Journal of Experimental Psychology:
Animal Behavior Processes
2006, Vol. 32, No. 2, 145–155

0097-7403/06/$12.00 DOI: 10.1037/0097-7403.32.2.145

Associative Activation of Stimulus Representations Restores Lost Salience: Implications for Perceptual Learning

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In 3 experiments, rats received preexposure to presentations of a compound flavor BX. The effective salience of B was then tested by assessing its ability to interfere with the aversion controlled by another flavor or the tendency to drink a saline solution after the induction of a salt need. It was found that the effective salience of B was maintained when during preexposure, presentations of BX alternated with presentations of X alone. This was true both when BX was presented as a simultaneous compound (Experiment 1) and as a serial compound (X → B; Experiments 2 and 3); salience was not maintained when the serial compound took the form B → X (Experiments 2 and 3a). It was argued that the salience of B declines during preexposure but is restored when presentations of X are able to activate the representation of B by way of the associative X–B link.

Keywords: rat, conditioning, perceptual learning, stimulus salience

In a recent report, Hall, Prados, and Sansa (2005) investigated the proposal (Hall, 2003) that the effective salience of a stimulus is subject to modification by experience. Specifically, Hall (2003) hypothesized that direct presentation of a stimulus would reduce its effective salience but that associative activation of the central representation of that stimulus, in the absence of the event itself, would restore lost salience. In the experiments by Hall et al., the critical stimulus was a shock. Rats in the control condition received exposure to the shock consistently signaled by a given stimulus (X+ trials, where X represents the signal and + represents the shock). Rats in the experimental condition received X+ trials alternated with presentations of X alone (X+/X training). It was argued that the X-alone trials would result in associative activation of the shock representation and thus alleviate the loss of effective salience produced by shock presentations on the X+ trials. The results confirmed this suggestion—the ability of the shock to serve either as a reinforcer or as conditioned stimulus in a subsequent conditioning phase was greater after X+/X training than after X+ training.

Hall et al. (2005) went on to argue that the principles demonstrated in their study could supply an explanation for the perceptual learning effect. An example of this effect is provided in a study by Blair and Hall (2003b). In this study, rats were given exposure to two compound flavor stimuli, AX and BX (where A and B represent unique features, and X represents a feature common to both), presented on alternate trials. They also received exposure to a third compound, CX, presented on a separate block of trials. An aversion subsequently conditioned to AX was found to generalize less readily to BX than to CX; that is, discrimination between AX and BX was enhanced by the preexposure procedure.

Blair and Hall (2003b) suggested, in explanation, that alternating presentations of AX and BX served to maintain the effective salience of the unique features of these compounds (A and B), whereas that of the control stimulus C was reduced during the block of CX trials. The more salient B would thus be better able to interfere with expression of the aversion conditioned to X on the BX test trials than would the less salient C on the CX test trials, producing the result obtained. Support for this interpretation came from a related study reported by Blair and Hall (2003a, Experiment 2), which used the same schedule of preexposure but with different flavor stimuli; in particular, saline was used as the X element. There was no conditioning phase, but a state of salt need was induced immediately prior to the test with BX and CX. The rats drank more of CX than of BX, consistent with the view that the X element (saline) was more readily perceived in the presence of the C element than in the presence of the B element.

The suggestion that appropriately scheduled exposure to similar stimuli will enhance the perceptual effectiveness of the unique features of the stimuli is not novel—Gibson's (1969) notion of *differentiation* postulates just this, for cases in which the preexposure procedure allows the possibility of stimulus comparison. Alternation of AX and BX is clearly such a case, but it is necessary to specify the mechanism responsible for the effect obtained. The results of Hall et al. (2005) suggest the following. Presentation of the compound stimulus BX will allow the formation of a within-compound excitatory association, which will be maintained, in spite of the intervening AX trials, by subsequent presentations of the BX compound. It is important to note that, for the present analysis, the existence of the X → B association will mean that, on the intervening AX trials, the representation of B will be activated associatively by the presence of X. According to the hypothesis, this should act to maintain the effective salience of B. No such effect will operate for the control stimulus C—the X → C asso-

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This work was supported by a grant from the United Kingdom Biotechnology and Biological Science Research Council.

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ciation will presumably be formed on CX trials, but in the absence of intermixed trials with some other compound containing X, there will be no opportunity for the associative activation of C in the absence of C itself. At the end of the preexposure phase, therefore, the effective salience of B should be higher than that of C, and, on the test trials, B will be better able to interfere with the response controlled by X, whether this be an aversion, as in the experiment by Blair and Hall (2003b), or an appetitive response, as in the experiment by Blair and Hall (2003a).

The experiments reported in this article were designed to provide a test of this interpretation. They focus on the suggestion that the critical factor in maintaining the salience of B is that the animal experiences presentations of B intermixed with trials on which the representation of B is activated associatively. Most previous studies of perceptual learning have given preexposure to two similar stimuli (i.e., AX and BX), sharing common features (X) but each also containing a distinctive feature (A or B; e.g., Blair & Hall, 2003a, 2003b; Mackintosh, Kaye, & Bennett, 1991; Mondragón & Hall, 2002; Symonds & Hall, 1995). An implication of the account being advanced here is that the presence of the unique feature (A) on the AX trials is not essential to producing the effect. Because it is the X element that is responsible (by way of the X → B association) for activating the B representation, the effect should be obtained just as readily when animals are given preexposure to presentations of BX intermixed with presentations of X alone. Support for this prediction comes from a recent study by Rodríguez and Alonso (2004). Their procedure involved a between-subjects comparison between a group given (in our terminology) alternating presentations of BX and X and a group given the BX and X trials as separate blocks. After an aversion had been established to X, the groups were tested with BX. It was found that the alternating group drank more of BX than did the blocked group. This parallels the result found in between-subjects demonstrations of the perceptual learning effect (e.g., Mondragón & Hall, 2002), which used the same procedure, apart from presenting an AX compound in place of the X-alone trials used by Rodríguez and Alonso.

In the present Experiment 1, we sought to demonstrate the effect reported by Rodríguez and Alonso (2004) in our own within-subject paradigm, using both the flavor aversion procedure of Blair and Hall (2003b) and the salt-need procedure of Blair and Hall (2003a). Using these same procedures, we went on, in Experiments 2 and 3, to seek evidence that the intermixed X presentations had their effect because of their ability to activate associatively the representation of B.

