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AQ1 : Please provide a short abstract of up to 250 words, giving a description of the findings of your article.

Response: Resolved

AQ2 : Reference Sanchez et al. (2022) has cited in text but not provided in the reference list. Please mark the reference (with complete publication details) into the reference list, or delete the citation from the text.

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AQ3 : Please expand SOP here.

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AQ14 : Please provide issue number in Ref. Recio et al. (2019).

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AQ15 : Please expand SEM in footnote in Figure 1-6.

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AQ16 : Should question mark (?) be defined here in Table 1 footnote?

Response: Resolved

Intermixed Rapid Exposure to Similar Stimuli Reduces the Effective Salience of Their Distinctive Features

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The data on which study conclusions are based are available in the APA's repository on the OSF. https://mfr.osf.io/render?url=https://osf.io/u6qfp/?direct%26mode=render%26action=download%26mode=render.

Isabel de Brugada served as lead for conceptualization, funding acquisition, and supervision and contributed equally to formal analysis, methodology, writing–original draft, and writing–review and editing.

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ABSTRACT

Intermixed exposure to two similar stimuli, e.g., AX and BX, improves subsequent discrimination between them compared to blocked exposure (the intermixed/blocked effect). Salience modulation models, developed mainly from research with nonhuman animals and exposure to widely spaced similar stimuli, explain this effect in terms of increased salience of the unique elements, A and B. Conversely, results from experiments initially conducted with humans and exposure to close spaced similar stimuli have led to the suggestion that it is the development of well-unitized representations of unique elements that leads to better discrimination, leaving the unique elements with less effective salience. The experiments carried out here aim to replicate the intermixed/blocked effect in rats using an exposure procedure with rapid succession between stimuli and to assess the effective salience of unique elements. In Experiment 1, an aversion to a new flavor, Y, was conditioned and then an external inhibition test with AY was given. In Experiment 2, an aversion to A was conditioned and its extinction was measured on unreinforced trials. In Experiment 3, an aversion to AY was conditioned and the associated aversion to Y was measured. We found after rapid intermixed preexposure a reduction in generalization from the aversive Y element to the compound AY (Experiment 1) as well as a reduction in A's salience (Experiments 2 and 3) compared to the effects of blocked preexposure. The results are discussed in terms of the various mechanisms underlying perceptual learning, which appear to depend on the details of the task.

~~Previous experience with similar stimuli, for example, AX and BX, improves subsequent discrimination between them, especially if they have been preexposed in an intermixed fashion. Salience modulation models, developed mainly from research with nonhuman animals and stimulus exposure procedures with long intervals between them, propose the increased salience of the unique elements, A and B, as the source of this improved discrimination. Conversely, the results of a series of experiments initially conducted with humans and stimulus exposure procedures with short intervals between them have led to the proposal that it is the development of well-unitized representations of the unique elements after intermixed exposure that leads to better discrimination, leaving the unique elements with less effective salience. The experiments carried out here aim to replicate the perceptual learning effect in nonhuman animals using an exposure procedure with rapid succession~~

between stimuli, assessing the effective salience of unique elements after rapid intermixed preexposure to test this second proposed mechanism. In Experiment 1, an aversion to a new flavor, Y, was conditioned and then an external inhibition test with AY was given. In Experiment 2, an aversion to A was conditioned and its extinction was measured on unreinforced trials. In Experiment 3, an aversion to AY was conditioned and the associated aversion to Y was measured. We found after rapid intermixed preexposure a reduction in generalization from the aversive Y element to the compound AY (Experiment 1) as well as a reduction in A's salience (Experiments 2 and 3) compared to the effects of blocked preexposure. The results are discussed in terms of the various mechanisms underlying perceptual learning, which appear to depend on the details of the task[AQ1].

