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BRIEF COMMUNICATIONS

Enhanced Discrimination Between Flavor Stimuli: Roles of Salience Modulation and Inhibition

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Rats were given intermixed preexposure to the compound flavors *AX* and *BX* and to the compound *CX* in a separate block of trials (4 presentations of each compound). In Experiment 1, rats showed less generalization of conditioned aversion from *AX* to *BX* than from *CX* to *BX,* a perceptual learning effect. Experiment 2 showed that the formation of an excitatory association proceeded more readily between *A* and *B* than between *C* and *B,* suggesting that intermixed preexposure maintains the effective salience of *A* and *B* and does not establish inhibition between them, a process that would require prolonged preexposure. According to this analysis, salience modulation and associative inhibition may contribute to perceptual learning at different stages of preexposure.

Keywords: perceptual learning, salience modulation, inhibition

Appropriately scheduled preexposure to a pair of similar stimuli can reduce the extent to which generalization occurs between them (can increase their discriminability). Specifically, if the stimuli are presented during preexposure according to an intermixed schedule, subsequent discrimination between them will be easier than if they are presented on separate blocks of trials (e.g., Artigas, Sansa, & Prados, 2006; Bennett, Scahill, Griffiths, & Mackintosh, 1999; Blair & Hall, 2003; Dwyer, Hodder, & Honey, 2004; Honey, Bateson, & Horn, 1994; Symonds & Hall, 1995). Blair and Hall (2003) provided an example of this effect by using a within-subject procedure. Rats received four exposure trials with each of three compound flavor stimuli, *AX, BX,* and *CX*. Presentations of *AX* and *BX* were given according to an intermixed schedule, and presentations of *CX* occurred as a separate block of trials (presented either before or after *AX* and *BX*). Preexposure was followed by aversion conditioning with *AX* as the conditioned stimulus (CS), and generalization to *BX* and *CX* was then tested. The rats drank *BX* more readily than *CX*, thus showing better discrimination between the stimuli that were preexposed according to an intermixed schedule (*AX* and *BX*) than between those stimuli preexposed in separate blocks of trials (*AX* and *CX*). This scheduling effect has been taken to be an instance of perceptual learning and is the focus of extensive research and theoretical debate.

Gibson (1969) attributed perceptual learning to a process of *stimulus differentiation,* whereby the opportunity to compare stimuli (as in the intermixed arrangement) enhances the perceptual effectiveness of their unique features and reduces the effectiveness of features they hold in common. Blair and Hall (2003; see also Hall, 2003) offered a similar interpretation. They suggested that exposure to a stimulus normally produces a reduction in its effective salience, but that experience of similar stimuli presented in alternation tends to maintain the effectiveness of the unique features that distinguish them. According to this account, the preexposure procedure used by Blair and Hall would lead to a loss of effectiveness by the *X* and *C* elements, but the effectiveness of the *A* and *B* elements would be maintained. After conditioning trials with *AX*, the degree to which the subjects show an aversion to *BX* and *CX* is determined by the readiness with which they perceive the conditioned element (*X*). The more salient *B* element interferes with perception of *X* more effectively than the less salient *C,* and the aversion shown to the compound containing *B* is less than that shown to the compound *CX*.

An alternative explanation of this effect, one based on standard associative learning principles, has been developed by McLaren and Mackintosh (2000). According to their account, preexposure to *AX*, *BX,* and *CX* establishes a range of within-compound associations: *A–X, B–X,* and *C–X*. Additionally, the activation of *B* in the *AX* trials (by way of the *X–B* link) and of *A* in the *BX* trials (by way of the *X–A* link) establishes inhibitory links between *A* and *B,* and between *B* and *A*. However, presentation of *CX* in a separate block of trials is less likely to establish inhibitory links involving the *C* element. The existence of inhibitory associations between *A*

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and *B* could influence the extent to which a conditioned response established to *AX* generalizes to *BX* and *CX*. Conditioning trials with *AX* results in the formation of associations between *A* and the unconditioned stimulus (US) and between *X* and the US. When animals are tested with *CX*, their response is determined not only by the direct *X*–US association but also by the ability of *X* to activate the representation of *A* (by way of the *X*–*A* association) and thus to contact a representation of the US by way of the chain *X*–*A*–US. This latter source of responding is not available in test trials with *BX* because the presence of *B* inhibits activation of the representation of *A*. The result is a weaker conditioned response to *BX* than to *CX*.