Table 1
Experimental Designs

Preexposure	Conditioning or salt need induction	Test
	Experiment 1a	
X group		
BX/X and CX	X+	BX and CX
No-X group		
BX/— and CX	X+	BX and CX
	Experiment 1b	
BX/X and CX	FuroDoca	BSal vs. CSal
	Experiment 2a	
Forward group		
X → B/X	X+	BX
Backward group		
B → X/X	X+	BX
	Experiments 2b and 2c	
Forward group		
X → B/X	FuroDoca	BSal
Backward group		
B → X/X	FuroDoca	BSal
	Experiment 3a	
Forward group		
X/X → B and X → C	X+	BX and CX
Backward group		
X/B → X and C → X	X+	BX and CX
	Experiment 3b	
X/X → B and X → C	FuroDoca	BSal vs. CSal

Note. Simultaneous compounds are represented as BX; serial compounds are represented as B → X. The dash indicates that no flavor was presented. Events separated by a forward slash (/) were presented on alternate trials. B, C, and X represent different flavors; Sal represents a saline solution; + indicates an injection of LiCl; FuroDoca indicates an injection of furosemide and deoxycorticosterone acetate; vs. indicates a choice test.

Experiments 1a and 1b

In these experiments, the subjects (rats) were given presentations of fluids twice a day during the preexposure phase. In Experiment 1a, rats in the critical experimental condition (the X group of Table 1) received 4 days of training on each of which the compound BX was presented on one of the drinking sessions, with X alone being presented on the other. They also received 2 days on which both drinking sessions consisted of presentations of CX. (There was no stimulus A in these experiments, but we maintain the nomenclature used in previous studies in which B and C were used to indicate the stimuli presented on the test.) The hypothesis under test suggests that the effective salience of B will be higher than that of C after this treatment. In order to test this hypothesis, we made use of the procedure previously used by Blair and Hall (2003b, Experiment 5a). The rats received flavor aversion conditioning, with X as the conditioned stimulus and lithium chloride (LiCl) as the reinforcer. They then received test trials with the BX and CX compounds. If B is more salient than C, it will be better able to interfere with the conditioned response governed by X; we predicted, therefore, that the rats would consume BX more readily than CX.

As Table 1 shows, Experiment 1a also included a control condition (the no-X group) in which the rats received the same treatment as in the experimental condition, except that there were no presentations of X alone. The preexposure schedule involved presentations of CX twice a day, whereas BX was presented only once a day. This difference in itself might, in principle, be responsible for any difference seen on the test trials with BX and CX in the experimental condition. But if the presentations of X alone are

necessary, no such difference should be obtained in the control group.

In Experiment 1b, we attempted to confirm the reliability and extend the generality of the findings of Experiment 1a. A single group of animals received a preexposure schedule identical to that given to the experimental group of the previous experiment but (following the procedure used by Blair & Hall 2003a, Experiment 2) with different flavors as the cues. There was no conditioning phase, but all subjects were given an injection capable of inducing a state of salt need. In the test phase, they received presentations of saline compounded with either B or C. Rats in a state of salt need can be expected to drink these solutions readily. But if B has greater effective salience than C, it will be better able to interfere with the perception of saline; with this procedure, therefore, we predicted that the rats would consume more of the solution containing C than of that containing B.

Method

Subjects and apparatus. The subjects in Experiment 1a were 16 male hooded Lister rats with a mean weight of 410 g at the start of the experiment. They had previously served in a study using operant conditioning techniques but were naive to the flavors and procedures used in the present study. They were assigned at random to two equal-sized groups (the X and no-X groups; see Table 1). Sixteen rats from the same stock, and with the same previous history, were used in Experiment 1b. They had a mean ad-lib weight of 498 g at the start of the experiment. The experiment was run in two replications, each using 8 subjects. The rats were singly housed with continuous access to food in a colony room that was artificially lit from 8 a.m. to 8 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 flavored solutions were used in Experiment 1a: 0.00003 molar (M) quinine sulfate, a compound consisting of 0.00003 M quinine sulfate and 0.16 M saline (NaCl), and a compound of 0.00003 M quinine sulfate and 0.165 M sucrose. Consumption was measured by weighing the tubes before and after trials, to the nearest 0.1 g. The unconditioned stimulus for the conditioning trials was an intraperitoneal injection of 0.15 M LiCl at 10 ml/kg of body weight. The following flavored solutions were used in Experiment 1b: 0.0825 M sucrose, a compound consisting of 0.0825 M sucrose and almond (2% vol/vol almond flavoring supplied by Supercook, Leeds, UK), a compound of 0.0825 M sucrose and vanilla (1% vol/vol Supercook vanilla flavoring), a compound of 0.16 M saline (NaCl) and almond (2% vol/vol), and a compound of 0.16 M saline and vanilla (1% vol/vol). 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.

Procedure. In both experiments, a schedule of water deprivation was initiated by removing the standard water bottles overnight. On each of the following 3 days, access to water was restricted to two daily sessions of 30 min, at 11 a.m. and 5 p.m. Presentation of fluids continued to be given at these times daily throughout the experiments.

Over the next 6 days (the preexposure phase), subjects in the X group of Experiment 1a received four presentations of each of the flavors X, BX, and CX. Half of the animals were first given 4 days of alternating trials with X and BX, with 10 ml of one being presented during the first daily drinking session and 10 ml of the other being presented during the second. For half of these animals, BX was the morning stimulus and X was the afternoon stimulus; for the rest, the arrangement was reversed. 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 was treated identically, except that they received the blocked presentations of CX on the first 2 days of the phase, followed by 4 days of X and BX. Half of the subjects received sucrose as B and saline as C; for the rest, the assignment was reversed. For all animals, X was quinine. The procedure for the rats in the no-X group was the same as that just described, except that presentations of X alone were replaced by presentations of 10 ml of unflavored water.

Three conditioning trials followed. The first was given in the morning session the day after preexposure ended. It consisted of a 30-min presentation of 10 ml of X followed immediately by an injection of LiCl. The rats were given free access to water in the afternoon session. The next day was a recovery day on which animals were given unrestricted access to water on both morning and afternoon drinking sessions. The second conditioning trial, given in the morning session of the next day, was identical to the first and was followed by a further recovery day. The third conditioning trial was identical to the second. Water was again available in the afternoon session following this conditioning trial, and one further recovery day preceded the test phase of the experiment.

On the following morning session, subjects were given a free-access test for 30 min, with half receiving BX and half receiving CX. Water was made available for half an hour in the afternoon session. The next morning, animals that had been tested with BX the previous day were given a test with CX and vice versa.

The preexposure procedure for Experiment 1b was identical to that described for the experimental group of Experiment 1a, except that X was sucrose and B and C (counterbalanced) were almond and vanilla.

One hour after the end of the final preexposure session, all subjects received an injection of FuroDoca. 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 the test (given in the morning session). On this test, the subjects were given access for 30 min to two tubes, one containing 30 ml of the B plus saline compound and one containing 30 ml of the C plus saline compound. 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 the rats were presented with C on the right, and half with B on the right.