KEYWORDS

- perceptual learning
- comparison
- intermixed/blocked effect
- effective salience
- unitization

Perceptual learning refers to the phenomenon by which mere exposure to similar stimuli (e.g., AX and BX) results in better subsequent discrimination between them. One of the earliest theories of this effect was proposed by Gibson (1963). This account supposes that any two stimuli will have some elements in common (e.g., X), and others that are unique (e.g., A and B), and according to Gibson (1969), the opportunity to compare these will launch a process of stimulus differentiation, whereby the effectiveness of the unique features will be enhanced relative to the common features. Gibson (1969) suggested that the opportunity to compare is critical for this process to occur; hence, a wide range of experiments have been conducted to evaluate the role of stimulus comparison in perceptual learning.

From an associative standpoint, the typical procedure used to study this process, generally with nonhuman participants, consists of giving subjects preexposure to two similar stimuli presenting them either in an intermixed (AX, BX, AX, BX ...) or blocked fashion (AX, AX ... BX, BX...). After this, one of the compounds is paired with a reinforcer to establish a conditioned response. The generalization of this response to the other similar stimulus is then measured. Usually, the intermixed presentation of the stimuli results in better discrimination between them than presentation in a series of blocks—the intermixed/blocked effect (I/B effect). This effect has been replicated numerous times in both nonhuman animals (e.g., Mondragón & Murphy, 2010; Prados et al., 2007; Recio et al., 2016, 2018, 2019; Sánchez et al., 2022; Symonds & Hall, 1995) and humans (e.g., Dwyer et al., 2011; Lavis et al., 2011; Mitchell et al., 2008; Mundy et al., 2007). One of the first proposals to explain this I/B effect comes from McLaren and Mackintosh's (2000) modification of McLaren et al.'s (1989) associative theory of the representation of stimuli. During exposure to compounds AX and BX, bidirectional within-compound excitatory connections (A−X and B−X) will form (McLaren et al., 1989). However, in addition, intermixed exposure will allow the formation of bidirectional inhibitory connections between the unique elements of each compound (A and B) (McLaren & Mackintosh, 2000). For example, when AX is present, the common element X will associatively activate the absent element B, leading to the formation of an inhibitory association between A and B. And the same will occur between B and A when BX is presented. Thus, less generalization of the conditioned response on the test will be expected after intermixed than blocked preexposure since one unique element signals the absence of the other.

A few years later, Hall's model (2003) accepted the proposal of McLaren et al. (1989) regarding the formation of excitatory associations during preexposure and, although it does not deny the formation of inhibitory links, proposes a rather different effect of the associative activation of the unique elements. Repeated experience during the preexposure phase causes all stimuli and their elements to undergo habituation, which implies a decrease in their effective salience and the ability to enter into new associations. The associative activation of the unique elements during intermixed preexposure is postulated to restore their salience and protect them from long-term habituation. Intermixed preexposure could keep the effective salience of the unique elements high and thus promote discrimination.

The mechanisms proposed by these two models can explain most of the results observed in nonhuman animal studies (for a review, see Mitchell & Hall, 2014). They are not incompatible with each other (Artigas et al., 2006), and both suggest that the effect depends on the associative activation of the unique elements in their absence. Indeed, these models have little to do with Gibson's idea of comparison. According to common sense, for the comparison process to operate, the representation of one stimulus must be active when the next one is presented, but, in fact, these exposure procedures involve long intervals between stimuli (hour or days) that do not favor comparison. Rather, these long intervals allow the representation of the first presented compound, for example, AX, to decay to inactivity, so that the representation of A can be associatively activated when the second compound, for example, BX, is presented (Wagner, 1981).

