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Mechanisms of Perceptual Learning: Prolonged Intermixed Preexposure Reduces the Effectiveness of the Unique and the Common Elements

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In three experiments, rats were given intermixed or blocked preexposure to two similar compound stimuli, AX and BX. In Experiment 1, following preexposure, animals were given appetitive conditioning training with the compound AX. A subsequent generalization test showed better discrimination between AX and BX in the group given intermixed than in the one given blocked preexposure. Experiments 2 and 3 assessed the nature of the learning mechanisms underlying this instance of the perceptual learning effect. Experiment 2 assessed the associability of the common and unique elements (X and A); animals in the group given intermixed preexposure showed poorer conditioning with both the X and the A elements than those given blocked preexposure. Experiment 3 further assessed the perceptual effectiveness of the distinctive element A using a superimposition test (the capacity of A to interfere with the conditioned response commanded by an independent conditioned stimulus). The results showed, in line with the outcome of Experiment 2, that the unique element A is more salient following blocked than intermixed preexposure. These results are discussed by reference to current theories of perceptual learning.

Keywords: perceptual learning, salience modulation, differential representation hypothesis, elemental learning, configural learning

Mere exposure to a stimulus is known to trigger learning processes that change its ability to serve as a classically conditioned stimulus or conditional stimulus (CS); an example would be the latent inhibition procedure (e.g., Lubow, 2010). Similarly, exposure to more than one stimulus without explicit consequences has been shown to modify their discriminability (e.g., Hall, 1991). For example, intermixed exposure to two similar stimuli sharing common elements, AX and BX, where A and B refer to the unique elements of each stimulus and X to their common features, has been shown to result in improved discrimination—comparison made to a group in which AX and BX are exposed in separate blocks of trials (e.g., Honey et al., 1994; Prados et al., 2004; Symonds & Hall, 1995). This intermixed/blocked effect, an instance of perceptual learning, has been intensively researched, and several processes have been shown to contribute to the enhanced discriminability between AX and BX after intermixed preexposure. The basic mechanism enhancing the discriminability of AX and BX seems to be associative in nature. According to McLaren and Mackintosh (2000) and Hall (2003), preexposure allows for the establishment of excitatory associations between the elements of the compound: between A and X and between B and X (see, e.g., Polack & Miller, 2018; Rodríguez & Alonso, 2014).

Although this within-compound association would increase the mediated generalization (through the common element, X) between the compound stimuli AX and BX, other learning processes counteract this tendency and contribute to enhance their discriminability. There is a strong body of evidence indicating that differential processing of the unique features (A and B) in the intermixed and blocked preexposure procedures determines the intermixed/blocked effect. Once the within-compound associations are established, the elements A and B can be associatively activated in the intermixed preexposure procedure (B is activated by X in the AX trials by virtue of its association with the common element, and A in the BX trials). On the contrary, the blocked preexposure procedure offers very limited opportunities for the associative activation of the unique elements. Associative activation of the unique elements in the intermixed schedule has been argued to counteract the X mediated generalization in two different ways.

McLaren and Mackintosh (2000; see also McLaren et al., 1989) suggested that associative activation of the unique elements A and B in alternating trials would result in the establishment of inhibitory associations between them. The development of such inhibitory links would require the completion of several steps: first, the

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development of excitatory links between the unique and common elements (A-X and B-X); this would allow an effective associative activation of A in the BX trials (and B in the AX trials). Given that A and B are predictors of the absence of each other, according to standard learning theory, we could expect the establishment of inhibitory links between A and B that would eventually match the strength of the within-compound excitatory associations. The establishment of effective inhibitory links between the unique elements would require a relatively long preexposure phase. The intermixed/blocked effect has been typically investigated in flavor discrimination tasks in which animals are given four preexposure trials with each flavor compound stimulus (Symonds & Hall, 1995). Artigas, Sansa and Prados (2006) compared the development of inhibitory links following short and long preexposure (four and 10 trials). Retardation and summation tests showed evidence of the establishment of inhibitory links between the unique elements only after long preexposure (the Espinet effect; see Artigas et al., 2001; Espinet et al., 1995; see also Polack & Miller, 2018, for converging evidence about the development of inhibitory associations following intermixed prolonged preexposure using a fear conditioning task). However, they observed the intermixed/blocked effect (improved discrimination between AX and BX) both after short and long preexposure. This study suggests that although the perceptual learning effect can indeed depend on the establishment of inhibitory links under some circumstances (long preexposure; see for additional evidence Bennett et al., 1999; and in human flavor aversion, Mundy et al., 2006), a different mechanism seems to be responsible for the effect when the animals are given short preexposure to AX and BX.

As an alternative, Hall (2003) has proposed that associative activation of the unique elements A and B protects their salience or effectiveness in the intermixed but not in the blocked procedure—in which the opportunities for the associative activation of the unique elements are limited (see Hall et al., 2005, for independent evidence on the role of associative activation in the modulation of the salience of stimuli). Following intermixed preexposure, the more salient A and B elements facilitate the discrimination between AX and BX (e.g., Artigas, Sansa, Blair, et al., 2006; Blair & Hall, 2003). Blair and Hall (2003) reported an ingenious procedure to assess the intermixed/blocked effect using a within-subjects procedure: Animals were given intermixed preexposure to AX and BX preceded or followed by a separate block of trials with a third similar compound, CX. Generalization tests showed that a conditioned aversion to AX generalized more readily to the CX than to the BX compound, showing that animals discriminate well between compound stimuli preexposed in alternation (AX and BX) but not so well between those preexposed in different blocks of trials (AX and CX). Blair and Hall reported additional evidence indicating that the unique element B, preexposed in alternation, was more salient than the unique element C, preexposed in a separate block of trials. Following preexposure to AX, BX, and CX, the animals were given conditioning trials with a new stimulus, Y, followed by test trials with the compounds YB and YC—a superimposition test. The results showed that, although the animals received the same level of preexposure to B and C, the presence of B interfered with the expression of the aversive conditioned response to Y significantly more than the presence of the C element. Additional evidence for the protected salience of the unique elements during the intermixed preexposure procedure has been reported by Mondragón and Hall (2002).

The two approaches reviewed above suggest that perceptual learning, exemplified by the intermixed/blocked effect, can be multidetermined. Although the two theories considered rely upon different associative mechanisms, they share the emphasis on the role of the unique elements A and B in the intermixed/blocked effect. According to these accounts, however, the salience or effectiveness of the common element X would be similar after both schedules of preexposure: The element X, present in every trial, is never associatively activated and receives equal amounts of preexposure in both preexposure procedures. This would suggest that the common element X does not play a significant role in the intermixed/blocked effect. A number of studies have assessed the salience of the X element following intermixed and blocked preexposure and using a variety of strategies.

