant main effect of group, $F(1, 14) = 1.05$, but a significant main effect of bin, $F(2, 28) = 406.21$, and a significant interaction between the variables, $F(2, 28) = 5.96$. Further analysis of the interaction revealed that the group means differed significantly for the first bin, $F(1, 41) = 10.9$, but not for the others (Fs < 2). Again there was no substantial effect of whether the CX trials were given in the first half or second half of the preexposure phase. For the subgroups given CX first, the scores for the first 10-min block of the test were 19.6 ml for the intermixed condition and 16.3 ml for the blocked condition. The equivalent scores for the subgroups given CX second were 21.0 ml and 17.9 ml. An ANOVA with group and order of presentation as the variables showed no significant effects of the order variable (Fs < 1, for the main effect and interaction).

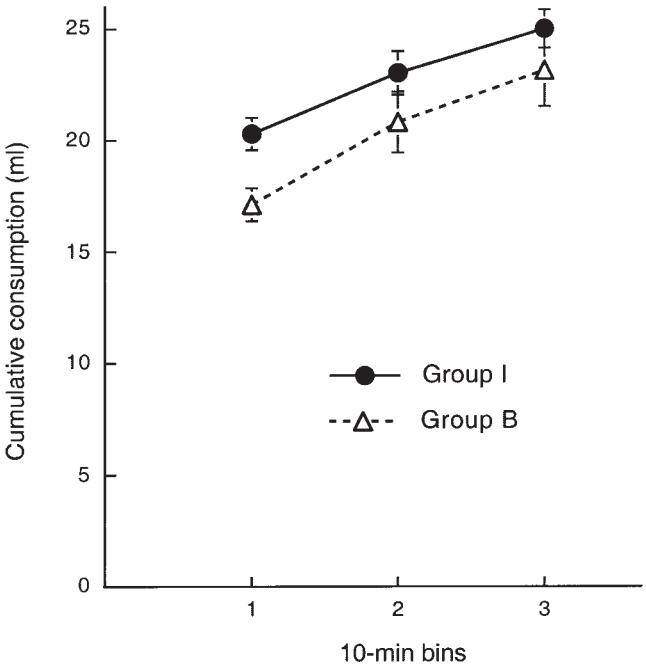

Figure 2. Experiment 1B: Consumption of a sucrose solution over successive 10-min periods of a 30-min test session (cumulative). Both groups had been preexposed to sucrose (presented in compound with another flavor). For Group I (intermixed) these preexposure trials had alternated with presentations of another, similar, flavor. For Group B (blocked), the sucrose compound was presented as a separate block of trials. Vertical bars represent standard errors of the means.

The pattern of results generated by these experiments is consistent with the hypothesis that the effective salience of the test flavor is greater after intermixed than after blocked preexposure—rats in the former condition behaved, on test, as if they had been given a stronger solution of quinine or of sucrose than rats in the latter condition. This is not to say that the intermixed arrangement actually enhances the salience of the test flavor. The treatment given during the preexposure trials for both groups amounts to an habituation procedure, and had we measured consumption on those trials (rather than giving the rats a fixed and limited amount), we might well have seen a decline in the UR (which we have equated with a decline in effective salience) in both. The critical finding is that some feature of the preexposure arrangement appears to attenuate this decline in the intermixed condition. We will consider possible accounts of what this feature might be after experiments investigating other measures of the same basic effect have been described.

It should be acknowledged that the results obtained in these experiments might be construed as instances of a contrast effect. Consider Experiment 1A: Rats in the intermixed group experienced presentations of the unpalatable quinine solution in alternation with presentations of a quinine-free solution. Rats in the blocked group received a continuous block of trials with the quinine solution. It is possible that the alternation of less and more palatable flavors generates a contrast effect that serves to enhance the aversiveness of the quinine solution, thus leading to the result obtained—a more marked reluctance to drink quinine in the test phase in the intermixed group. It is not clear, however, that this description necessarily implies the operation of a mechanism other than that already discussed. That is, the hypothesis that alternating presentations of the two solutions maintains or boosts the effective salience of the quinine could be seen as the mechanism that generates the contrast effect. The matter could perhaps be resolved by a study in which the various solutions used were closely matched in their palatability.