From these studies with nonhuman animals, a series of human studies were initiated to examine the generalization of the perceptual learning phenomenon and its mechanisms. The procedures used differ in several ways from those used with nonhuman animals. In particular, preexposure takes place at a very fast pace with very short intervals between stimuli (interstimulus interval [ISI]) and in a single session. Furthermore, complex visual stimuli and a same/different discrimination test are used (for a review of the procedural differences, see Mitchell & Hall, 2014). For instance, Mundy et al. (2007) preexposed participants to intermixed or blocked pairs of similar faces with a short ISI (1–2 s), after which they were required to learn to discriminate whether these faces belonged to right-handed or left-handed people. They found that the intermixed pair of preexposed faces was discriminated more readily than the blocked pair (see also Lavis et al., 2011 with checkerboards as stimuli). According to Mundy et al. (2007), rapid intermixed presentation of stimuli causes their common elements to undergo short-term habituation and thus processing resources are biased in favor of the unique elements. In successive exposure with a short ISI, the presentation of a compound (e.g., AX) will activate a number of units corresponding to the common and unique elements. When the second compound (e.g., BX) is presented, some of the units of the common element (x) will remain in a secondary activation state (A2). According to Wagner (1981), these already primed units (in an A2 state) cannot be activated again in an A1 state of processing and therefore cannot be fully processed. These circumstances would increase the likelihood of activating a greater number of units of the unique element (b), thus favoring its processing. This bias encodes well-defined representations of the unique elements in memory, which when retrieved on the test will facilitate their discrimination. In the case of blocked exposure, common and unique elements would be habituated together and compete for processing resources.

In a subsequent study, Dwyer et al. (2011) found that the introduction of a distractor (either a face or a checkerboard) in the middle of the pairs during preexposure reduced the discriminative advantage of the intermixed preexposure. The authors explain this latter effect in terms of interrupted short-term habituation of the common elements that eliminates the processing bias, and they conclude that "The opportunity to compare stimuli plays a causal role in supporting perceptual learning" (Dwyer et al., 2011; see also Mitchell & Hall, 2014).

In this regard, our laboratory has conducted a series of experiments with rats as subjects using a rapid alternating exposure procedure, one that more closely resembles the procedure used with humans and have demonstrated the I/B effect (Recio et al., 2018, 2019; Sánchez et al., 2022 **[AQ2]**). In one of these experiments (Experiment 1 in Recio et al., 2018), the rats were exposed to pairs of similar flavors (AX and BX) in intermixed or blocked succession with a short ISI (5 min), after which a new element Y was aversively conditioned and followed by a consumption test in which Y was presented in compound with one of the already preexposed unique elements (AY). They found higher consumption of the AY compound for the intermixed group than the blocked group, suggesting that there was less generalization of the Y aversion after intermixed than blocked preexposure. Recio et al. (2018) interpreted these results in the same terms as Mundy et al. (2007); that is, rapid stimulus alternation promotes short-term habituation of the common elements, and this biases processing resources toward the unique elements. As a consequence, the well-defined representation of A after intermixed exposure could decrease the similarity between the conditioned element Y and the test compound AY, resulting in less generalization between them. Furthermore, they found in their Experiments 2 and 3 that this effect was abolished by the presentation of a novel stimulus (sugar) between AX and BX during preexposure, replicating the distractor effect found in humans (Dwyer et al., 2011).

This external inhibition test had previously been used in rats by Blair and Hall (2003, Experiments 5A and 5B) with a long ISI preexposure procedure, and like Recio et al. (2018), they also found lower generalization for subjects given an intermixed scheme. However, Blair and Hall's (2003, Experiments 5A and 5B) long-ISI results have been explained in terms of increased salience of the unique elements after intermixed preexposure, which interferes with the conditioned response to Y on the test (Hall, 2003). At this point it is important to note that, the short ISI procedures, as used by Recio et al. (2018), would not be able to promote the associative activation of unique elements and, therefore, the restoration of their salience. When the second compound (BX) is presented shortly after the presentation of the first compound (AX), most of the unique elements of the first compound (a) will be in a marginal processing state (A2). According to Wagner's Sometimes opponent process (SOP) **[AQ3]** model (Wagner, 1981), if the unique elements of a stimulus are in the A2 state because they have been recently presented, they cannot be activated associatively and thus no salience modulation would take place. So how can a well-represented element in memory be able to produce this external inhibition effect? To elucidate this, Recio et al. (2018) rely on McLaren and Mackintosh's (2000) unitization mechanism, which refers to the formation of associations between the different features that comprise each stimulus and can be understood as the formation of a representation of the stimulus; thus, the greater the unitization, the better the representation. This is relevant for perceptual learning because what drives discrimination between two very similar stimuli is the representation of the elements that make them different. Recio et al. (2018) suggested that stimuli are composed of several subunits, of which our limited sensory system can only sample a few