Bennett and Mackintosh (1999) and Mondragón and Hall (2002), using a flavor aversion preparation, assessed the associability of the common element X when used as a CS. The two studies failed to observe any differences in conditioning following intermixed and blocked preexposure to AX and BX. However, Mondragón and Hall (2002) found evidence that X was more resistant to extinction after blocked preexposure. This result could be taken as evidence for better learning during the acquisition phase, suggesting that the common element acquires higher associative strength. However, as the authors of the study pointed out, it could also reflect the rate at which the animals learn during the extinction phase: Higher levels of extinction in the intermixed condition could indicate that the common element X is actually more salient or effective than in the blocked preexposure procedure. Hall (2020a) reports a number of very similar experiments (using flavor aversion) that failed to observe any differences in the rates of acquisition and extinction of the X element following intermixed and blocked preexposure. Additionally, the perceptual effectiveness of X was assessed by measuring its capacity to interfere with the expression of a conditioned response commanded by an effective CS (a superimposition test). These experiments revealed no differences between the intermixed and blocked conditions, reinforcing the notion that the salience of the common element X is not differentially affected by the intermixed and blocked preexposure procedures (Hall, 2020a).

In contrast with the studies that have used flavor aversion conditioning, studies using a standard Pavlovian appetitive task have reported some evidence to suggest that the salience of the common element could be better preserved in the blocked than in the intermixed condition. Mondragón and Murphy (2010) gave rats preexposure to two similar auditory stimuli, AX and BX, according to an intermixed or a blocked procedure. This was followed by conditioning trials in which AX was reinforced with a food unconditioned stimulus and, finally, test trials with the BX compound (a generalization test). The animals showed better discrimination between AX and BX following intermixed than blocked preexposure, the basic intermixed/blocked effect. Interestingly, in two separate experiments, Mondragón and Murphy also found evidence that X was less salient or effective following intermixed than blocked preexposure. When the animals were given conditioning trials with the X element, although there were no differences in the acquisition of the conditioned response, subsequent test trials showed better extinction in the group that had been given intermixed preexposure. However, as suggested above, this could be evidence for higher extinction learning in the intermixed condition (which might suggest that X is actually more salient than in the blocked condition). In a final experiment, they found that the X element was more effective in the group given blocked preexposure in overshadowing the acquisition of a conditioned response by a new element, Y, in YX conditioning trials (Mondragón & Murphy, 2010, Experiment 4).

The suggestion that the salience of X might be better preserved in the blocked than in the intermixed preexposure procedure led Artigas and Prados (2014, 2017) to hypothesize that preexposure to AX and BX could improve the discrimination between two new compound stimuli, NX and ZX, on the condition that they shared the same common elements. Assuming that no generalization is observed from the preexposed unique features, A and B, to the novel features used in a test, N and Z, this perceptual learning transfer could be taken as additional evidence for the differential salience of X after intermixed and blocked preexposure. In two series of experiments using flavor aversion and appetitive conditioning procedures, Artigas and Prados reported this perceptual learning transfer effect, reinforcing the notion that blocked preexposure triggers learning mechanisms that preserve the salience of the common element X. Some doubts have been cast on this conclusion on the basis that generalization from the highly salient unique features A and B could be generalized to N and Z (e.g., Hall, 2020b). This possibility was cast off in the experiments using aversion conditioning, where the two pairs of stimuli (AB and NZ) belonged to different sensory modalities, flavors and odors (Artigas & Prados, 2014). In the experiments using an appetitive conditioning task, however, this possibility could not be easily avoided since the two pairs of stimuli belonged to the same modality—they were all pure tones (Artigas & Prados, 2017).

All in all, the evidence supporting the notion that intermixed and blocked preexposure differentially affect the salience of the common element X is limited. We can rely on a single experiment, using an appetitive task in which the X element was found to be a more effective overshadowing cue after blocked than intermixed preexposure (Mondragón & Murphy, 2010), and the perceptual learning transfer reported by Artigas and Prados (2014), using an aversive conditioning task.

The existent literature (reviewed above) has shown that the salience of the unique elements tends to be protected in the intermixed preexposure procedure (e.g., Artigas, Sansa, Blair, et al., 2006; Blair & Hall, 2003; Mondragón & Hall, 2002). However, some studies (Contel et al., 2011; see also Prados, 2000; Trobalon, 1998) have shown that the salience of the unique elements decreases as exposure lengthens. Following a short or a long amount of preexposure to AX and BX, Contel et al. (2011) gave taste aversion conditioning trials with the AX compound to all animals, and this was followed by a preference test with the A and X elements presented simultaneously. With short preexposure (four exposure trials to each compound), in comparison to blocked animals, the intermixed condition showed a larger rejection of the A flavor in favor of the X element, suggesting that the associability of the A element was relatively high as a result of the short intermixed preexposure. With long preexposure (eight preexposure trials to each compound), these differences disappeared, indicating that the salience of the unique elements that was transiently high had been significantly reduced with additional preexposure trials.

The results reported by Contel et al. (2011) strongly suggest that the length of preexposure can play an important role in the modulation of the effectiveness of the unique elements; it could also, of course, affect the salience or effectiveness of the common element X. Independent of the nature of the processes triggered by preexposure, the effect of these processes would be gradual and would require some time to differentially alter the salience of the unique and common elements in the intermixed and blocked preexposure conditions. Assuming the salience or effectiveness of the common element X is differentially affected in the different preexposure procedures, a more reliable effect could emerge extending the amount of preexposure used in previous studies using auditory compound stimuli and an appetitive task (Artigas & Prados, 2017; Mondragón & Murphy, 2010). It could be the case that with the level of preexposure used in these experiments, although the modified salience of the common element affects the ease at which animals discriminate between the compound stimuli AX and BX, it is not sufficient to guarantee an effect on the acquisition of associative strength when the common element X is used as a CS in Pavlovian conditioning.

The experiments reported below were designed with the primary objective of assessing this issue. Experiment 1 aimed to replicate the basic intermixed/blocked effect reported by Mondragón and Murphy (2010) and Artigas and Prados (2017) under slightly different preexposure conditions, with a prolonged preexposure (4 days; 20 preexposure trials to each compound instead of the 2 days and 10 preexposure trials used in the previous experiments). Experiment 2 assessed the associability of X and the unique element A (that had not yet been assessed in this appetitive task) under the same preexposure conditions of Experiment 1, as well as using the same preexposure parameters of previous experiments (2 days/10 trials). Experiment 3 extended the assessment of the salience or perceptual effectiveness of the unique element, A, using a superimposition test.