Experiment 2

Conditioning proceeds more rapidly the more intense (the more salient) the US. It follows from our hypothesis then, that if, after preexposure of the type given in Experiment 1, cues B and C were to be used as USs, an association with B as the US would be formed more readily than an association with C as the US. To test this proposal we made use of a version of the sensory preconditioning procedure pioneered by Fudim (1978). The subjects were given preexposure as in Experiment 1 except that a saline solution was used as the critical stimulus (i.e., as the C stimulus for the blocked group and the B stimulus for the intermixed group). All subjects then received pairings of a new flavor (vanilla) and saline. Our interest was in the strength of the vanilla–saline association, and to assess this we then rendered saline motivationally signifi-

cant by giving the rats an injection designed to produce a state of salt need. Rats is this state show an enhanced readiness to consume a flavor that has been associated with salt (Fudim, 1978; see also Symonds, Hall, & Bailey, 2002) and thus both groups can be expected to drink vanilla readily when it is presented alone in a final test. But if the saline solution paired with vanilla was effectively more salient for the intermixed group than for the blocked group, then the former group should drink more vanilla on test than the latter.

Method

The subjects were 16 male hooded Lister rats, with a mean ad-lib weight of 400 g at the start of the experiment. They had previously been used in another, unrelated, experiment, but were naive to all aspects of the current procedure. The following solutions were used as experimental stimuli: A compound consisting of 0.00003 M quinine sulphate and 0.16 M saline (NaCl), a compound of 0.00003 M quinine sulphate and 0.165 M sucrose, a compound of 0.00003 M quinine sulphate and 2% lemon (2% lemon by volume; ReaLemon natural strength lemon juice, supplied by ReaLemon, Ramsdonk, Belgium), a compound of 0.16 M saline and 1% vanilla (1% [vol/vol] Supercook vanilla flavoring, Leeds, United Kingdom), and a solution of 1% vanilla (1% [vol/vol] Supercook vanilla flavoring). The treatment used to induce a sodium appetite was a subcutaneous injection of 0.5 ml of a mixture of 10 mg furosemide (Furo) and 5 mg of deoxycorticosterone acetate (Doca) dispersed in 20 ml of distilled water with one drop of Tween 80 (Uniqema, New Castle, DE).

The rats received preexposure schedules similar to those used in Experiment 1. For all the rats, the X element, present on all preexposure trials, was quinine. For half of the rats (the intermixed group), the compound containing saline was BX and was presented in alternation with AX; CX was presented on a separate block of trials. For half of the rats in this group, A was lemon and C was sucrose; for the remainder the arrangement was reversed. For the remaining subjects (the blocked group), the saline compound was the CX stimulus, and the sucrose and lemon compounds were AX and BX (again, counterbalanced). As before, half of each of these groups received intermixed preexposure first, and the remainder received blocked preexposure first.

Two pairings of saline with a novel flavor followed. In the morning session of the day directly following the end of preexposure, both groups were given a presentation of 10 ml of the saline + vanilla compound. In the afternoon drinking session, free access to water was given. This was repeated on the next day. Following the afternoon drinking session on the second of these 2 days, all rats received an injection of Furo-Doca. The food was then removed from the home cages in the colony room, and the subjects were given free access to distilled water overnight. On the following day, the distilled water was removed from the cages 3 hr prior to a test session (given at 2:00 p.m.). A free-access choice test was given, with rats receiving 30 ml of 1% vanilla solution and an identical volume of water in two separate drinking tubes, presented simultaneously. The two tubes were inserted into the cage on either side of the aperture used for presentations of the single tube given during earlier stages of training. The two spouts were separated by a distance of 5 cm. The position of the tubes was counterbalanced such that half of the rats were presented with vanilla on the right and half with water on the right.