Indirect support for this associative hypothesis comes from experiments on the Espinet effect—the observation that, after prolonged intermixed preexposure to *AX* and *BX*, pairing *A* with a reinforcer allows *B* to act as an inhibitor for that reinforcer (Espinet, Iraola, Bennett, & Mackintosh, 1995). According to McLaren and Mackintosh (2000), the Espinet effect (like the perceptual learning effect) occurs because of the ability of *B* to inhibit *A* (and its associate, the US) at the time of test. It may be noted, however, that although the Espinet effect is found only after prolonged preexposure to *AX* and *BX* (Espinet et al., 1995, Experiment 4), perceptual learning has been shown to occur after shorter preexposure. In a recent study, Artigas et al. (2006) observed that long intermixed (as opposed to blocked) preexposure produced a reliable Espinet effect, which was not found after shorter preexposure (confirming the original findings of Espinet et al., 1995). However, perceptual learning was observed after both short and long preexposure, and thus under conditions in which no evidence could be found for inhibitory properties of *B*. This result casts doubts on the associative analysis proposed by McLaren and Mackintosh (2000). However, as Artigas et al. acknowledged, this conclusion rests on a null result—on the failure to find inhibitory properties in *B* after short intermixed preexposure. It remains possible that inhibitory links between *B* and *A* were formed even during short preexposure but that the tests that were used in this study were less sensitive to the inhibitory properties of *B* than the generalization test used in the perceptual learning procedure.

A more direct, and possibly more sensitive, measure of inhibition between *A* and *B* has been used by Dwyer, Bennett, and Mackintosh (2001; see also Dwyer & Mackintosh, 2002). In their procedure, rats received direct pairings of *A* (a saline solution) and *B* after either intermixed or blocked preexposure to *AX* and *BX*. A state of salt need was then induced, and the animals were tested with flavor *B*. The readiness with which *B* is consumed in these circumstances can be taken to reflect the strength of the excitatory association formed between *B* and saline (*A*) as a result of the *A*–*B* pairing. Dwyer et al. found that subjects given intermixed preexposure to *AX* and *BX* drank less of *B* than did subjects given blocked preexposure. They interpreted this result as indicating that intermixed preexposure had established inhibitory links between *A* and *B* that retarded the acquisition of excitation during the *A*–*B* pairing. Although this result is consistent with the associative account of perceptual learning proposed by McLaren and Mackintosh (2000), it should be noted that it was obtained after prolonged preexposure (eight trials with each compound stimulus). It still has not been established, therefore, whether evidence for inhibition between *A* and *B* can be obtained with the briefer exposure durations that have been used in recent demonstrations of the perceptual learning effect. This was our aim in the experiments reported here.

Our experiments used a version of the within-subject preexposure procedure developed by Blair and Hall (2003). Rats received preexposure consisting of alternating trials with *AX* and *BX*, and a separate block of *CX* trials (with just four presentations of each compound). For half the subjects (the intermixed group) the *A* stimulus was salt, and for the other half (the blocked group) the *C* stimulus was salt (see Table 1). We then gave all subjects the pairing of *B* and salt and assessed the strength of the *B*–salt association by measuring consumption of *B* when the animals were in a state of salt need. According to the associative inhibition account, the *B*–salt association should have been less strong in the intermixed group than in the blocked group, and consumption of *B* on test should have been lower in the former group (as in the effect reported by Dwyer et al., 2001). Alternatively, the salience modulation account predicts that the preexposure procedure leaves *A* and *B* with higher effective salience than *C*. This being the case, there was no reason to expect a retardation of acquisition of the *A*–*B* association—in fact, if both stimuli are high in salience, the association should be formed more readily than that between *A* and *C* (for which one of the stimuli, *C,* is presumed to have a low level of effective salience).