Experiment 1

Since the length of preexposure seems to play a role in the modulation of the salience of the unique elements in flavor aversion tasks (i.e., A; see Contel et al., 2011), we wanted to expand the parametric conditions under which the perceptual learning effect is assessed using an appetitive conditioning task. In previous reports (Artigas & Prados, 2017; Mondragón & Murphy, 2010), the animals were given 10 preexposure trials to each compound, AX and BX. In the present experiment, we extended the amount of preexposure to 20 preexposure trials per compound. Animals in the intermixed group were given presentations of AX and BX in an alternated schedule (AX, BX, AX, BX . . .), whereas animals in the blocked group were exposed to the same stimuli in two separate blocks of identical trials (AX, AX . . . BX, BX). Following the preexposure phase, all the animals were given conditioning trials in which the AX compound was paired with the presentation of a food unconditioned stimulus. The animals were then given a generalization test with the BX compound (see experimental designs in Table 1).

Table 1
Experimental Designs

Experiment	Group	Preexposure (4)	Conditioning (2)	Test (1)
Experiment 1	Intermixed	AX / BX	AX +	BX
	Blocked	AX — BX	AX +	BX
		Preexposure Exp. 2A (2); Exp. 2B (4)	Conditioning (3)	
Experiment 2	Intermixed-A	AX / BX	A +	
	Blocked-A	AX — BX	A +	
	Intermixed-X	AX / BX	X +	
	Blocked-X	AX — BX	X +	
		Preexposure (4)	Conditioning (3)	Test (1)
Experiment 3	Intermixed	AX / BX	Y +	AY
	Blocked	AX — BX	Y +	AY

Note. A, B, X, and Y represent different acoustic stimuli. Stimuli separated by a forward slash (/) in the preexposure phase were presented on alternate trials; stimuli separated by a dash (—) were presented in separate blocks of trials. The numbers in parentheses refer to the number of sessions within each phase of the experiments. + represents the delivery of a food unconditioned stimulus (two food pellets). Exp. = experiment.

Method

Subjects

The subjects of Experiment 1 were 16 experimentally naïve hooded Long Evans rats, eight males with an ad lib body weight range 376−437 g and eight females with an ad lib body weight range 213−265 g at the beginning of the experiment. They were housed in standard transparent plastic cages that were 24 × 50 × 14.5 cm, in groups of two or three animals, in a colony room that was artificially lit from 9:00 a.m. to 9:00 p.m. daily, and with free access to water. The animals were handled, weighed, and fed a restricted amount of food at the end of each session to keep them at 85% of their ad lib body weight for the course of the experiment. In the 2 days that preceded the start of the experiment, the animals were presented with 10 pellets per animal mixed with the usual diet to reduce neophobia to the reinforcer in the appetitive conditioning task. They were assigned, at random, to two experimental groups matched by sex: intermixed and blocked.

Apparatus

Four identical Modular Operant Box chambers (25 × 25 × 25 cm) from Panlab (Model LE1005, Panlab/Harvard Apparatus) were used. The chambers were inserted in sound- and light-attenuating boxes (Model LE26, Panlab/Harvard Apparatus), with background noise produced by ventilation fans (≈70 dB). Each chamber was dimly illuminated by a shielded houselight operating at 20 V located on the wall opposite to the food tray. The floor of each chamber consisted of 20 tubular stainless-steel bars; these bars were perpendicular to the wall where the food tray was located (Model LE100501, Panlab/Harvard Apparatus). This wall and the opposite one were made of aluminum; the ceiling and remaining walls were made of clear methacrylate. A magazine pellet dispenser (Model LE100550, Panlab/Harvard Apparatus) delivered 45-mg Dustless Precision Pellets (Bio Serv; Rodent Purified Diet) into the food tray. A head entry into the food tray was recorded by interruption of a LED photocell (Model LE105-51, Panlab/Harvard Apparatus). Two speakers (Model LE100543, Panlab/Harvard Apparatus) were attached to the top sides of the front wall. The left speaker could deliver two different 15-s tones. A 3.2 kHz (80 dB) tone and a 9.5 kHz (80 dB) tone were used as the elements A and B of the experimental design. The right speaker delivered a 75-dB white noise, the X element of the experimental design. A computer running the Packwin software platform 2.0 for Windows XP controlled experimental events.

Procedure

There were three phases in the experiment: preexposure, conditioning, and test. Throughout the experiment, rats were presented with trials separated by a variable intertribal interval with a mean of 240 s. During the first 4 days of preexposure, animals were exposed to the compound stimuli AX and BX (five presentations of each compound every day). The identity of the first stimulus was counterbalanced changing every day, and the initial order (counterbalanced) in which the stimuli were exposed in Days 1 and 3 was reversed on Days 2 and 4. In the intermixed group, the stimuli were exposed in an alternated fashion (e.g., AX, BX, AX, BX . . .). In the blocked group, the stimuli were presented in separate blocks of identical trials (e.g., AX, AX . . . BX, BX). Two sessions of conditioning followed, each of which comprised 10 presentations of AX followed by two pellets of food. During the final day of the experiment, the animals were given a test in which the compound BX was presented six times in extinction. The amount of time the animals kept their head in the food tray was recorded during the stimulus presentation (CS period) and during the 15 s that preceded it (the pre-CS period). A difference score in which time responding during the pre-CS was subtracted from that recorded during the CS was computed and used as a response measure.

Data Analysis

The analysis of this measure of performance was conducted with analyses of variance (ANOVAs) using a rejection criterion of $p < .05$. The reported effect size for ANOVA with more than one factor is partial eta squared, while for comparisons between two means, it is eta squared. For both measures of effect size, 95% confidence intervals were computed using the method reported by Nelson (2016).

Results and Discussion

One animal in group blocked only showed magazine activity in three of the 20 conditioning trials with the compound AX (Trials 7, 14, and 18), showing a total of 5.68 s of magazine activity in the pre-CS periods and 3.95 s in the presence of the CS. The unusual low level of magazine activity and the negative overall CS − pre-CS score (−1.73 s) indicates that the animal did not develop a conditioned response to the CS and would be pointless to measure the generalization of the conditioned response to the compound BX. The data from this animal were therefore excluded from the analyses.

Figure 1 shows the group means for the magazine approach response during the conditioning trials with the compound AX. An ANOVA with preexposure (intermixed vs. blocked) and blocks of trials as factors showed a significant effect of blocks of trials, $F(3, 39) = 21.03$, $MSE = 87.59$, $p < .01$, $\eta_p^2 = .62$, 95% CI [.38, .72]. The preexposure factor and the Preexposure × Blocks of Trials interaction were nonsignificant, maximum $F(1, 13) = 3.18$.

The same analyses were carried out on the pre-CS scores during the conditioning phase of the experiment. The overall mean pre-CS scores for the four blocks of conditioning trials were 1.99 (*SEM* ± .37) for group intermixed and 1.84 (± .39) for group blocked. An ANOVA with preexposure (intermixed vs. blocked) and blocks of trials as factors showed no significant effects, maximum $F(3, 39) = 2.52$.