Results and Discussion

Neophobia was evident on the 1st day of the preexposure phase. The group mean consumption scores for the morning and afternoon sessions were 7.5 ml and 7.2 ml for the intermixed group, respectively; the equivalent scores for the blocked group were 7.2 ml and 7.2 ml. Thereafter (with one exception—1 rat given the quinine + lemon compound drank only 7.3 ml on the morning of Day 2), all rats drank all the fluid offered. The saline + vanilla compound presented after preexposure was consumed readily, with no evidence of neophobia on either trial.

The results of the test session, means for the consumption of vanilla and water for the two groups, are shown in Figure 3. Overall levels of consumption were low in both groups, but this is unsurprising given that subjects had been deprived of water for only 3 hr prior to the test. However, rats in the intermixed group showed a preference for vanilla over water, as would be expected of animals in a state of salt need for whom vanilla had become associated with saline. No such effect was evident in the blocked group, which showed, if anything, a slight preference for water over saline. Because other unpublished studies in our laboratory have found that rats will often show a substantial preference for plain water over vanilla, the absence of a difference in the blocked group does not show that no vanilla–saline association was formed—but the magnitude of this association must clearly be rather less than that formed in the intermixed group.

This description of the results was confirmed by statistical analysis. An ANOVA, with the variables of group and stimulus (water or vanilla), produced significant main effects neither for stimulus, $F(1, 14) = 1.36$, nor for group ($F < 1$), but there was significant interaction between these two variables, $F(1, 14) = 6.62$. Analysis of simple effects showed that the difference between vanilla and water was statistically significant in the intermixed group, $F(1, 14) = 7.00$, but that there was no reliable difference between these scores for the blocked group ($F < 1$). As in the previous experiments, order of stimulus presentation (i.e., CX first or CX second) had little effect on the results obtained. For rats in the intermixed condition, the subgroup given CX first drank 1.8 ml of vanilla and 1.0 ml of water; the subgroup given CX second drank 2.3 ml of vanilla and 1.6 ml of water. For rats in the blocked condition the subgroup given CX first drank 1.4 ml of vanilla and 1.4 ml of water; the subgroup given CX second drank

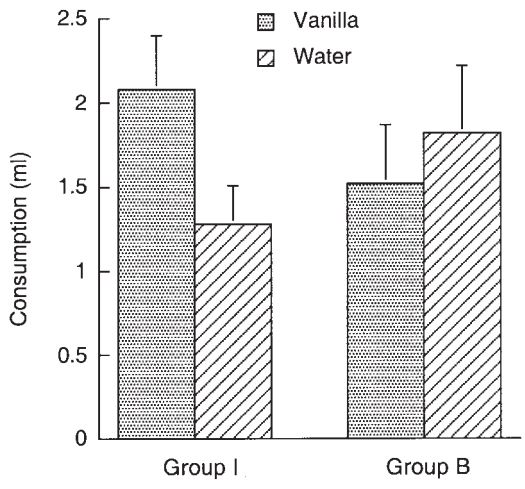

Figure 3. Experiment 2: Group means for consumption of water and a vanilla solution after an injection of 0.5 ml of a mixture of 10 mg furosemide and 5 mg of deoxycorticosterone acetate. All rats had previously experienced vanilla in compound with saline. Group I had received preexposure to saline in an intermixed arrangement; Group B had received preexposure to saline in the blocked arrangement. Vertical bars represent standard errors of the means.

1.6 ml of vanilla and 2.3 ml of water. Statistical analysis revealed no significant effects of the order variable: $F(1, 12) = 1.65$ for the main effect of order, and Fs < 1 for the interaction of group and order and for the triple interaction.

When animals in a state of salt need show a preference for a neutral flavor that has been associated with saline, this constitutes evidence that a flavor–saline association has been formed. The magnitude of this preference will depend on the strength of this association, which, in turn, will depend on the strength or salience of the saline that has been paired with the flavor (see Symonds et al., 2002, Experiment 1). The present results are therefore consistent with the proposition that the effective salience of the saline solution on the conditioning (the saline + vanilla) trials was greater in the intermixed group than in the blocked group.