The study we just outlined forms our Experiment 2. Its implications for the interpretation of the perceptual learning effect rest on the assumption that the preexposure procedures it uses would be effective in generating such an effect. However, because the specific stimuli and procedures were rather different from those

Table 1
Design of Experiments 1 and 2

Group	Phase 1 (preexposure)	Phase 2	Phase 3 (test)
	Experiment 1		
Intermixed	*A*(salt)*X*/*BX*–*CX*	salt–*X* (+)	*BX*
Blocked	*AX*/*BX*–*C*(salt)*X*	salt–*X* (+)	*BX*
	Experiment 2		
Intermixed	*A*(salt)*X*/*BX*–*CX*	salt–*B*	(SA) *B*
Blocked	*AX*/*BX*–*C*(salt)*X*	salt–*B*	(SA) *B*

Note. *A, B, C,* and *X* represent different flavors. *X* was citric acid. For the intermixed group, *B* and *C* were vanilla and almond (counterbalanced), and *A* was salt; for the blocked group, *A* and *B* were vanilla and almond (counterbalanced), and *C* was salt. + represents an intraperitoneal injection of LiCl, 0.15 M, 10 ml/kg; SA represents the induction of a sodium appetite. Flavors separated by a forward slash (/) in Phase 1 were presented on alternate trials; the other flavor was presented on a separate block of trials.

used in previous studies using this general experimental design, we thoughT it necessary to confirm this assumption directly in a preliminary experiment (Experiment 1).

Experiment 1

In Experiment 1, we gave rats preexposure identical to that just described (see Table 1) but followed this with aversive conditioning with the salt–*X* compound as the CS. We then tested generalization to *BX*. A perceptual learning effect would be demonstrated if the intermixed group, which had received presentations of *BX* in alternation with salt–*X* in preexposure, showed less generalization than the blocked group, which had received these two compounds on separate blocks of trials during preexposure.

Method

Subjects and apparatus. The subjects were 16 male hooded Long Evans rats (*Rattus norvegicus*), with a mean ad lib weight of 415 g at the start of the experiment. The animals had previously been used in an experiment involving a spatial task in the Morris swimming pool. They were housed in individual cages in a colony room that was artificially lit from 9:00 a.m. to 9:00 p.m. daily. They were given continuous access to food, but access to water was restricted as detailed below.

The solutions used as experimental stimuli were administered in the home cages at room temperature in a 50-ml plastic centrifuge tube fitted with a rubber stopper and a stainless steel drinking spout. The following flavor solutions were used: a compound consisting of 0.05% wt/vol of citric acid and 1% vanilla solution (1% vol/vol vanilla flavoring supplied by Supercook, Leeds, United Kingdom); a compound consisting of 0.05% wt/vol of citric acid and 2% almond solution (2% vol/vol Supercook almond flavoring); a compound consisting of 0.05% wt/vol citric acid and 1% wt/vol saline. Fluid consumption was measured by weighing the tubes.

Procedure. The experiment started with a water deprivation schedule. The standard water bottles were first removed overnight. On the following 4 days, access to water was restricted to two daily sessions of 30 min each initiated at 11:00 a.m. and 4:00 p.m. Subjects continued to receive fluids at these times throughout the experiment. On the last day of this cycle, water intakes were measured, and subjects were assigned to two equal-sized groups matched by levels of water consumption. During the course of the experiment, 2 animals belonging to the intermixed group died, so the data for this condition are for a group of 6 subjects.

Over the next 6 days (the preexposure phase), all the subjects received four 10-ml presentations of the three flavors, *AX*, *BX*, and *CX*, always presented for 30 min at 11:00 a.m. and 4:00 p.m. In the intermixed group, half of the subjects were given 4 days intermixed access to flavors *A*(salt)–*X* and *BX*; half the rats were given access to *A*(salt)–*X* in the morning session and *BX* in the afternoon session, whereas for the other half, the order was reversed. The next 2 days consisted of blocked presentations of *CX*. The remainder of the subjects received the blocked presentations of *CX* on the first 2 days of the phase, followed by 4 days of intermixed access to *A*(salt)–*X* and *BX*. In the blocked group, half of the animals were given 4 days intermixed access to *AX* and *BX*. Half the rats were given access to *AX* in the morning session and *BX* in the afternoon session, whereas for the other half the order was reversed. The next 2 days consisted of blocked presentations of *C*(salt)–*X*. The remainder of the subjects received the blocked presentations of *C*(salt)–*X* on the first 2 days of the phase, followed by 4 days of intermixed access to *AX* and *BX*. For all the animals, *X* was citric acid. The flavors *A* and *B* were counterbalanced, with half of the animals receiving almond as *A* and vanilla as *B* and half receiving the reverse arrangement.