Results

Experiment 1a. There was some evidence of neophobia on the first trial of the preexposure phase in that the mean consumption score was 7.9 ml (range = 5.5–9.8 ml) for rats in the X group and 6.7 ml (range = 6.1–8.1 ml) for rats in the no-X group (excluding those that received access to unflavored water on this trial). The corresponding scores for the second trial were 9.1 ml and 8.6 ml, respectively. Thereafter, the rats consumed all of the available fluid. (This pattern of consumption was seen during the preexposure phase of all subsequent experiments, and the data from this phase will not be considered further.)

The conditioning procedure successfully established an aversion to X in both groups. The X group drank a mean of 9.1 ml on the first conditioning trial, 8.7 ml on the second conditioning trial, and 3.3 ml on the third conditioning trial; the corresponding scores for the no-X group were 9.3 ml, 6.9 ml, and 2.1 ml, respectively. An analysis of variance (ANOVA), with group and trial as the variables, produced a significant main effect of trial, $F(2, 28) = 145.07$, no main effect of group, $F(1, 14) = 3.48$, and no significant interaction, $F(2, 28) = 3.16$. (Here and elsewhere, a significance level of $p < .05$ was adopted.) The trend toward faster

conditioning in the no-X group is presumably a consequence of the fact that this group received four fewer presentations of X than did the X group over the course of preexposure.

The results of the test phase are presented in Figure 1, which shows group means for consumption of the compounds BX and CX. The no-X group drank rather little of either compound, demonstrating that the different schedules of preexposure given to BX and CX did not, in themselves, generate a difference in test performance. The X group, on the other hand, drank little of CX but consumed BX more readily. An ANOVA was conducted on the data summarized in the figure. The variables of principal interest were group and stimulus (BX or CX). We also included as variables the counterbalanced factors of preexposure order (whether CX was presented over the first or last 2 days of the preexposure phase) and preexposure time (whether X was presented in the morning or afternoon session during preexposure—because conditioning with X was given in a morning session, we were concerned that there might be a difference between animals that had previously experienced X in the morning and those that had only previously encountered it in the afternoon).

This analysis showed there to be significant main effect of group, $F(1, 8) = 7.18$, and of stimulus, $F(1, 8) = 4.61$. All other Fs < 2, apart from that for the interaction of group and preexposure time, $F(1, 8) = 3.27$, $p > .1$, and, critically, that for the interaction of group and stimulus, $F(1, 8) = 3.68$. Although this interaction fell short of significance ($p < .09$), simple main effects analysis confirmed the reliability of the difference between BX and CX in the X group, $F(1, 16) = 10.55$, and absence of such a difference in the no-X group ($F < 1$).

Experiment 1b. On the test session, the rats consumed less of the compound containing B than of that containing C. Group mean scores were as follows: 8.7 ml of B plus saline and 12.0 ml of C plus saline. There was, however, considerable variability in individual scores, and the difference between means was not statistically reliable, $F(1, 15) = 1.10$. Closer inspection of the scores showed that although most of the animals drank at least 2 ml from each of the bottles, the remainder drank exclusively, or almost exclusively, from one bottle. We were concerned that these latter animals had failed to sample both alternatives before making a choice and that their scores did not truly reflect the effects of B and C on consumption of saline. Accordingly, we calculated the means excluding the scores of 4 subjects that drank less than 2 ml of one of the solutions on offer (for 2 rats, this was the compound containing B, and for 2, it was the compound containing C). The results are presented on the right side of Figure 1. An ANOVA was conducted on the data summarized in the figure, the variables being stimulus (B plus saline or C plus saline) and preexposure order (whether CX was presented at the beginning or the end of the preexposure phase). There was a significant main effect of stimulus, $F(1, 10) = 11.69$, confirming, what the figure suggests, that the subjects drank C plus saline more readily than B plus saline. (For preexposure order and the interaction, Fs < 1.)

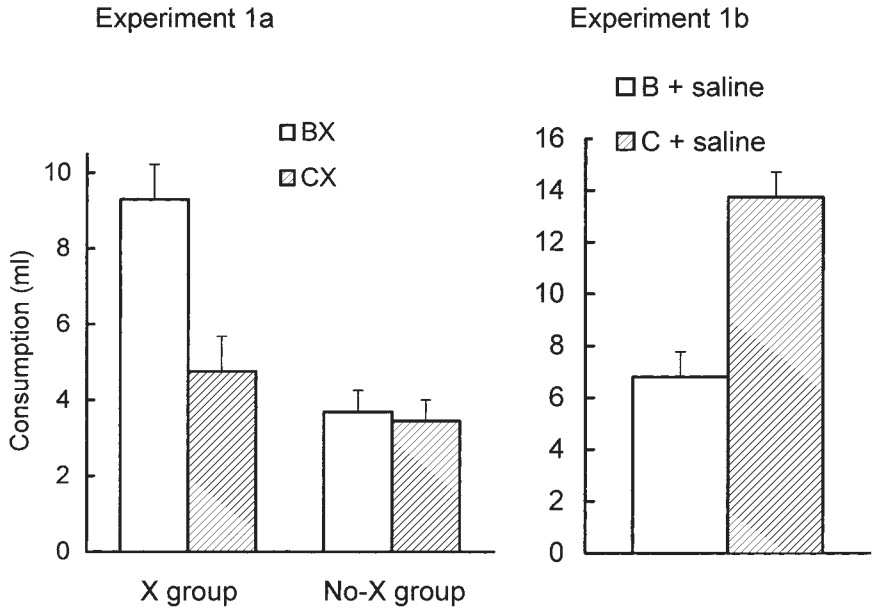

Figure 1. Experiment 1a: Group mean consumption of the compound flavors BX and CX after aversion conditioning with X. Rats in the X group received initial preexposure to a block of CX trials and to trials with X and BX presented in alternation. Rats in the no-X group received just the CX and BX trials in preexposure. Vertical bars represent, for each group, within-subject standard errors, computed on scores adjusted for variation between subjects (Bakeman & MacArthur, 1996). Experiment 1b: Mean consumption of flavor compounds B plus saline and C plus saline on the choice test. The rats had all received preexposure consisting of a block of trials with CX and alternating trials with X and BX, followed by the induction of a salt need immediately prior to the test. Vertical bars represent within-subject standard errors.

Discussion

The treatment given to the X group in Experiment 1a was the same as that used in studies of the perceptual learning effect in flavor aversion learning (e.g., Blair & Hall 2003b, Experiment 1), except that presentations of X alone took the place of the AX trials used in the previous experiments. And the outcome was the same—in both procedures, the aversion controlled by BX was less marked than that controlled by CX. Evidently this effect does not depend on the presence of the A feature during preexposure, confirming the results recently reported by Rodríguez and Alonso (2004).