Experiments 3A and 3B

Conditioning with a given US proceeds more rapidly the more salient the CS. Our hypothesis predicts, therefore, that, after our standard preexposure procedure, B should be a more effective CS than C. We tested this prediction in the present experiment by using these cues as CSs in the flavor aversion paradigm, with an injection of lithium chloride (LiCl) as the US. In Experiment 3A the flavors used as cues and the conditioning parameters were the same as those that we had used previously in the series of studies by Blair and Hall (2003b) on the effects of preexposure on generalization. We found (to anticipate) that these procedures resulted in very rapid learning, obscuring, to some extent, the effect of interest. Accordingly, in Experiment 3B, we changed the conditioning regime (using a weaker US), and chose different flavors that we thought would be intrinsically less salient, in the hope of seeing more gradual acquisition in the conditioning phase.

Method

The subjects for Experiment 3A were 16 male hooded Lister rats with a mean ad-lib weight of 505 g at the start of the experiment. The rats had previously been used in another experiment, but were naive to all aspects of the current procedure.

The flavor compounds used in preexposure were the same as those used in Experiment 2. All rats received preexposure to AX, BX, and CX, the procedures being identical to those described for Experiment 2. For all rats, Flavor A was lemon and Flavor X was quinine. The critical test flavors, B and C, were counterbalanced, with half of the rats receiving sucrose as B and saline as C, and half the reverse arrangement. The rats were divided into two equal-sized groups for the conditioning phase. For the intermixed group, Flavor B was used as the CS; for the blocked group, Flavor C was used as the CS. For half of each of the groups, therefore, the CS was saline (0.16 M), and for the remainder it was sucrose (0.165 M). The first conditioning trial was given in the morning session the day after preexposure ended. It consisted of a 30-min presentation of 10 ml of the CS flavor followed immediately by an intraperitoneal injection of 0.15 M LiCl at 10 ml/kg of body weight. The rats were given free access to water in the afternoon session, followed by a recovery day in which free access to water was given in both morning and afternoon drinking sessions. There were two further conditioning trials, each followed by a recovery day. On each of these trials the rats were given free access to the conditioned flavor for 30 min prior to the injection. The conditioning was followed by a nonreinforced test phase during which the rats were given access for 30 min, over each of 12 consecutive morning drinking sessions, to the flavor that had been conditioned. Free access to water was given in the afternoon session of each day. One rat in the intermixed group died prior to the second conditioning trial, meaning that data were available for 15 subjects. Procedural details not specified here were the same as those described for the preceding experiments.

The subjects for Experiment 3B were 16 experimentally naive male hooded Lister rats, with a mean ad-lib weight of 480 g at the start of the experiment. The flavors were the same as those used by Blair and Hall (2003a) in their experiments on the effect of stimulus preexposure. They consisted of a compound of 0.08 M saline (NaCl) and almond (2% [vol/vol] almond flavoring supplied by Supercook, Leeds, United Kingdom), a compound of 0.08 M saline and vanilla (1% [vol/vol] Supercook vanilla flavoring), and a compound of 0.08 M saline and peppermint (0.5% [vol/vol] Supercook peppermint flavoring). The flavors used in the conditioning phase were a solution of 2% almond and a solution of 1% vanilla. All rats received preexposure to AX, BX, and CX, according to a schedule identical to that described for Experiment 3A. For all rats Flavor A was peppermint and X was saline; for half of the rats vanilla was B and almond was C; for the rest this arrangement was reversed. As before, the intermixed group received conditioning with Flavor B as the CS and the blocked group with C as the CS (for half of each of these groups, the stimulus conditioned was vanilla, and for the remainder it was almond). The conditioning procedure was the same as described for Experiment 3A, except that the volume of LiCl injected was reduced to 1 ml/kg of body weight, and the number of reinforced trials was increased to eight. In respects not specified here, the procedure was the same as for Experiment 3A.