The next 6 days constituted the conditioning phase. On the day after the end of the preexposure, the first conditioning trial was given in which all the subjects were presented with 10 ml of salt–*X* followed by an intraperitoneal injection of 0.15 M LiCl at 10 ml/kg of body weight. The next day constituted a recovery day, on which rats received two 30-min sessions of free access to water. This 2-day cycle was then repeated twice. Over the next 2 days, all subjects were given free access to *BX* in the morning drinking session for 30 min.

Results and Discussion

Although the rats often did not drink the full 10 ml offered on the preexposure trials, there were no marked differences in consumption between the groups or among the different flavors. Group means for consumption of salt–*X* over the four preexposure trials with this compound were 6.16 ($\pm SEM = 0.46$) ml for the intermixed and 6.46 (0.40) ml for the blocked group. The equivalent means for the almond–*X* compound were 5.32 (0.71) ml and 4.59 (0.46) ml, and the equivalent means for the vanilla–*X* compound were 5.90 (0.37) ml and 5.03 (0.66) ml. An analysis of variance (ANOVA) conducted on these data, with group and flavor as the variables, showed that there were no significant differences between the groups or the flavors and that the Group × Flavor interaction was not significant; largest $F(2, 24) = 3.27$. (Here and elsewhere, a significance level of $p < .05$ was adopted.)

Conditioning successfully established an aversion to the salt–*X* compound in both groups. Group means for consumption of salt–*X* during the three conditioning trials were 8.61 ($\pm SEM = 0.23$), 3.87 (1.52), and 0.44 (0.12) ml for the intermixed group and were 8.35 (0.23), 4.28 (1.05), and 0.30 (0.07) ml for the blocked group. An ANOVA with group and trial as the variables revealed a significant effect of trial, $F(2, 24) = 36.01$. Neither the effect of group nor the Group × Trial interaction was significant; largest $F(2, 24) = 1.05$.

Figure 1A shows group mean scores for consumption of *BX*, pooled over the two test trials. Subjects in the intermixed group drank more of *BX* than subjects in the blocked group. An ANOVA conducted on the data for *BX* consumption showed a significant

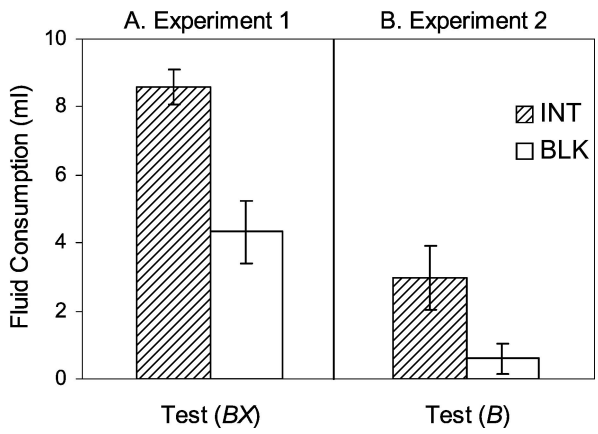

Figure 1. (A): Group means for consumption of flavor *BX* (pooled over two trials) in the test phase of Experiment 1. (B): Group means for consumption of flavor *B* in the test phase of Experiment 2. Vertical bars represent the standard error of the mean. In Experiment 1, all subjects received aversion conditioning with salt–*X* as the CS; for the intermixed (INT) group, salt–*X* had been preexposed in alternation with *BX*; for the blocked (BLK) group, salt–*X* had been preexposed on a separate block of trials. In Experiment 2, the same preexposure schedule preceded pairing of salt and *B,* and the final test was given in a state of salt need.

effect of group, $F(1, 12) = 12.44$. This outcome confirms that the perceptual learning effect (less generalization from salt–*X* to *BX* after intermixed than after blocked preexposure) can be obtained with the preexposure regime used here.

This result can be attributed either to inhibition between salt and *B* in the intermixed preexposure condition or to differential changes in salience among the elements of the preexposed stimuli. According to the associative inhibition account, the formation of inhibitory associations between *A* and *B* in the intermixed group during the preexposure phase reduced generalization from *AX* to *BX* because *B* inhibited the *A* element (and thus prevented activation of its associate, the US) in the test trials with *BX*.