Given that the effect of preexposure to alternating trials of BX and X is comparable with that produced by preexposure to alternating trials of AX and BX, it seems appropriate to seek a common explanation for them. As Rodríguez and Alonso (2004) pointed out, this presents a difficulty for the account of perceptual learning proposed by McLaren, Kaye, and Mackintosh (1989; see also McLaren & Mackintosh, 2000). According to this account, the relatively high level of consumption of BX shown on the test trial after preexposure to alternating trials of AX and BX is a consequence of the formation of inhibitory associative links between the unique features of these compounds, between A and B. No such effect can be expected, therefore, in a procedure in which the A feature is omitted, and some other explanation must be contrived for the results reported here (and by Rodríguez & Alonso, 2004).

The hypothesis proposed by Hall (2003) can accommodate both sets of results. The proposal is, for the case of perceptual learning, that alternating trials with AX and BX maintain the effective salience of B because the presentation of X on the AX trials is capable of associatively activating the B representation on those trials. According to this account, the presence of A is irrelevant to this process, and the effect should also be produced by alternation of BX and X. In both cases (i.e., both when A is presented and when it is not), the effective salience of B should be maintained, making B better able to interfere with the expression of an aversion established to X.

A further implication of this analysis is that the difference between B and C should be evident in tests other than that traditionally used in studies of perceptual learning, in which these cues are compounded with one that has undergone aversion conditioning. B should be more effective than C in attenuating any response controlled by an element with which it is compounded—if this element is particularly valued by the rat, the presence of B in the compound can be expected to produce a lower level of consumption than would the presence of C. This prediction was confirmed by the results of Experiment 1b. In this experiment, B and C were tested in compound with a saline solution (valued by the rat as a consequence of the injection of FuroDoca), and it was found that consumption of the compound containing C was greater than that of the compound containing B.

Experiments 2a and 2b

Our suggested explanation for the result obtained in Experiment 1 holds that the X-alone trials serve to offset, to some extent, the reduction in the effective salience of the B cue produced by its exposure on the BX trials. We have hypothesized that this effect is a product of associative learning—that the critical feature of presenting X alone is that the association between X and B formed on the BX trials allows X to activate the representation of B in the absence of B itself. The present experiments attempt to provide a test of this hypothesis by examining the effects of a preexposure schedule intended to reduce the likelihood that an excitatory X → B association will be formed on the compound trials.

The experimental design is outlined in Table 1. Its critical feature is that the preexposure phase involved the presentation of a serial compound rather than the simultaneous compound used in Experiment 1. Thus, the forward groups of Table 1 received preexposure consisting of alternating trials of X and the serial compound X → B. On trials of the latter type, they were allowed to drink a quantity of X; the drinking tube was then removed and was replaced by one containing the B flavor. This procedure can be expected to establish an excitatory X → B association, so that X will be able to activate the representation of B when X is presented alone on the intermixed trials. According to our hypothesis, the effective salience of B will be maintained at a higher level than in the control (backward) condition. Rats in the backward groups received just the same flavor presentations as those in the forward group, except that on the compound trials, the B flavor was made available before the X flavor (i.e., they received B → X trials). Our standard accounts of association formation (e.g., Wagner, 1981; Wagner & Larew, 1985) anticipate that no excitatory X → B association will be formed under these conditions or that any such association will be weaker than that formed by X → B presentations. X will not, therefore, be able to activate the B representation on the X-alone trials, and the decline in salience will proceed unopposed.

The procedures used to assess the effective salience of B in the two groups matched those used in Experiment 1. Thus, in Experiment 2a, the rats received conditioning trials designed to establish an aversion to X and then received test trials with BX. We predicted that B, being more salient in the forward group than in the backward group, would interfere with the expression of the aversion more effectively in the former than in the latter and that consumption on the test would be greater in the forward than in the backward group. In Experiment 2b, an injection of FuroDoca followed the preexposure phase, and the test consisted of a presentation of B plus saline. We predicted that in this case, consumption would be less in the forward group than in the backward group.

Method

The subjects for Experiment 2a were 16 male hooded Lister rats with a mean ad-lib weight of 474 g at the start of the experiment; a further 16 (with a mean ad-lib weight of 470 g at the start of the experiment) were used in Experiment 2b. The rats were maintained in the same way and on the same water deprivation schedule as was described for Experiment 1. The solutions used as experimental stimuli in Experiment 2a were as follows: as X, 0.00003 M quinine sulfate; as B, either 0.16 M saline (NaCl) or 0.165 M sucrose. The solutions used in Experiment 2b were as follows: 0.0825 M sucrose (X), 1% vanilla (B), and a compound of 1% vanilla and 0.08 M NaCl (B plus saline).

In both experiments, the animals were divided into two equal-sized groups for the preexposure phase. This lasted for 4 days. In one of the two daily drinking sessions in this phase, animals in the forward groups received access to a tube containing 5 ml of X for 5 min. At the end of this time, the tube was removed and replaced immediately with another tube

containing 5 ml of B; this tube was also removed after 5 min. Subjects in the backward groups received an identical treatment, except that the order of presentation of the solutions was reversed, with B being given first and X second. In the other daily session, all rats were given access to 5 ml of X for 5 min. For half of the subjects, the compound trial was presented in the morning session; for the remainder, it was presented in the afternoon session. In Experiment 2a, half of the subjects in each group received saline as X, and half were given sucrose.

After completion of the preexposure phase, all subjects in Experiment 2a were given two conditioning trials in which consumption of X was followed by an injection of LiCl. (We gave two trials, rather than the three given in Experiment 1a, on the assumption that acquisition would proceed more rapidly in this experiment, given that the preexposure phase involved fewer presentations of X and thus less opportunity for the development of latent inhibition.) There was a single test trial in which the simultaneous compound BX was presented. In Experiment 2b, all subjects received an injection of FuroDoca at the end of the preexposure phase, followed, on the next day, by a test trial in which 30 ml of the compound B plus saline was made available for 30 min. We were concerned that, with this single-bottle test procedure, rats in a state of salt need might drink so readily that any difference between the groups might be obscured. To address this potential problem, we attempted to increase the sensitivity of the test by weighing the drinking tubes at 10-min intervals during the test session. Any details not specified here were the same as those described for Experiment 1.

Results and Discussion

The conditioning trials of Experiment 2a were effective in producing an aversion to X. Both groups drank a mean of 9.4 ml on the first trial; on the second trial, the forward group drank 6.1 ml, and the backward group drank 5.0 ml. An ANOVA, with the variables of group and trial, produced a significant main effect of trial, $F(1, 14) = 34.07$. Neither the main effect of group nor the Group $\times$ Trial interaction were significant.