Results and Discussion

On the first conditioning trial of Experiment 3A all rats drank almost all of the 10 ml made available (the mean scores were 9.5 ml for the intermixed group and 9.6 ml for the blocked group). When the rats were given free access on the second trial, consumption was lower in the intermixed group (at 10.3 ml) than in the blocked group (13.0 ml), a difference consistent with the suggestion that the aversion was forming more readily in the former group. By the third trial, however, consumption was almost totally suppressed in both groups (the means were 1.1 ml for the intermixed group and 1.5 ml for the blocked group). An ANOVA conducted on the conditioning data, with the variables of group and trial, yielded only a significant main effect of trial, $F(2, 26) = 99.41$. Although neither the main effect of group ($F < 1$) nor the Group $\times$ Trial interaction, $F(2, 26) = 1.62$, was significant, an analysis of simple main effects showed there to be a significant difference between the groups on Trial 2, $F(1, 35) = 4.52$.

The results of the 12 nonreinforced test trials are presented in Figure 4. For the intermixed group, consumption remained profoundly suppressed throughout the test phase, but showed a substantial recovery toward the end of testing in the blocked group. These data were submitted to an ANOVA with group and trial as the variables. The main effect of group fell short of significance, $F(1, 13) = 3.90$, $p < .10$, but there was a significant effect of trial, $F(11, 143) = 6.01$, and a significant Group $\times$ Trial interaction, $F(11, 143) = 3.26$. Analysis of simple main effects showed that the groups differed on each of the last five trials, smallest $F(1, 156) = 4.28$. The difference between the groups was evident both in the subgroups given CX first during preexposure and in the subgroups given CX second during preexposure. For the former subgroups the total consumption, pooled over all test trials, was 13.1 ml in the blocked condition and 3.4 ml in the intermixed condition. The equivalent scores for the other pair of subgroups were 30.2 ml and 5.7 ml. Statistical analysis revealed no significant effects of the order variable: $F(1, 11) = 1.29$ for the main effect of order, and $F < 1$ for the Group $\times$ Order interaction.

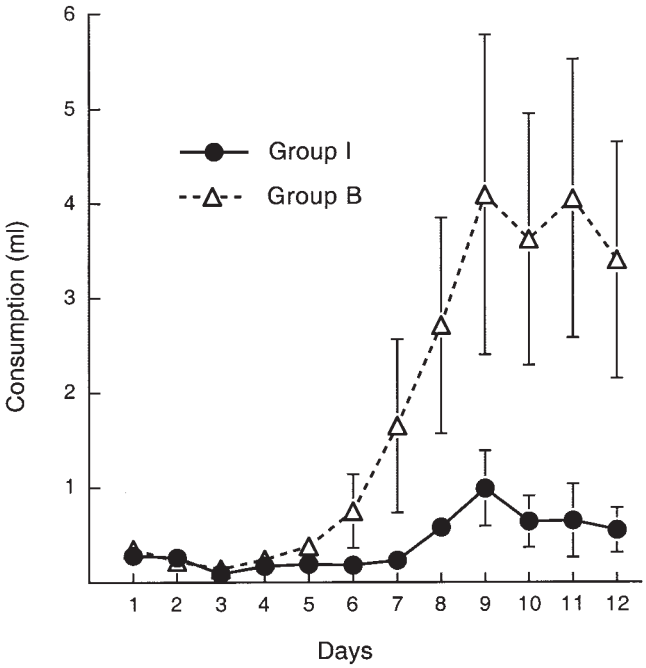

Figure 4. Experiment 3A: Group mean consumption of a conditioned flavor over nonreinforced daily test trials. Both groups had been preexposed to a compound containing this flavor. For Group I (intermixed), these preexposure trials had alternated with presentations of another, similar, flavor. For Group B (blocked), the critical flavor compound was presented as a separate block of trials. Vertical bars represent standard errors of the means.

This pattern of results exactly matches those previously reported by Mondragón and Hall's (2002) Experiment 4 (although Bennett, Scahill, Griffiths, & Mackintosh, 1999, reported, in their Experiment 3, a formally equivalent study producing the opposite outcome). The pattern obtained here is consistent with the proposal that conditioning proceeded more readily in the intermixed than in the blocked condition, the difference in associative strength being obscured by a floor effect at the end of conditioning, but becoming evident as extinction occurred during the test trials. It must be acknowledged, however, that a difference observed during an extinction test may be open to other interpretations, and that a more convincing confirmation of the hypothesis under investigation would be provided by demonstrating a difference during the course of initial acquisition. Experiment 3B was intended to address this issue.