The salience modulation account predicts the same outcome but for different reasons. Alternated preexposure to *A*(salt)–*X* and *BX* in the intermixed group (and the presentation of *CX* in a separate block of trials) would lead to a loss of effectiveness by the *X* and *C* elements, but the effectiveness of the salt and *B* elements would be maintained. For the blocked group, presentations of *C*(salt)–*X* in a separate block of trials (and alternated trials with *AX* and *BX*) would lead to a loss of effectiveness by the salt and *X* elements but would maintain the salience of the *A* and *B* elements. The presence of a relatively salient salt element in the salt–*X* compound during conditioning in the intermixed group would interfere with the processing of the *X* element, thus reducing the likelihood that *X* would become a good predictor of the US. For the blocked group, however, the presence of the less salient salt element would allow *X* to become a better predictor of the US. Better conditioning of the common element *X* in the blocked condition would result in more generalization from salt–*X* to *BX*.

The salience modulation account might also be taken to predict that the presence of the salient salt element should result in acquisition to the salt–*X* compound occurring more rapidly in the intermixed than in the blocked condition. That no such effect was observed during the conditioning trials of this experiment is, however, not surprising. The rapid learning produced by the conditioning parameters used in this experiment makes the course of acquisition quite insensitive to differences in CS salience. Previous experiments with preexposure and conditioning parameters comparable with those used here (Blair, Wilkinson, & Hall, 2004; Hall, 2003; Mondragón & Hall, 2002) have uniformly found no evidence for CS salience effects over the course of acquisition (even though the presence of the expected differences was readily revealed subsequently over a series of tests carried out in extinction).

The results of Experiment 1 cannot (indeed were not intended to) allow a choice between the alternative interpretations (i.e., between associative inhibition and salience modulation). They do, however, demonstrate the existence of the basic perceptual learning effect for the preexposure procedure that we used in Experiment 2.

Experiment 2

The experiment involved two groups that were given intermixed or blocked preexposure, as in Experiment 1. After preexposure, salt was paired with *B*. We then induced a state of salt need in the animals and tested the appetitive properties of *B* in a final test trial. According to the associative inhibition account, inhibitory associations between the unique elements salt and *B* interferes with the establishment of an excitatory *B*–salt association, and consumption of *B* on test should be lower in the intermixed than in the blocked group. On the other hand, the salience modulation account states that *B* and salt elements maintain their effectiveness after alternated preexposure in the intermixed group, but the salt element is less effective after blocked preexposure. In accordance with this account, the *B*–salt association should be stronger in the intermixed group, and consumption of *B* on test should be higher in that group than in the blocked group.

Method

The subjects were 16 naive male hooded Long Evans rats, with a mean ad lib weight of 356 g at the start of the experiment. They were maintained in the same way and on the same water-deprivation schedule as was used in Experiment 1. In addition to the flavors used in Experiment 1, we made use of the following compounds in Phase 2: 1% wt/vol saline and 1% vol/vol vanilla; 1% wt/vol saline and 2% vol/vol almond. The solution presented in Phase 3 was either 1% vol/vol vanilla or 2% vol/vol almond. The treatment used to induce a sodium appetite was a subcutaneous injection of 0.5 ml of a mixture of 200 mg of furosemide (Furo) and 100 mg of deoxycorticosterone acetate (Doca) dispersed in 10 ml of distilled water with 1 drop of Tween 80.

Phase 1 of the experiment (preexposure) proceeded exactly as described for Experiment 1. On the day following the final day of preexposure, all the animals were given access to 10 ml of a salt–*B* compound at 11:00 a.m. Five hours later, all the subjects received an injection of Furo–Doca. The food was then removed from the home cages in the colony room, and the subjects were given access to distilled water overnight. On the next day, the distilled water was removed from the cages 3 hr prior to the test session. The test was initiated at noon and consisted of a 30-min session in which the subjects had free access to flavor *B* (almond or vanilla).

Results and Discussion

The mean consumption of the salt–*X* compound during the four preexposure trials was 6.46 ($\pm SEM = 0.42$) ml for the intermixed and 7.27 (0.17) ml for the blocked group. The equivalent scores for the almond–*X* compound were 6.22 (0.22) ml and 6.03 (0.61) ml, respectively, and the equivalent scores for the vanilla–*X* compound were 6.05 (0.41) ml and 6.01 (0.50) ml, respectively. An ANOVA conducted on these data, with group and flavor as the variables, showed that there were no significant differences between groups or flavors and that the Group × Flavor interaction was not significant; largest $F(2, 28) = 2.06$.