at a time (Estes, 1959). Therefore, during preexposure with a short, intermixed ISI, the processing bias would increase the likelihood that a greater number of subunits, which, for example, form the unique element A on AX trials, could be sampled together, increasing the possibility of forming excitatory associations between them. These associations would lead to further unitization of the unique element A, developing a well-defined representation of that element in memory. As a consequence, a more unitized A should cause more external inhibition of Y on the test because more of its features will be retrieved from memory. Sampling any subunit of A on the test will associatively prime the rest and easily activate this representation, which will be better discriminated than after blocked preexposure, reducing its similarity to Y and hence interfering to some extent with the conditioned response (CR) **[AQ4]** (McLaren & Mackintosh, 2000). During blocked preexposure, the unique elements will tend to form a stronger association with the common elements at the expense of other unique elements and therefore the unitization of these will be lower, interfering less with the CR on test.

Paradoxically, this unitization mechanism is expected to decrease the effective salience of the unique elements after intermixed exposure, in contrast to what salience models propose for long ISI procedures in this respect. Well-unitized elements might be expected to suffer greater latent inhibition, so their ability to enter into new associations would also be reduced (McLaren et al., 1989; McLaren & Mackintosh, 2000). The representation of a unitized element would so accurately match the real perceived elements during preexposure that the value of the subjects' expectation discrepancy will approach zero (the internal input matching the external input), and consequently, the salience of this element would decrease (Ballesta et al., 2021). Some evidence for these unitization implications comes from flavor aversion experiments conducted by Artigas et al. (2012) and from appetitive experiments carried out by Ballesta et al. (2021), which have shown reduced salience of the unique elements after short ISI intermixed presentations of similar auditory stimuli.

Salience modulation models (e.g., Hall, 2003) propose that the increased salience of the unique elements improves discrimination in perceptual learning. However, the associative activation that protects the salience of these elements is not likely to operate in the rapid exposure procedures that have shown to be successful in improving discrimination (Dwyer et al., 2011; Mundy et al., 2007; Recio et al., 2018, 2019; Sanchez et al., 2022). In view of this, Recio et al. (2018) proposed that during rapid intermixed preexposure, the processing bias toward unique elements favors their unitization. And according to McLaren and Mackintosh (2000), a well-unitized representation should be more easily discriminated from other stimuli while suffering greater latent inhibition. Although this model does not make a clear prediction about the role of unitization in the I/B effect, certain hypotheses can be proposed. Intermixed preexposure with a long ISI allows for increased sampling of the common elements, resulting in more rapid unitization of these elements and greater latent inhibition. The latter favors the subsequent unitization of the unique elements (see also Ballesta et al., 2021). In any case, this would be a less rapid and effective process than the one proposed by Recio et al. (2018) for short ISI procedures in terms of processing bias. The following experiments aimed to find evidence of these mechanisms proposed by Recio et al. (2018) to explain perceptual learning in terms of greater unitization of the unique elements resulting from a short-term habituation process of the common elements. For this purpose, we conducted three experiments with rats using a preexposure procedure involving short ISIs. Experiment 1 aimed to replicate the perceptual learning effect obtained by Recio et al. (2018, Experiment 1) with this short ISI procedure. The remaining two experiments were designed to measure the associability of the unique elements, either directly by measuring their subsequent conditioning (Experiment 2) or indirectly by measuring their ability to overshadow the conditioning of a new stimulus (Experiment 3). We expected to find that the unique elements are more discriminable and less effective in entering into a new association after short ISI intermixed preexposure than after blocked exposure (see Honey & Hall, 1989 for a demonstration of the dissociation between effective salience and discriminability after exposure to a stimulus).