Group means for consumption of BX on the test trial are presented in Figure 2. It is apparent that the forward group drank substantially more than the backward group. An ANOVA conducted on these data, with group and time of preexposure (i.e., whether X alone was presented in the morning or the afternoon during preexposure), confirmed the reliability of the difference between the groups, $F(1, 12) = 8.57$. There was also a main effect of the time-of-preexposure variable, $F(1, 12) = 5.69$; the subgroup given X in the morning during preexposure drank less than the subgroup given X in the afternoon, the group means being 2.4 ml and 4.5 ml, respectively. This difference may reflect the fact that latent inhibition was a more powerful influence in the subjects that experienced exposure to X and conditioning at the same time of day. There was, however, no interaction between the variables ($F < 1$).

Figure 2 also shows the results for the test trial of Experiment 2b (cumulative means for consumption of B plus saline over the three 10-min bins of the test session). Here the pattern was reversed, with the forward group drinking less than the backward group. An ANOVA, with group and bin as the variables, produced a significant main effect of group, $F(1, 14) = 7.37$, and a significant main effect of bin, $F(2, 28) = 182.91$. The interaction between the variables was not significant ($F < 1$).

The pattern of results shown in Figure 2 is that predicted by the hypothesis that motivated these experiments. We argued that the effective salience of the B stimulus would be higher in the forward group than in the backward group and thus better able to interfere

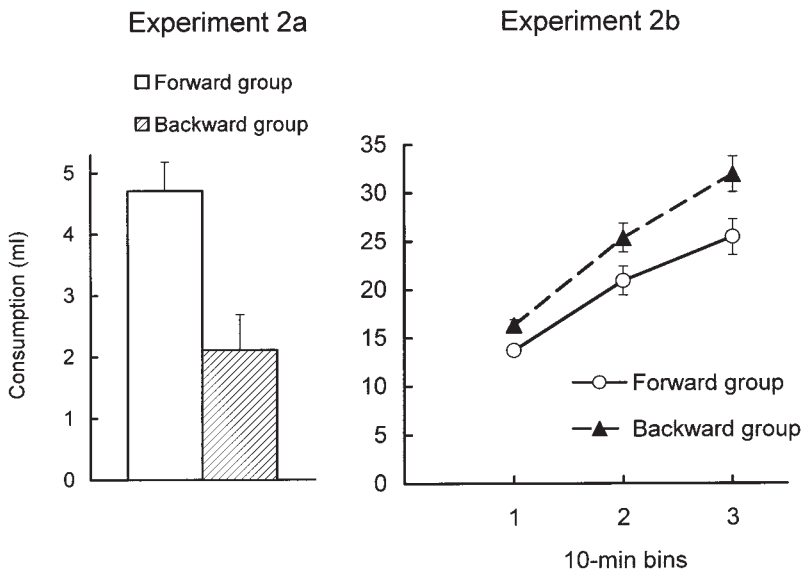

Figure 2. Experiment 2a: Group mean consumption of the compound flavor BX after aversion conditioning with X. The rats had received preexposure consisting of alternating trials with X and the BX compound. For the forward group, X preceded B on the compound trials; for the backward group, X followed B. Vertical bars represent the standard errors of the means. Experiment 2b: Group mean consumption of the compound B plus saline over the three 10-min bins of the test session, following induction of a salt need. The rats had received preexposure consisting of alternating trials with X and the BX compound. For the forward group, X preceded B on the compound trials; for the backward group, X followed B. Vertical bars represent the standard errors of the means.

with the response controlled by the stimulus with which this stimulus was compounded on the test. It should thus, for the forward group of Experiment 2a, attenuate the aversive response to X and enhance consumption of BX; in Experiment 2b, it should attenuate the appetitive response to saline, reducing consumption of B plus saline.

These results are thus consistent with the proposal that modulation of the effective salience of B depends on the formation of an excitatory X → B association. Given the nature of the stimuli used in these experiments, it is possible that such an association would be formed in both groups—the backward arrangement does not rule out the possibility that the immediate aftereffects of consuming B will be present when X is experienced, and in this case, an association might be formed that would allow X to activate B. But our standard accounts of association formation (e.g., Wagner, 1981) point to the conclusion that, whatever is true of the backward case, the excitatory X → B association will be better formed in the forward group.

Experiment 2c

Our explanation for the results of Experiments 2a and 2b holds that the X → B association is effective in maintaining the salience of B because it allows for the associative activation of B on X-alone trials during preexposure. But another possible interpretation requires consideration. It is known (e.g., Capaldi, Hunter, & Lyn, 1997; Fanselow & Birk, 1982) that flavor preferences can be modified by conditioning procedures in which the target flavor is paired with another that has a different hedonic value. Rats in the backward condition of Experiment 2a experienced the test flavor B followed by the (presumably somewhat aversive) quinine solution during preexposure. The formation of an association between B and its consequences might endow B with aversive properties, reducing the amount of BX consumed on the test (recall that in this experiment, the backward group consumed less than the forward group). In Experiment 2b, X was the (presumably valued) sucrose solution, and an association between B and X in the backward group might have served to increase the positive value of B and thus increase the amount consumed on the test of the compound containing B (recall that in Experiment 2b, the backward group drank more of B plus saline than did the forward group).

We do not think it likely that this process can be wholly responsible (if at all) for the results reported here. As applied to Experiment 2a, the hypothesis requires that consumption of BX on test be suppressed in the backward group by virtue of B's ability to activate the representation of X. It is difficult to see that this would have a major effect on behavior, given that the X representation would be directly activated by the relevant stimulus, which is actually present in the compound. (Indeed, according to Wagner's, 1981, theory, associative activation of the X representation should act to reduce the impact of the presentation of X itself in these circumstances.) Experiment 3a provides further data directly relevant to this matter.

The situation is different for Experiment 2b, as the X element was not present on the test (B being tested in compound with the novel saline solution), and in this case, we must acknowledge that the association of B with sucrose in the backward group might contribute to test performance shown by that group. In order to address this issue, we carried out a further experiment, identical to Experiment 2b, except that hedonically neutral solutions were used as B and X.

Method

The subjects were 16 male hooded Lister rats. They had served previously in a study of appetitive conditioning using operant techniques, but they were naive to the present stimuli and procedures. Their mean ad-lib weight at the start of this experiment was 380 g. The solutions used as experimental stimuli in the preexposure phase were 1% almond and 2% vanilla. The test phase made use of the following compounds: 0.08 M saline plus vanilla and 0.08 M saline plus almond.

As in Experiment 2b, the rats were divided into two groups for preexposure. On one of the two daily sessions, those in the forward group received access to X followed by access to B; those in the backward group received B and then X. X-alone was presented on the other daily session. For half of the rats in each group, X was almond and B was vanilla; for the remainder, the arrangement was reversed. All rats received an injection of FuroDoca at the end of the preexposure phase and a test of B plus saline on the following day. In respects not specified here, the procedure was the same as that described for Experiment 2b.