Group mean consumption of the salt–*B* compound during the Phase 2 trial was 8.20 ($\pm SEM = 0.25$) ml for the intermixed group and 8.30 ($\pm SEM = 0.28$) ml for the blocked group. A one-way ANOVA showed no significant difference between the groups on this trial ($F < 1$). The results for the test trial with *B* are shown in Figure 1B. Levels of consumption were low—the rats were only mildly water deprived in an attempt to ensure that their drinking would be controlled by the state of salt need rather than by thirst. Indeed, subjects in the blocked condition barely drank any of solution *B*, suggesting that for them, the association between *B* and saline was weak or nonexistent. This is the outcome to be expected on the basis of the suggestion that the salience of saline was low for this group. As the figure shows, however, subjects in the intermixed condition drank *B* rather more readily, and the difference between the groups proved to be statistically reliable, $F(1, 14) = 5.06$. This result indicates that the *B*–salt association was better formed in the intermixed group than in the blocked group. It lends no support, therefore, to the hypothesis that intermixed preexposure establishes inhibition between *B* and salt—such inhi-

bition would be expected to retard the formation of the *B*–salt association. It is consistent, however, with the prediction of the salience modulation account, that the effective salience of salt will be higher in the intermixed than in the blocked condition.

General Discussion

In both experiments reported here, the rats received preexposure consisting of alternating trials with *AX* and *BX* and a separate block of *CX* trials. There were four presentations of each compound cue, and the schedule of presentation followed that used by Blair and Hall (2003) in their study of perceptual learning. Experiment 1 showed that generalization between *AX* and *BX* was less marked than that between *CX* and *BX*, confirming that this procedure generates a perceptual learning effect. Experiment 2 demonstrated that the formation of an excitatory association proceeded more readily between *B* and *A* than between *B* and *C*. This outcome is anticipated by the salience modulation account of perceptual learning, which supposes that the *B*–*A* association involves cues that are both high in salience, whereas the association between *B* and *C* involves a cue, *C,* that is low in salience. The suggestion that the preexposure procedure used here establishes inhibitory links between *A* and *B* receives no support from this result; that is, there was no evidence that formation of an excitatory association between *A* and *B* was retarded as a result of preexposure.

Taken together with the results of Artigas et al. (2006), the present findings confirm that the development of inhibition between *B* and *A* is not necessary for the perceptual learning effect to be observed. (Artigas et al., 2006, demonstrated that 4 preexposures to each of the cues produced the perceptual learning effect but not the Espinet effect, which was taken to be diagnostic of inhibition.) This is not to assert that alternating exposure to *AX* and *BX* is incapable of establishing inhibition between the unique features. When Artigas et al. gave more extensive preexposure (10 presentations of each cue), the Espinet effect was observed. Further, Dwyer et al. (2001) obtained direct evidence of inhibition (retardation of the formation of an excitatory *A*–*B* association) in rats given 8 presentations of each cue in preexposure.

The implication of this pattern of results may be that, although salience modulation is responsible for the perceptual learning effect seen after relatively brief preexposure, associative inhibition is responsible for, or contributes to, the effect seen after longer preexposure. Indeed, this conclusion may be a necessary corollary of accepting the salience modulation mechanism proposed by Hall (2003). According to this account, the salience lost when a stimulus is presented on one trial during alternating preexposure is restored (at least to some extent) when the representation of that stimulus is activated associatively on the next—thus, for example, *A* loses salience on an *AX* trial, but salience is restored when *A* is activated associatively (by way of an *X*–*A* link) on the following *BX* trial. This hypothesis does not preclude the possibility that such a sequence of trials will lead to the formation of inhibition between *A* and *B*—a mechanism that would help discrimination of *AX* from *BX*. This may take many trials to develop, but once it has developed, *B* is able to inhibit activation of *A* on *BX* trials, and *A* is able to inhibit activation of *B* on *BX* trials. At this point, the salience modulation mechanism envisaged by Hall (2003) is unable to operate—*A* and *B* continue to lose salience on the trials on which they are presented, and this loss is not opposed by associative activation of their representations on the intervening trials. Therefore, it may be inappropriate to treat the theoretical accounts discussed here as alternatives. Instead, we conclude that salience modulation and associative inhibition contribute to perceptual learning at different stages of preexposure.

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