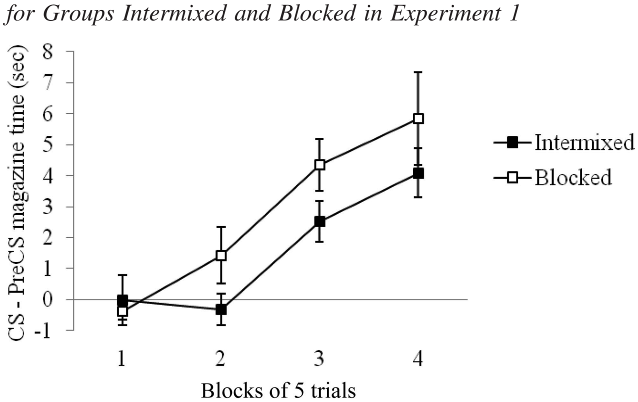
Figure 2 shows the group means for the magazine approach response during the generalization test with the BX compound. A one-way ANOVA performed on the test data showed a significant difference between the intermixed and blocked groups, $F(1, 13) = 5.27$, $MSE = 33.88$, $p = .04$, $\eta_p^2 = .29$, 95% CI [.00, .56].

The same analyses were carried out on the pre-CS scores during the test phase. The overall mean pre-CS scores for the test trials were 1.64 (*SEM* ± .45) for group intermixed and .92 (± .49) for group blocked. A one-way ANOVA revealed no differences between the two groups, $F(1, 13) = 1.14$.

The AX acquisition results displayed in Figure 1 suggest a tendency of animals in group blocked to respond at a higher level than those in group intermixed. Although the difference is nonsignificant, it might cast doubt about the key results reported in Figure 2, where animals in the blocked condition also show higher levels of responding (this time the differences were statistically significant). However, it is worth noting that animals in group intermixed showed higher levels of pre-CS responding than the blocked group during the test (although, again, these differences were nonsignificant). To further address this issue, we compared the performance of the animals in the last block of training trials with the AX compound and the block of test trials with BX. The mean response levels in group intermixed were 4.09 (*SEM* ± .79) for AX and 1.67 (±.69) for BX, and in group blocked, 5.83 (±1.49) for AX and 4.68 (±1.16) for BX. Paired-samples *t* tests confirmed a significant drop in responding to BX as compared to AX in the intermixed group, $t(7) = 2.43$, $p < .05$, but not in the blocked group, $t(6) = .617$. This supports the notion that animals in the intermixed group discriminate well between AX and BX (a perceptual learning effect), whereas those in the blocked group tend to generalize between the two compounds.

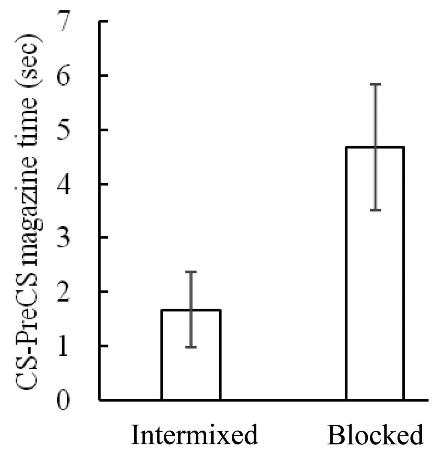
The present results replicate the basic intermixed/blocked effect reported by Mondragón and Murphy (2010; also Artigas & Prados, 2017) using different preexposure parameters, with a longer preexposure phase (20 trials to each compound rather than the 10 trials used in the original experiments). In Experiment 2, we assessed the salience of the unique and common elements (A and X) both under the short and long preexposure conditions.

Figure 1
Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) During the Four Blocks of Conditioning Trials With the Compound Stimulus AX for Groups Intermixed and Blocked in Experiment 1



Note. CS = conditioned stimulus.

Figure 2
Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) During the Generalization Test Trials With the Compound BX for Groups Intermixed and Blocked in Experiment 1



Note. CS = conditioned stimulus.

Experiment 2

In Experiment 2A, four groups of rats received short preexposure to AX and BX (10 exposure trials to each compound over 2 days, as in the experiments reported by Mondragón & Murphy, 2010) according to either the intermixed or the blocked procedure.

Following preexposure, half of the animals in each preexposure condition were given conditioning trials with the common element, X, whereas the other half were given conditioning trials with the unique element, A. (Note that, to simplify, although A and B were always counterbalanced across the different phases of all the experiments reported here, we will refer to the unique elements as A.) Experiment 2B replicated the procedure of Experiment 2A with the exception of the preexposure length, 20 exposure trials to each compound over 4 days as in Experiment 1.

Experiment 2A

Method

Subjects and Apparatus. The subjects were 32 male hooded Long Evans rats (ad lib body weight range 273.8−432.8 g) that had been previously used in a spatial learning experiment using the water maze. The stimuli used were the same described for the previous experiments. The animals were assigned at random to four experimental groups: intermixed-X, intermixed-A, blocked-X, and blocked-A.

Procedure. The procedure of Experiment 2A replicates the preexposure procedure of Experiment 1 but using a shorter preexposure phase: 10 preexposure trials to each compound, AX and BX, over 2 days. Following preexposure, half of the animals were given conditioning trials with the common element, X, whereas the other half were given conditioning trials with the unique element, A. Conditioning followed the procedure described in Experiment 1 for the compound AX and took place over 3 consecutive days at a rate of 10 conditioning trials per day.

Results and Discussion

Figure 3 shows the group means for the magazine approach response during the conditioning trials with the X stimulus (left-hand panel) and the A stimulus (right-hand panel). An ANOVA with stimulus (X vs. A), preexposure (intermixed vs. blocked), and blocks of trials as factors showed a significant effect of stimulus, $F(1, 28) = 5.01$, $MSE = 53.61$, $p = .03$, $\eta_p^2 = .15$, 95% CI [0, .38], and blocks of trials, $F(5, 140) = 33.88$, $MSE = 182.92$, $p = .00$, $\eta_p^2 = .54$, [.41, .61]. All the other factors and interactions were nonsignificant, maximum $F(1, 28) = 2.97$.