On the first conditioning trial of Experiment 3B, all rats consumed the full amount of fluid (10 ml) offered. Figure 5 shows the mean amount consumed by each of the groups during the seven subsequent free-access conditioning trials. As is clear from the figure, the modified conditioning procedure used in this experiment was successful in establishing an aversion that was acquired only slowly, allowing differences between the groups in their rate of acquisition to become evident. The aversion was acquired more readily by the intermixed group than by the blocked group. An ANOVA conducted on the data summarized in the figure, with group and trial as the variables, revealed no reliable main effect of group, $F(1, 14) = 2.65$, but there was a significant effect of trial, $F(6, 84) = 25.39$, and a significant interaction between these two variables, $F(6, 84) = 2.21$. An analysis of simple main effects showed that the groups differed significantly on Trial 4, $F(1, 98) = 6.38$; Trial 6, $F(1, 98) = 3.95$; and Trial 7, $F(1, 98) = 4.18$. This result accords with the hypothesis that the CS flavor was effectively more salient in the intermixed group than in the blocked group.

The difference between the intermixed and blocked groups was present both in the subgroups given the CX trials in the first half of preexposure and in the subgroups given CX in the second half of preexposure. The mean daily consumption scores, over all seven test trials, for subjects given CX first were 6.9 ml in the intermixed condition and 8.5 ml in the blocked condition. The equivalent scores for the subjects given CX second were 6.7 ml and 10.2 ml. The effect of interest was thus somewhat larger in the second pair of groups, but statistical analysis revealed no significant effects of the order-of-presentation variable ($F < 1$, both for the main effect of this variable and for the Group $\times$ Order interaction).

General Discussion

The aim of the experiments reported here was to test the hypothesis that exposure to stimuli can modify their effective salience and that different forms of preexposure are differentially effective in this respect. Specifically, we proposed that the salience of the distinctive features of a stimulus (those that distinguish it from another similar stimulus) would be maintained at a relatively high level by preexposure in which the two similar stimuli were

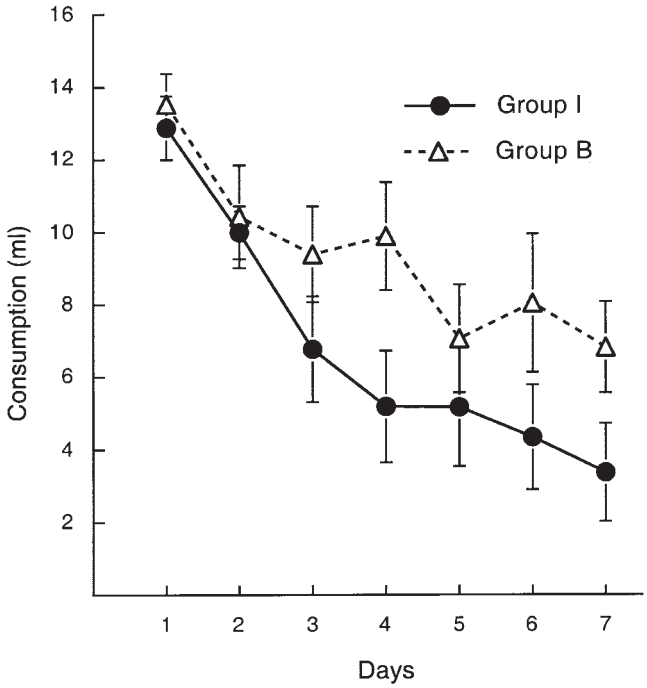

Figure 5. Experiment 3B: Group mean consumption over the seven free-access conditioning trials. Both groups had been preexposed to a compound containing the flavor used as the conditioned stimulus. For Group I (intermixed), these preexposure trials had alternated with presentations of another, similar, flavor. For Group B (blocked), the critical flavor compound was presented as a separate block of trials. Vertical bars represent standard errors of the means.