Results and Discussion

The results of the test session (cumulative means over three 10-min bins) are presented in Figure 3. As in Experiment 2b, the forward group drank less than the backward group. An ANOVA, with group and bin as the variables, revealed significant main effects of group, $F(1, 14) = 9.79$, and of bin, $F(2, 28) = 50.740$, and a significant interaction between the variables. Analysis of simple main effects showed there to be a significant difference between the groups in the amount consumed in Bin 1, $F(1, 42) = 27.15$, and in Bin 2, $F(2, 42) = 5.32$, but not in Bin 3 ($F < 1$).

This experiment has thus replicated the central finding of Experiment 2b using a procedure that rules out an explanation in terms of flavor preference conditioning. The critical flavors (al-

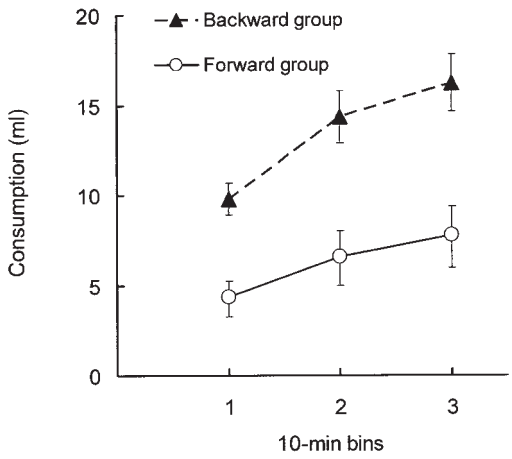

Figure 3. Experiment 2c: Group mean consumption of the compound B plus saline over the three 10-min bins of the test session, following induction of a salt need. The rats had received preexposure consisting of alternating trials with X and the BX compound. For the forward group, X preceded B on the compound trials; for the backward group, X followed B. Vertical bars represent the standard errors of the means. B, X, and C refer to flavors.

mond and vanilla) cannot be expected to support such conditioning as sucrose might, and furthermore which flavor served as B and which served as X in preexposure was counterbalanced. The result obtained follows directly from the suggestion that the maintained salience of B in the forward group allows that stimulus to interfere with the rat's normal appetitive response to saline.

Experiments 3a and 3b

The aim of these experiments was to confirm the reliability of the effect observed in Experiment 2 and to add a further control condition. We have attributed the effects seen in that experiment to the formation of an excitatory association between X and B in the groups given forward (i.e., X → B) pairings during preexposure, and we have suggested that this association is important because it allows the associative activation of B on the intermixed X-alone trials. We have already noted how flavor preference conditioning might occur in this procedure and now acknowledge that there is another possible mechanism by which this procedure might produce the results obtained. According to Wagner (1976, 1979), the progress of habituation of a target stimulus (B in our experiments) will be attenuated if it is either preceded or followed by some other event (a distractor) during the exposure trials. We know of no evidence that directly supports the proposition, but we must allow the possibility that a pretrial distractor might be more effective at retarding habituation than a posttrial distractor. If so, B would suffer less habituation in the forward (X → B) condition than in the backward (B → X) condition. The resulting difference in the effective salience of B might then generate the results obtained in Experiment 2, for just the reasons we have already discussed (i.e., the more salient cue will be better able to interfere with the response controlled by some other stimulus with which it is compounded on test). But the source of the difference would not lie, as we have hypothesized, in the ability of X to activate the B representation associatively. Indeed, the effect would be independent of presentations of X alone.

The present experiments examined this issue by investigating the case in which the subjects were given serial presentations of X and the target cue in preexposure but no intermixed presentations of X alone. The design of Experiment 3a is outlined in Table 1. The subjects received the same preexposure treatments as were used in Experiment 2a; that is, they received presentations of the serial compounds X → B or B → X intermixed with presentations of X alone. But in addition, they received a block of compound trials in which X was accompanied by another cue; that is, they received X → C (the forward group) or C → X (the backward group) without intermixed X-alone trials. As before, the test procedure consisted of establishing an aversion to X prior to trials on which the BX and CX compounds were presented. If maintenance of the effective salience of the target cue depends on the associative mechanism described previously, the effect should only be found for the case in which the subject experiences forward pairings, intermixed with X-alone trials. This account predicts, therefore, that consumption of BX should be greater than that of CX in the forward group but not in the backward group. In addition, consumption of BX should be greater in the forward group than in the backward group (replicating the finding of Experiment 2a). There is no reason, however, to predict a difference between BX and CX on the basis of differences in habituation, as, for the forward group, both B and C were preceded by a pretrial distractor during the exposure phase.

The results of this experiment will also be relevant to the attempt to explain the outcome of Experiment 2 in terms of flavor preference conditioning. The arrangement for the forward group, in which X (quinine) precedes the target cue, is unlikely to establish the relevant association, and to the extent that it does, its effects should be evident both for B and for C. Flavor preference conditioning could not, therefore, explain a difference in the forward group in consumption of BX and CX on the test. The relevant association could well be formed, however, in the backward group, in which X follows the target cue during preexposure; and the test with CX provides the opportunity to assess its effects on behavior. That is, when tested with CX, the C element should be able to activate the representation of X for the backward group but not for the forward group. We suggested, in discussing Experiment 2, that this asymmetry would be unlikely to produce any marked effect on behavior, given that the X element is physically present during the test. A failure to find a difference in the groups in their consumption of CX in the present experiment would confirm this suggestion. And if flavor preference conditioning is unable to generate a difference between the groups on the CX test, it seems implausible that it could be responsible for any difference between them observed on the test with BX.

Experiment 3b applied the same general logic to the salt need testing procedure, although in this case, we restricted investigation to the forward case. Thus, all subjects received preexposure consisting of intermixed trials of X → B and X, and a block of X → C trials. They were then tested in a state of salt need with the compounds B plus saline and C plus saline. If the X-alone trials play no part in producing the effect obtained in Experiment 2b, there should be no difference on test in consumption of these compounds. Our associative hypothesis, however, predicted that consumption of CX should be greater than that of BX.

Method

The subjects for Experiment 3a were 32 male hooded Lister rats with a mean ad-lib weight of 354 g at the start of the experiment. The experiment was run in two identical replications. In each replication, half of the animals were assigned to the forward group, and half were assigned to the backward group. The animals had previously been used in another experiment but were naive to all aspects of the current procedure. The subjects for Experiment 3b were 24 male hooded Lister rats with a mean ad-lib weight of 441 g at the start of the experiment. The experiment was run in three replications, each using 8 subjects. Of these 3 sets of rats, the 1st had previously been used in an unrelated procedure; the other 2 were experimentally naive.