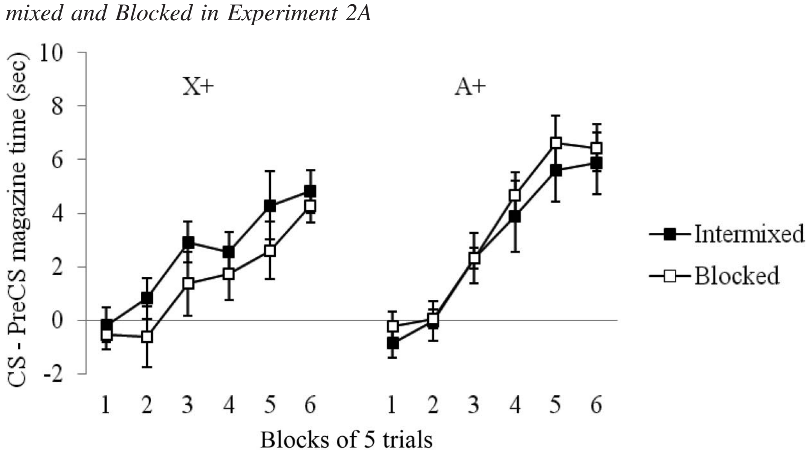
The same analyses were carried out on the pre-CS scores during the conditioning phase of the experiment. The overall mean pre-CS scores for the six blocks of conditioning trials were 3.40 (± .41) for group intermixed-X, 3.56 (± .41) for group blocked-X, 3.57 (± .41) for group intermixed-A, and 3.98 (± .41) for group blocked-A. An ANOVA with stimulus (X vs. A), preexposure (intermixed vs. blocked), and blocks of trials as factors showed a significant effect of blocks of trials, $F(5, 140) = 7.44$, $MSE = 40.03$, $p = .00$, $\eta_p^2 = .21$, 95% CI [.08, .30]. This reflects an increment in the time animals spent on the food tray during the pre-CS period as training progressed. The other factors and interactions were nonsignificant, Fs < 1.

On the one hand, the results of Experiment 2A confirm that the common element X is less effective as a CS than the unique element A both after intermixed and blocked preexposure. This is hardly surprising given that X receives double amount of exposure than the unique elements both after intermixed and blocked preexposure; this finding is easily accommodated by associative explanations of perceptual learning. On the other hand, the results also replicate the absence of differences between the intermixed and the blocked groups during conditioning either with the common or the unique elements (e.g., Mondragón & Hall, 2002, in flavor aversion tasks; Mondragón & Murphy, 2010, in appetitive conditioning of the X element). Mondragón and Murphy, however, observed a quicker extinction of the X element after intermixed preexposure, a result they interpreted as evidence for acquisition of associative strength—and hence lower salience of X—but could also be seen as higher acquisition of extinction—and hence higher salience—leaving that result inconclusive.

Although the preexposure parameters used here successfully enhance the discriminability of AX and BX in the intermixed

Figure 3

Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) During the Six Blocks of Five Conditioning Trials With Element X (Left-Hand Panel) and A (Right-Hand Panel) for Groups Intermixed and Blocked in Experiment 2A



Note. CS = conditioned stimulus.

condition (see Artigas & Prados, 2017, for an identical experiment with a generalization test; also Mondragón & Murphy, 2010), they seem to be insufficient to differentially affect the salience of the unique and common elements in the two preexposure procedures, intermixed and blocked. As mentioned above, it could be the case that the modified salience of the unique and common elements affect the ease at which animals discriminate between the compound stimuli AX and BX, but it is not sufficient to guarantee an effect on the acquisition of associative strength when used as a CS in Pavlovian conditioning.

Experiment 2B

Method

Subjects and Apparatus. The subjects were 32 male hooded Long Evans rats (ad lib body weight range 331.6−484.6 g) that had been previously used in a spatial learning experiment using the water maze. The stimuli used were the same described for the previous experiments.

Procedure. The procedure of Experiment 2B replicates the one described for Experiment 2A but using a longer preexposure phase: 20 preexposure trials to each compound, AX and BX, over 4 days (as in Experiment 1). As in the previous experiment, following preexposure half of the animals were given conditioning trials with the common element, X, whereas the other half were given conditioning with the unique element, A.

Results and Discussion

One animal in group blocked-A only showed magazine activity in three of the 30 conditioning trials with A (Trials 1, 28, and 29), showing a total of 4.97 s of magazine activity in the pre-CS periods and only 0.10 s in the presence of the CS in the whole conditioning phase (just one brief entrance to the magazine in Trial 29). The extremely low level of magazine activity and the negative overall CS − pre-CS score (−4.87 s) suggests that the animal was highly sensitive to the auditory stimuli used in the experiment and failed to engage with the conditioning task. This animal's data were withdrawn from the experiment.

Figure 4 shows the group means for the magazine approach response during the conditioning trials with the X stimulus (left-hand panel) and the A stimulus (right-hand panel). An ANOVA with stimulus (X vs. A), preexposure (intermixed vs. blocked), and blocks of trials as factors showed a significant effect of stimulus, $F(1, 27) = 6.72$, $MSE = 107.19$, $p = .01$, $\eta_p^2 = .19$, 95% CI [.01, .43], preexposure, $F(1, 27) = 4.99$, $MSE = 79.79$, $p = .03$, $\eta_p^2 = .15$, [0, .39], and blocks of trials, $F(5, 135) = 40.45$, $MSE = 208.72$, $p < .01$, $\eta_p^2 = .60$, [.48, .66]. All the other factors and interactions were nonsignificant, maximum $F(5, 135) = 1.5$.

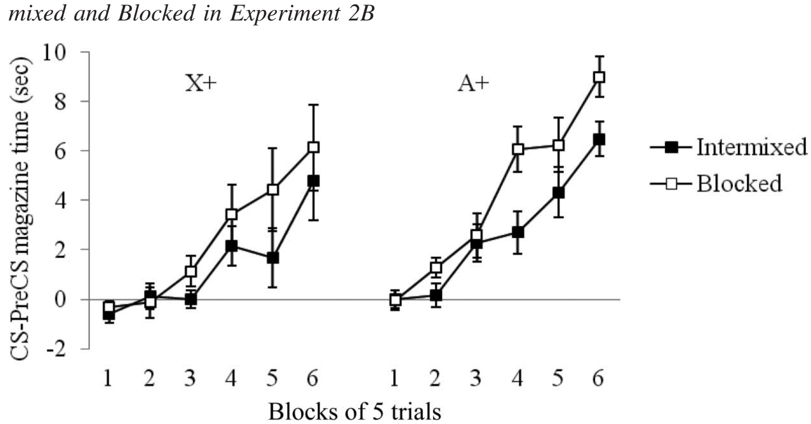
The same analyses were carried out on the pre-CS scores during the conditioning phase of the experiment. The overall mean pre-CS scores for the six blocks of conditioning trials were 1.57 (*SEM* ± .49) for group intermixed-X, 1.15 (± .20) for group blocked-X, 1.72 (± .37) for group intermixed-A, and 1.41 (± .32) for group blocked-A. An ANOVA with stimulus (X vs. A), preexposure (intermixed vs. blocked), and blocks of trials as factors showed no significant effects, maximum $F(5, 135) = 2.08$.

The results of Experiment 2B confirm again that the common element X is less effective than A as a CS both after intermixed and blocked preexposure. Furthermore, the results showed a lower conditioning in the intermixed than in the blocked group of the common element X and the unique element A, suggesting a larger decline in their salience in the intermixed condition. Notably, the results of Experiment 2B with prolonged preexposure show, for the first time, a decline in the salience of the common element X during a conditioning phase following intermixed preexposure, a result that has been elusive in previous studies where differences were only apparent during a subsequent test in extinction (see Mondragón & Hall, 2002; Mondragón & Murphy, 2010).