presented in alternation. In our experiments we compared the effects of such preexposure with those produced by a procedure in which the stimulus was presented the same number of times but in a continuous block of trials. We presented three tests of stimulus salience. We showed that a stimulus presented according to the intermixed (alternating) preexposure schedule was more effective than one presented according to the blocked schedule in eliciting its UR (Experiment 1), as a US in classical conditioning (Experiment 2), and as a CS in classical conditioning (Experiment 3). All three results are what would be expected if the intermixed stimulus was more salient than the blocked stimulus.

It should be acknowledged that the last of these results may be open to another interpretation. Although formal theories of conditioning have usually supposed that the salience of a stimulus is directly determined by its sensory properties and is not subject to change (e.g., the S parameter in the theories proposed by Mackintosh, 1975, and Pearce & Hall, 1980, is a fixed value, related to stimulus intensity), these theories have also postulated the existence of another parameter associated with the CS that determines how readily the CS enters into associations and may be changed by experience. Both of the theories just mentioned incorporate an associability parameter, alpha, that changes according to how well the CS predicts its consequences. Although neither of these theories can easily predict that the alpha value of a stimulus will be higher after intermixed than after blocked preexposure, it remains possible that the difference in rate of acquisition observed in Experiment 3 could be a consequence of a difference in associability rather than a difference in effective salience (as these terms are being used here). The response measures used in Experiments 1 and 2, however, are less subject to this ambiguity. If we accept that alpha reflects only associability and does not influence performance (an assumption made explicitly by Pearce & Hall, 1980, and accepted by Mackintosh, 1975; but see Kruschke, 2001, for a different view), there is no reason to expect an effect on the vigor of the UR, the measure used in Experiment 1. And none of these theories has suggested that the alpha value of a stimulus will influence its ability to act as a US, the measure used in Experiment 2. Both these measures, however, should be sensitive to the salience of the stimulus.

The results reported here thus converge on the conclusion that stimulus salience, although determined initially by stimulus intensity, can change as a consequence of exposure to the stimulus. They indicate that the level of salience attained after the intermixed preexposure procedure is higher than that produced by blocked preexposure, but they do not provide any information about the absolute value of effective salience in the two cases. Perhaps the most natural assumption is that any form of preexposure produces a loss of salience through the operation of an habituation mechanism, but that the specific circumstances of the intermixed arrangement work to attenuate this loss. In this case, both forms of preexposure would produce a loss of salience, but the effect would be less marked after the intermixed version. It should be noted, however, that this interpretation does not fully accord with the results of Experiment 1B (in which the UR to a sucrose solution was monitored). Unpublished observations from our laboratory show that the rat's response to sucrose does not habituate—after a short-lived initial neophobic response, consumption levels tend to be high and to remain at the same high level over the course of successive presentations. The observation, in Experiment 1B, that rats drank more sucrose after intermixed preexposure than after blocked preexposure, may indicate that the former procedure actually increases the effective salience of sucrose above its initial starting level. This possibility requires further experimental investigation.

Why should the intermixed procedure be more effective in maintaining (or enhancing) salience than the blocked procedure? According to the hypothesis advanced by Hall 2003 (see also Blair & Hall, 2003a), the critical property of the alternating arrangement is that it allows for the central representations of distinctive stimulus features to be activated associatively on each trial after the first. Presentations of AX and BX can be expected to establish and maintain excitatory associations between X and A, and between X and B, allowing B to be activated associatively on AX trials, and A on BX trials. By contrast, because CX is given in a separate block of trials, there will be less (or no) opportunity for the associative activation of C in its absence. Hall (2003) suggested that associative activation of the representation of a stimulus, in the absence of that stimulus, will tend to reverse the loss of salience produced by prior presentations of the stimulus itself.