The preexposure procedure used in Experiment 3a was similar to that described for Experiment 2a. That is, all subjects received 4 days' intermixed preexposure to the BX compound and to X, with rats in the forward group receiving X → B on the compound trials, and rats in the backward group receiving B → X. In addition, there were 2 days of blocked preexposure to the CX compound (to X → C for the forward group and to C → X for the backward group). Half of the subjects in each group were given the CX trials on the first 2 days of preexposure, and half were given the CX trials on the last 2 days of preexposure. As in Experiment 2a, X was quinine, and B and C were sucrose and saline (counterbalanced).

After completion of the preexposure phase, the subjects in Experiment 3a were given three conditioning trials in which consumption of X was followed by an injection of LiCl. Four test trials followed, two with each

of the compounds. Half of the rats in each group received the trials in the order BX, CX, CX, BX; half received them in the order CX, BX, BX, CX. In details not specified here, the procedure was as described for Experiments 1a and 2a.

The preexposure procedure in Experiment 3b was identical to that described for the forward group of Experiment 3a, except that the flavors used were sucrose as X and almond and vanilla (counterbalanced) as B and C. FuroDoca was administered 1 hr after the last preexposure session, and a choice test, between B plus saline and C plus saline, was given on the following day. In details not specified here, the procedure was as described for Experiment 1b and 2b.

Results and Discussion

The conditioning trials successfully established an aversion to X in Experiment 3a. Group means for the consumption of X in the conditioning phase were 9.1 ml on Trial 1, 8.8 ml on Trial 2, and 2.3 ml on Trial 3. All subjects consumed less on Trial 3 than on Trial 1. The results of the test phase are shown in Figure 4. Consumption was less suppressed on the second test trial than on the first, presumably reflecting the effect of extinction. But on both trials, the same pattern of within-group and between-groups differences was obtained. Rats in the forward group drank more of BX than of CX, rats in the backward group drank BX and CX equally, and the level of consumption in the backward group was the same as that shown for CX in the forward group.

An ANOVA was conducted on the data summarized in Figure 4, with trial, group, and stimulus (BX or CX) as the variables of principal interest. As in Experiment 1a, we also included in the analysis the counterbalanced factors of order of preexposure (whether trials with the CX serial compound were given in the first or last 2 days of preexposure) and time of preexposure (whether X-alone trials were given in the morning or afternoon sessions). This analysis revealed significant effects of trial, $F(1, 24) = 116.43$, and of group, $F(1, 24) = 4.10$, and a significant interaction of group, stimulus, trial, and preexposure order, $F(1, 24) = 5.10$. For all other effects and interactions, $F < 2$, except for the following: main effect of stimulus, $F(1, 24) = 2.18$; interaction of stimulus and preexposure order, $F(1, 24) = 2.28$; and interaction of trial, time, and order of preexposure, $F(1, 24) = 2.89$.

In order to elucidate the source of the significant four-way interaction, we conducted separate analyses, paralleling that just described, for each of the groups. The analysis for the forward group revealed a significant main effect of trial, $F(1, 12) = 104.26$, and of stimulus, $F(1, 12) = 4.94$. There was also a significant main effect of time of preexposure, $F(1, 12) = 5.23$, reflecting the fact that the aversion appeared to be stronger in subjects that were preexposed to X alone in the afternoon sessions; the group means, pooled over all test trials, were 5.7 ml for the subjects preexposed in the morning and 3.8 ml for the subjects preexposed in the afternoon. No other effects or interactions achieved significance. The equivalent analysis conducted on the data for the backward group revealed a significant main effect of trial, $F(1, 12) = 36.39$, but not of the critical variable, stimulus ($F < 1$). All other main effects and interactions were nonsignificant (largest $F = 1.46$), apart from the three-way interaction of trial, stimulus, and preexposure order, $F(1, 12) = 7.13$. This effect appears to reflect the fact that, on Trial 1 of the test, the subgroup given CX trials at the

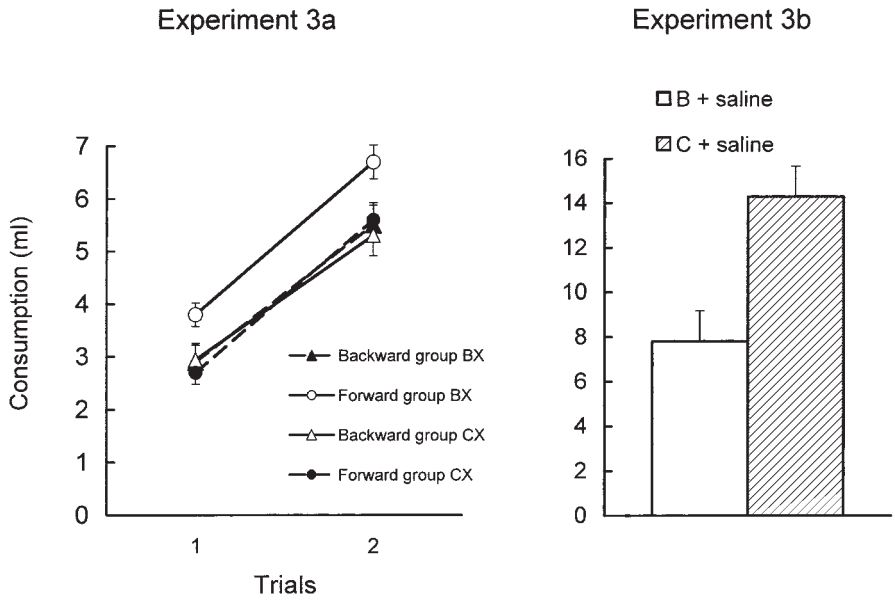

Figure 4. Experiment 3a: Group mean consumption of the compound flavors BX and CX after aversion conditioning with X. The rats had received initial preexposure to a block of trials with the serial compound CX and to alternating trials with X and the serial compound BX. For the forward group, X was presented first on the compound trials; for the backward group, X was presented second on the compound trials. Vertical bars represent within-subject standard errors. Experiment 3b: Mean consumption of flavor compounds B plus saline and C plus saline on the choice test given after induction of a salt need. The rats had received initial preexposure to a block of trials with the serial compound XC and to alternating trials with X and the serial compound XB. Vertical bars represent within-subject standard errors.

start of preexposure drank more of BX ($M = 3.7$ ml) than of CX ($M = 2.3$ ml), whereas the reverse was the case for the subgroup given CX trials at the end of preexposure (Ms = 2.1 for BX and 3.6 for CX). We do not know why this should have occurred, and separate analyses conducted on the data for these two subgroups revealed, in each case, no significant effects apart from that of trial.