The most original and relevant finding reported in Experiment 2 is undoubtedly the advantage of the blocked preexposure procedure protecting the associability of the unique elements over a prolonged preexposure phase (Experiment 2B). This is the oppo-

Figure 4

Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) During the Six Blocks of Five Conditioning Trials With Element X (Left-Hand Panel) and A (Right-Hand Panel) for Groups Intermixed and Blocked in Experiment 2B



Note. CS = conditioned stimulus.

site of what most theories of perceptual learning would predict (e.g., Hall, 2003). The associative approach based on differential representations put forward by Artigas and Prados (2014) could accommodate these results; however, before we discuss this approach in the "General Discussion" section, we need to confirm the deleterious effect of long intermixed preexposure on the salience of the unique element A. Experiment 3 was designed to provide convergent evidence by using an alternative procedure—a superimposition test.

Experiment 3

Experiment 3 assessed the salience of the unique element, A, following prolonged intermixed and blocked preexposure. In this experiment we assesed the capacity of the unique element A to interfere with the expression of a conditioned response to a new element Y (the superimposition test used by Blair & Hall, 2003, Experiment 5b).

Method

Subjects

The subjects were 24 naïve hooded Long Evans rats, 18 males with ad lib body weight range 348−442 g and six females with ad lib body weight range 204−255 g at the beginning of the experiment. The animals were assigned at random to two experimental groups matched by sex: intermixed and blocked. In addition to the stimuli used in the previous experiments, a 15-s intermittent tone (200 ms on/off; 5 kHz; 80 dB) was used as the stimulus Y of the experimental design (see Table 1).

Procedure

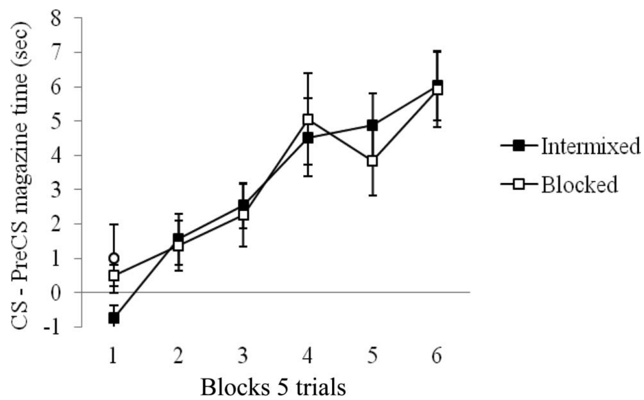
The procedure of Experiment 3 replicated the preexposure procedure of Experiment 1 (20 exposures to each compound over four daily sessions). Following preexposure, the animals were given conditioning trials with a novel stimulus Y followed by the presentation of two food pellets. Conditioning took place over 3 consecutive days at a rate of 10 conditioning trials per day. Following conditioning, all the animals received a single test session consisting of six presentations of the simultaneous compound stimulus AY in extinction.

Results and Discussion

Figure 5 shows the group means for the magazine approach response during the conditioning trials with the novel stimulus Y. An ANOVA with preexposure (intermixed vs. blocked) and blocks of trials as factors showed a significant effect of blocks of trials, $F(5, 110) = 25.39$, $MSE = 126.24$, $p < .01$, $\eta_p^2 = .54$, 95% CI [.40, .62]. The preexposure factor and the Preexposure × Blocks of Trials interaction were both nonsignificant, $F\text{s} < 1$.

The same analyses were carried out on the pre-CS scores during the conditioning phase of the experiment. The overall mean pre-CS scores for the six blocks of conditioning trials were 1.29 (*SEM* ± .23) for group intermixed and 1.28 (± .23) for group blocked. An ANOVA with preexposure (intermixed vs. blocked) and blocks of trials as factors showed no significant effects, maximum $F(5, 110) = 2.09$.

Figure 5
Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) During the Six Blocks of Five Conditioning Trials With the Y Element Used as the CS for Groups Intermixed and Blocked in Experiment 3



Note. CS = conditioned stimulus.

Figure 6 shows the group means for the magazine approach response during the superimposition test with the AY compound. A one-way ANOVA revealed a significant effect of group, $F(1, 22) = 4.46$, $MSE = 10.70$, $p = .04$, $\eta_p^2 = .17$, 95% CI [.00, .42].

The same analysis was carried out on the pre-CS scores during the test phase. The overall mean pre-CS scores for the test trials was .24 (*SEM* ± .15) for group intermixed and .51 (± .15) for group blocked. A one-way ANOVA revealed no significant differences between the two groups, $F(1, 22) = 1.61$.

This experiment demonstrates that the conditioned response controlled by a CS, Y, is differentially modulated by the presence of another preexposed stimulus (the unique element A). The conditioned response was weaker when Y was presented in compound with the A element following blocked preexposure than in the group given intermixed preexposure. This is in line with the results of Experiment 2B, strongly suggesting that the salience or perceptual effectiveness of the unique element is somewhat protected following blocked preexposure—in comparison to the intermixed preexposure procedure.

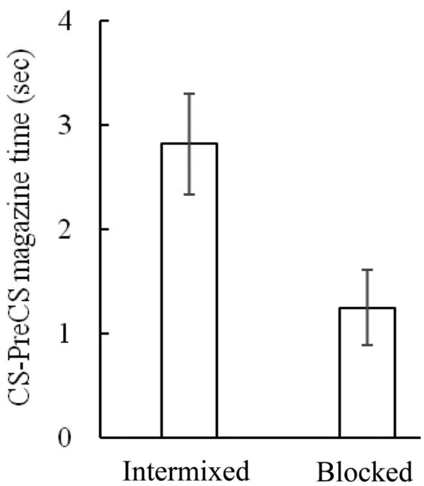
Most associative learning theories (e.g., Hall, 2003; McLaren & Mackintosh, 2000) tend to predict that the salience/effectiveness of the unique elements would be higher following intermixed than blocked preexposure. The results of the present experiment (together with those from Experiment 2B) seem to challenge this principle.