Comparison of the counterbalanced subgroups (those given CX first in the preexposure phase, and those given CX second) could, in principle, produce data relevant to this hypothesis. For both these subgroups the alternating schedule given to AX and BX ensures that associative activation of B will occur reliably on AX trials, and the salience of B should be maintained or enhanced in both. But for those given CX exposures in the second block, B will also be activated associatively on at least the first of the CX trials (extinction of the X-B association over the course of this phase of training will make activation of B less likely on trials after the first), further sustaining the salience of B in this condition. The fate of C will also be slightly different in the two subgroups. When CX is presented second during preexposure, there will be no possibility of the representation of C being activated associatively in the absence of the stimulus, and its decline in salience should proceed unopposed. But when CX is presented first, the X-C association formed on these presentations will mean that C should be activated associatively on subsequent AX and BX trials (up to the point at which the X-C association is extinguished). C should therefore suffer less loss of salience in this subgroup. It follows that the difference in effectiveness between B and C on the test should be greater in the subgroup given CX second than in the subgroup given CX first. In fact none of our experiments revealed any statistically reliable difference between the counterbalanced subgroups, but this is not, perhaps, a cause for concern given that the small size of the subgroups ($n = 4$) will make it difficult to detect what could well be only a small difference between them. It is worth pointing out that in no case was there a more substantial difference in a subgroup given CX first than in a subgroup given CX second—a result that would be damaging for the theory under consideration.

It remains to be explained why associative activation of a stimulus representation should help restore the salience lost during previous presentations of that stimulus. One possibility can be derived from certain features of the theory of associative learning recently proposed by McLaren and Mackintosh (2000). These authors maintain that the amount of activation produced by a stimulus in its central representational unit will depend, not only on the value of its external input, but also on the extent to which this unit receives input via associations established with units representing other stimulus elements (internal input). The value of

the difference between the external and internal inputs determines the magnitude of a "boost" applied to the external input. A novel stimulus (having no associates) will receive a sizeable boost; one that has been experienced before will not (not only will it be associated with the context of presentation, but the formation of within-stimulus associations among its various elements will provide another source of internal input). Although the only major application of this process within the theory has been to account for the phenomenon of latent inhibition (McLaren & Mackintosh, 2000, pp. 220–221), the modulation of salience it envisages can be expected to influence other measures of the effectiveness of the stimulus (such as those used in the present Experiments 1 and 2).

The issue now is to explain why the preexposure procedures used in these experiments should leave stimulus B with a greater salience boost than stimulus C. One possibility (there may be others, given the multifaceted nature of the theory) comes from the associative learning rule it adopts, which assumes that an associative link between two units will lose strength if both are activated internally (i.e., associatively) in the absence of external input. As we have already argued, associative activation of B can be expected to occur regularly during the course of preexposure, whereas associative activation of C will be less frequent. It follows that associations among the various elements of the B stimulus will tend to lose strength, one of the sources of internal input to these elements will be attenuated, and the salience boost will be enhanced when B is next presented (e.g., on test). The chief problem for this otherwise elegant account comes from doubts about the validity of its associative learning rule. What learning might occur when two stimulus representations are activated associatively has recently been the subject of much debate and is not yet resolved. Wagner's influential (1981) theory asserts that no associative change will occur in these circumstances. Others (e.g., Holland & Forbes, 1982; see also Hall, 1996) have argued in favor of the possibility, espoused by the McLaren and Mackintosh (2000) theory, that inhibitory learning will occur. Yet others have argued that the learning will be excitatory (e.g., Dickinson & Burke, 1996; see also Shevill & Hall, in press). It will be evident that, should the last of these suggestions prove well founded, the McLaren and Mackintosh theory, as presented here, will be constrained to make quite the wrong prediction—that stimulus B will be less likely to receive the salience boost than will stimulus C.

A fully satisfactory account of the mechanisms responsible for the effects reported here is thus not yet available. But whatever form the explanation might take, the fact that effective salience can change with experience is something that will need to be accommodated by future theories of conditioning. Because associative learning depends on the ability of the stimulus to activate its central representation, it follows that a comprehensive theory needs to include a specification of the rules that determine changes in the sensitivity of event representations (i.e., of the effective salience of stimuli).

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