Figure 4 also shows the results of the test session of Experiment 3b. Ten of the subjects consumed less than 2 ml of one of the flavors on offer during the test, and the means presented are for the remaining 14 subjects. (Of the subjects excluded, 5 drank very little of the compound containing B, and 5 drank very little of the compound containing C.) As Figure 4 shows, in this experiment, the animals drank saline compounded with B less readily than saline compounded with C. An ANOVA, with test stimulus and preexposure order as the variables, revealed a significant effect of stimulus, $F(1, 12) = 5.57$; neither the effect of preexposure order, $F(1, 12) = 1.29$, nor the interaction between the variables ($F < 1$) was significant. (The group mean scores with all subjects included were similar to those shown in Figure 4: 7.4 ml of B plus saline and 12.3 ml of C plus saline, $F[1, 23] = 3.35$, $.05 < p < .10$).

The results of Experiment 3b and of the forward group of Experiment 3a indicate that B is better able to interfere with the response controlled by X than is C. These two stimuli received the same treatment during preexposure in that each was preceded on each trial by a presentation of the X stimulus. Any pretrial distractor effects that operate in this situation should thus be equated for the two stimuli. It seems unlikely that excitatory associations between X and B and between X and C will be formed in this situation, but, to the extent that they are, they should be formed equally for both stimuli. The difference between the stimuli in their effects on the test trials may thus be attributed to the fact that BX was presented in alternation with presentations of X alone, whereas CX was not. This result appears to be uniquely predicted by the suggestion that, when preexposure allows the formation of an X → B association, X-alone trials are capable of restoring the salience lost by B as a consequence of its presentation on the compound trials.

The results for the backward group of Experiment 3a are in accord with this analysis. These subjects received preexposure equivalent to that given to the forward group, except that, for them, the order of presentation on the serial trials (with B preceding X) precluded the formation of a strong X → B association. In these circumstances, the inclusion of alternated X-alone trials was without effect—consumption of BX was no greater than that of CX.

General Discussion

Perceptual learning is demonstrated when preexposure to a pair of similar stimuli enhances the ability to discriminate between them. It has been suggested that the perceptual leaning effect will be best obtained with preexposure that allows the possibility that the subject will be able to compare the stimuli (e.g., when they are presented in alternation). Just such an effect has been frequently demonstrated with rats as the subjects and flavors as the stimuli. For example, rats given preexposure consisting of alternating trials with the flavor compounds AX and BX, and also a block of trials with the compound CX, subsequently showed better discrimination between BX and AX than between CX and AX—specifically, an aversion established to AX will generalize less readily to BX than to CX (e.g., Blair & Hall, 2003b). Here the critical stimuli (A, B, and C) were rendered similar by the addition of an explicit common element (X). Discrimination was better between the compounds presented in alternation (AX and BX) than between those presented on separate blocks of trials (AX and CX).

The explanation offered by Hall (2003) for these results (see also Blair & Hall, 2003b; Blair, Wilkinson, & Hall, 2004) was in terms of changes in the effective salience of the cues during preexposure. It was suggested that direct presentation of a cue will produce a reduction in its effective salience but that this reduction will be reversed, to some extent, on occasions when the central representation of the cue is activated associatively, in the absence of the cue itself. Alternating trials with AX and BX will thus maintain the effective salience of B, as the X → B association established on the BX trials will allow the presentation of X (on the AX trials) to activate the representation of B on the intermixed AX trials. When presented with BX after conditioning to AX, the relatively salient B will interfere with the expression of the aversion controlled by X, thus attenuating the magnitude of the generalized response.

The results obtained in the experiments reported here are in accord with this analysis. One implication of our account is that, because the critical feature of the intermixed AX trials is that the X element is able to activate the B representation, the presence of the A element is unnecessary—the salience of B should be maintained by alternating presentations of BX and X alone. Such a result has previously been reported by Rodríguez and Alonso (2004), and it was confirmed, for our training procedures, in the present Experiment 1. Our novel findings come from Experiments 2 and 3, which tested the hypothesis that the effectiveness of the X-alone trials depends on the existence of an excitatory X → B association. They showed that the salience of B was maintained when the presentations of X alone were alternated with X → B trials, a procedure likely to establish the X → B association. Alternation of X with B → X trials (a procedure less likely to establish the required association) was not effective in maintaining the salience of B.

Finally, it is appropriate to consider the mechanisms that might underlie changes in the effective salience of stimuli. That repeated presentation of a stimulus should result in a reduction in its effective salience is uncontroversial, to the extent that this effect can be equated with the phenomenon of habituation. The important question then becomes that of how theoretical accounts of habituation might accommodate the proposal that associative activation of a stimulus representation can reverse this process. The account of habituation offered by Groves and Thompson (1970) amounts to little more than the assertion that the organism becomes less sensitive to a stimulus (specifically that the pathway from stimulus to response becomes less effective) with repeated presentations of that stimulus. This seems to be offered as a basic, irreducible fact about how biological systems operate; that associative activation of a stimulus representation restores sensitivity could be given the same status.

The influential theory of habituation developed by Sokolov (1963) provides a more detailed possible account. According to Sokolov, habituation depends on the formation of a *neuronal model* of the stimulus, the gradual decline in responsiveness to the stimulus being a consequence of the improving match between the input and the, increasingly accurate, model. If presentations of BX

result in the formation of a model in which the co-occurrence of the two stimulus elements is represented, then it might be argued that presentations of X alone would disrupt this representation and reverse the habituation process. It is not immediately apparent, however, why such an effect should be best achieved by a procedure in which the BX and X trials are intermixed, nor why the effect should apparently depend on the formation of an excitatory association between X and B.

In these respects the, rather similar, account offered by McLaren and Mackintosh (2000) has an advantage. These authors proposed that preexposure to a complex stimulus results in the formation of a network of associations among its constituent elements; these will include not only associations between B and X but also associations among the various elements that constitute each of these notional stimuli. The theory holds that the loss of salience suffered by the target stimulus (B in our experiments) is largely a consequence of the formation of associations among its elements. (More precisely, but equivalently for our purposes, their theory postulates a mechanism that acts to boost the salience of a stimulus element that lacks associations.) Extinction of these associations will thus restore salience. According to the theory, extinction occurs when associated stimulus elements are activated associatively in the absence of the stimulus itself. Because intermixed presentations of X will produce just this state of affairs (by way of the association between X and the B elements), the theory can predict that this procedure will restore the salience of B.

Whatever the mechanism, the conclusion supported by the results of these and related experiments (e.g., Hall et al., 2005) is that the effective salience of a stimulus is determined not solely by the physical intensity of the event but by learning processes that can both reduce and enhance it. Any account of the nature of association formation that has a valid claim to comprehensiveness will need to incorporate an account of these processes.

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Received March 3, 2005
Revision received November 23, 2005
Accepted November 29, 2005 ■