General Discussion

It is well established that alternating preexposure to two compound stimuli sharing explicit common elements (AX, BX, AX, BX . . .) triggers learning mechanisms that enhance their discriminability—compared to the same amount of preexposure to the two stimuli but in separate blocks of trials (AX, AX . . . BX, BX). Doubling the amount of preexposure (20 preexposure trials to each compound instead of 10) used in previous studies using the same appetitive conditioning procedure (i.e., Artigas & Prados, 2017; Mondragón & Murphy, 2010), Experiment 1 showed the

Figure 6

Mean Time (± SEM) of Magazine Approach Response Calculated From Difference Scores (CS − Pre-CS) in the Superimposition Test With the Compound YA for Groups Intermixed and Blocked in Experiment 3



Note. CS = conditioned stimulus.

intermixed-blocked effect (an instance of perceptual learning). It is worth noting that most animal studies of perceptual learning used a blocked design that consisted of a block of AX trials followed by the presentations of BX in a separate block of trials (in such a way that there was only one alternation between AX and BX). In present experiments, we used a slightly different blocked preexposure procedure in which animals are given separate blocks of five trials to AX and BX within each session (since the order of presentation of AX and BX was balanced across days, the animals experienced four alternations between AX and BX; animals in the intermixed preexposure group experienced 39 alternations). We adopted this preexposure procedure to be able to make comparisons with the previous studies by Mondragón and Murphy (2010) and Artigas and Prados (2017), which showed a clear advantage of the intermixed procedure on the ability to discriminate between AX and BX. However, the fact that there is some level of alternation between AX and BX even in the blocked preexposure condition might underestimate the differences that typically arise when comparing the effects of intermixed and blocked preexposure.

The intermixed blocked effect observed in Experiment 1is known to depend, at least to some extent, on the salience or effectiveness of the unique and common elements following preexposure (e.g., Hall, 2003). Experiments 2 and 3 aimed to assess the effectiveness of the unique and common elements following preexposure to AX and BX in alternation or in different blocks of trials. In Experiment 2, following either short (Experiment 2A) or long (Experiment 2B) preexposure to AX and BX, animals were given conditioning trials with either the common element X or the unique feature A as the CS. All the animals showed lower levels of conditioning with the common than the unique feature. This replicates a common finding in the literature, which is hardly surprising: Since X is present in every trial and A and B are present only in half the preexposure trials, X is likely to accumulate higher levels of latent inhibition (e.g., Lubow, 2010). In Experiment 2A, using the same preexposure parameters used by Mondragón and Murphy (2010), we did not observe differences in the conditioning rate of A and X between the groups given intermixed and blocked preexposure. This replicates the absence of differences reported by Mondragón and Murphy during the acquisition phase of the element X of their Experiment 3 (they found differences between the two groups in a subsequent phase in which the animals were given extinction test trials). The absence of differences in the conditioning rate of the unique element A also replicates previous findings reported by Mondragón and Hall (2002) using a flavor aversion task; however, they reported evidence for lower extinction of the unique element A, suggesting it had higher associability in the intermixed than in the blocked condition.

In contrast with the null result observed in Experiment 2A, in Experiment 2B, using a long preexposure phase (20 instead of 10 preexposure trials to each compound), the animals in group intermixed showed lower levels of conditioning of both the common and the unique elements than the animals in the blocked condition. Using a prolonged preexposure therefore seems to reduce the associability of both elements A and X. The lower conditioning of A is an unusual finding at odds with most of the literature that has assessed the effectiveness of the A element. As pointed out in the introduction of Experiment 1, there is a precedent in which the effectiveness of A was found to be higher after short intermixed than blocked preexposure, but these differences vanished following prolonged preexposure (Contel et al., 2011). This would support the notion that the length of preexposure is a key factor in the modulation of the associability or effectiveness of the unique element A. However, this was found in an experiment using a flavor aversion preparation (conditioning of the compound AX was followed by a preference test with the elements A and X). Before attempting to discuss how long preexposure might negatively affect the salience or associability of the unique element A, it would be worth obtaining some convergent evidence using the appetitive conditioning task used in Experiments 1 and 2 to confirm the unusual outcome of Experiment 2B.

In Experiment 3, we assessed the perceptual effectiveness of the unique element by using a superimposition test: Following the long preexposure phase (20 trials to each compound), all animals were given conditioning trials with a new stimulus, Y. The animals were then tested in the presence of the AY compound. The results showed higher interference with the expression of the conditioned response to Y in the group given blocked preexposure. This indicates that the unique element A is less salient following long intermixed than blocked preexposure. Taken together, the results of Experiments 2B and 3 strongly suggest that long intermixed preexposure reduces the effectiveness of the unique element A.

The results of Experiment 3 are in conflict with the results reported by Blair and Hall (2003, Experiment 5b) showing that the unique elements preexposed in alternation had more effective salience than the unique elements of compound stimuli preexposed in a separate block of trials. Although it is difficult to compare between these experiments using different sensory modalities (flavor and auditory stimuli) as well as different conditioning paradigms (aversive and appetitive), there are reasons to belief that the preexposure phase used by Blair and Hall was relatively short (four preexposure trials to each compound; see, e.g., Artigas, Sansa & Prados, 2006, and Contel et al., 2011, for examples of long preexposure using eight and 10 exposure trials to each compound in flavor aversion conditioning experiments). The contrasting results of Experiments 2A and 2B in the present study suggest that the length of preexposure is a key factor in the modulation of the elements' salience, and the amount of preexposure used in the present Experiment 3 can be deemed to be relatively long. We need to be cautious, however, and not overlook the differences between the experimental paradigms used in the present study and the report by Blair and Hall (2003).

Theories of perceptual learning assume that nonreinforced preexposure can alter the perceptual characteristics of complex stimuli. In her pioneering approach to the phenomenon, Gibson (1969) suggested that nonreinforced preexposure that allowed comparison between the to-be-discriminated stimuli would increase the salience of the unique distinctive features and simultaneously reduce the effectiveness of the common, nondistinctive elements. Most modern theories have emphasized the increased effectiveness of the unique elements A and B following intermixed preexposure (e.g., Hall, 2003; Honey & Bateson, 1996; McLaren & Mackintosh, 2000; Mitchell et al., 2008; for a review, see Mitchell & Hall, 2014); however, they tend to assume that the salience or effectiveness of the common element would be equivalent after intermixed and blocked preexposure (X is present in every exposure trial in both preexposure arrangements). Therefore, these theories struggle accommodating instances of perceptual learning that are most likely due to a differential salience of effectiveness of the common element in the intermixed and blocked procedures (i.e., the perceptual learning transfer; Artigas & Prados, 2014).

To account for the reduced salience of X after intermixed preexposure, Mondragón and Murphy (2010) suggested that stimuli that associatively activate others (X activates a representation of A and B in alternating trials) would lose their own effective salience in a selective attention process. This is reminiscent of the Pearce-Hall model principles (Pearce & Hall, 1980), where stimuli that are strongly associated with an outcome are supposed to lose perceptual effectiveness or associability; however, if that were the mechanism that reduces the salience of X in the intermixed preexposure procedure, the loss of associability should be higher in the blocked condition, where the X element is consistently associated with one element within a block of training trials (in the intermixed procedure, X is paired with A and B on alternating trials, increasing the uncertainty that is supposed to protect the associability of the signal according to the Pearce-Hall model). Alternatively, Mondragón and Murphy proposed an approach based on the attentional theory by Mackintosh (1975): X, paired with A and B on alternating trials in the intermixed condition, would be perceived as a relatively poor predictor of its consequences and would lose perceptual effectiveness or associability to a greater extent than in the blocked condition, where it is consistently paired with the same stimulus over a block or preexposure trials. If we extend this analysis to the unique features, given that A and B are always paired with the X element both in the intermixed and blocked preexposure conditions (and are therefore likely to be perceived as good predictors), the attentional theories might predict similar salience or associability (high in the case of Mackintosh, 1975; low in the case of Pearce & Hall, 1980). These complications suggest the need for an alternative theoretical approach to accommodate the results reported here.

Artigas and Prados (2014) proposed that intermixed and blocked preexposure to AX and BX may lead to the establishment of elemental (A, B, and X) or configural-like (AX, BX) representations, respectively. Combining elemental and configural processes is not a novel approach (see, e.g., McLaren et al., 2012). However, Artigas and Prados presented their approach as a development of the elemental theory of stimuli proposed by McLaren and Mackintosh (2000; also McLaren et al., 1989) that assumes the traditional stimulus sampling theories (e.g., Atkinson & Estes, 1963; Estes, 1959).

During blocked preexposure to AX, for example, the elements of A and X can confidently be expected to be sampled at the same rate—A and X can be assumed to be equally salient. Coactivation of the elements of A and X in each preexposure trial would lead to the establishment of associations among them (X-A associations), as well as associations between the elements of X (X-X) and A (A-A). The existence of strong X-A associations would contribute to the establishment of a unique configural-like representation of AX. Consistent with this assumption, Rodríguez & Alonso (2014, 2015) have reported persuasive evidence showing stronger within-compound associations (i.e., A-X) following blocked than intermixed preexposure.

Following Artigas and Prados (2014), alternation of AX and BX in the intermixed preexposure would result in a different sampling rate for the unique and common elements: The X elements would be sampled in every trial, whereas the A (and B) elements would be sampled only every two trials. In the first AX trial, for example, we can expect the establishment of associations between the X elements (X-X), the A elements (A-A), and the X and A elements (X-A); however, the X-A associations can be expected to weaken in the absence of A during the subsequent BX trial. Similarly, a BX trial will result in further X-X, as well as B-B, and X-B associations that will weaken in the following AX trial. Therefore, the X elements will lose salience more rapidly than the A and B elements, and as a consequence of this, the A (and B) elements will tend to develop associations between one another in preference to associations with the X elements (McLaren & Mackintosh, 2000, p. 227).

In the long term, the final outcome of intermixed preexposure would therefore tend to be elemental well-formed representations of the elements X, A, and B. These elemental representations would be subject to preexposure effects (reduced salience or effectiveness) according to their level of exposure, double in the case of X compared to A and B. The configural-like representations that emerge during blocked preexposure would be subject to the same processes as the elemental representations. However, the existence of strong x-a and x-b associations would limit the extent to which the actual elements (A, B and X) loss salience or effectiveness. When one element is presented alone (i.e., A), there would be a number of established a-a and a-x associations; however, the absence of the x element would result in a differential internal and external input. Given that this error term will be larger in the blocked than in the intermixed procedure, the blocked condition would limit the extent to which A, B, and X loss salience or effectiveness, which would just be reduced according to their similarity to the configural-like representations AX and BX. Latent inhibition would generalize to X from both the AX and BX representations, resulting in lower effectiveness of the common element than the unique elements, to which latent inhibition is generalized from either AX (A) or BX (B).

This approach allows us to introduce the amount of exposure as a key factor in determining the stimulus salience following short and long levels of preexposure. As indicated above, in the intermixed preexposure procedure, a representation of X would emerge relatively soon and would then be subject to the preexposure effects (typically loss of salience and associability). The building up of the representation of the unique elements (dependent on sampling and association of the A elements) would be slightly delayed compared to X given that the unique elements are present only in every other trial. Once a representation of the stimulus is established—through the process of unitization—we can assume that its effectiveness would be temporarily increased: The existence of a central tendency would facilitate the recognition of the elemental stimulus. However, with continuous exposure, further strengthening of the associations between its elements will tend to reduce its salience or effectiveness when the error term is reduced because the internal input matches the external input (see McLaren & Mackintosh, 2000, p. 213). We can therefore predict that the elemental stimuli representations that emerge during intermixed preexposure would transiently increase their perceptual effectiveness during the early stages of preexposure and subsequently lose their salience due to the reduction of the error term. The representation of the common element emerges first and suffers from earlier and deeper loss of salience. The unique elements A and B take longer to complete the central tendency, and their loss of salience is delayed. In other words, with relatively short preexposure (like the one presumably used by Blair & Hall, 2003), the unique elements presented in alternation could be relatively salient, improving the discriminability of AX and BX; with prolonged preexposure, the salience or effectiveness of these elements would decline gradually, as shown by the present Experiments 2B and 3. This is consistent with the literature that shows that the salience of the unique elements tends to be protected in the intermixed preexposure procedure (e.g., Artigas, Sansa, Blair, et al., 2006; Blair & Hall, 2003; Mondragón & Hall, 2002), as well as with the reports that have shown that the salience of the unique elements decreases as exposure lengthens (e.g., Contel et al., 2011).

As discussed in the introduction, there is evidence for different mechanisms that enhance the discriminability of the compound stimuli AX and BX following intermixed preexposure, including differential associability of the unique and common elements, enhanced perceptual effectiveness of the distinctive elements A and B, reduced salience of the common element X, and the establishment of inhibitory associations between the unique elements A and B. The differential representation hypothesis, a version of the McLaren and Mackintosh (2000) model with the add-on of the differential representation following intermixed (elemental) and blocked (configural-like) preexposure, can easily accommodate the establishment of inhibitory links between A and B, which can be expected to boost the distinctiveness of the unique elements, facilitating the discrimination between AX and BX. With short preexposure, the transient high salience of the unique elements seems to be a main contributor to the intermixed/blocked effect; with prolonged preexposure, the salience of the unique elements is likely to decline, but other mechanisms—including the existence of accurate representations of the unique elements inhibitory linked (e.g., McLaren & Mackintosh, 2000)—can still put the animals that received intermixed preexposure in an advantageous position to discriminate between AX and BX.

To conclude, independent of the merits of this theoretical approach, it emerges that a key element that contributes to modify the associability and perceptual effectiveness of both the common and the unique elements is the number of preexposure trials: The longer the preexposure phase, the lower the relative salience of both X and A in the intermixed condition (by contrast to the blocked condition, where the salience of the elements seems to be protected). Future research should systematically assess the effects of the different schedules and lengths of preexposure to unveil the nature of the learning mechanisms responsible for the perceptual learning effect.

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