Experime[AQ5]nt 1

This experiment is a replication of Experiment 1 of the study by Recio et al. (2018), the design of which is summarized in Table 1. In that study, we used a short ISI preexposure procedure and an external inhibition test to measure the I/B effect (see also Blair & Hall, 2003). Two groups of rats received daily exposure to two compound flavors (AX and BX) separated by a 5-min ISI. Group intermixed (INT) received both stimuli each day while group blocked (BLK) received each stimulus in blocks of 2 days. After preexposure, both groups received a new flavor Y paired with a LiCl injection that generates an aversion, and Y was then tested in compound with one of the unique preexposed elements (AY).

On the basis of previous findings, we expected to find less generalization of the aversion in the intermixed group, that is, a higher consumption of AY than the blocked group in the test phase. After intermixed exposure, sampling any subunit of A on the test will associatively prime the rest and easily activate this representation, which will be better discriminated than after blocked preexposure, reducing its similarity with Y and hence interfering to some extent with the CR. The unique feature—which is well unitized and therefore better represented in memory—will be retrieved readily and hence be more

discriminable.

Method

Subjects and Apparatus

The experiment was carried out in two batches with 16 naïve male Wistar rats as subjects in each. For the first batch, the mean ad libitum weight was 332 g (range: 300–370 g), while the mean ad libitum weight of the second batch was somewhat lower, 304 g (range: 283–345 g). The rats were housed individually in transparent plastic boxes measuring 35 × 22 × 18 with sawdust for the bedding. They were maintained on a 12-h light/dark cycle that began at 8:00 a.m.

All the solutions used were prepared with tap water on the same day as the experimental session. They were administered in the home cages using 50-ml inverted centrifuge tubes with stainless steel ball-bearing-tipped spouts. The consumption of the solutions was calculated by weighing the tubes before and after the sessions. Stimuli AX and BX were commercial salt solutions (9 g/l) with hazelnut or caramel odors (counterbalanced) at 0.05% of the total volume of the solution. The odors were from the Manuel Riesgo brand (Madrid, Spain). The conditioned element Y was a 0.5 g/lsolution of citric acid. For conditioning, 0.15 M intraperitoneal injections of LiCl were administered at 1% of the subject's body weight.

Procedure

All the procedures used here were approved by the Animal Research Ethics Committee (Comité de Ética en Experimentación Animal, CEEAOH, number 05/11/2020/125) from the University of Granada and are classified as low severity according to European guidelines. Rats were monitored daily by those responsible for animal welfare in the research center. Rats from the first batch were divided into two groups (INT and BLK) of eight rats with equivalent weight and consumption (mean INT weight: 330 g and BLK: 333 g), while rats from the second batch were divided into two groups (INT and BLK) of eight rats, also with equivalent weight and consumption (mean INT weight: 301 g and BLK: 307 g). Access to water was restricted for all rats, and they could only drink on two 30-min sessions per day, at 11:00 and 16:00. The rats received three baseline days in which their water consumption was measured during the morning session since no relevant manipulations were to be carried out during the afternoon session. The subjects were divided into equivalent groups based on their level of consumption.

The preexposure phase lasted 4 days (Days 1–4). During the morning session, all rats received access to compounds AX and BX. The INT group first received 6 ml of one solution for 10 min, followed by 4 ml of water for 5 min, and finally 6 ml of the other solution for 10 min. The BLK group received the same presentation scheme, but they always received the same compound on the first 2 days and the other compound on the last 2 days. The order of presentation of the stimuli was counterbalanced for both groups during the 4 days of preexposure. During the afternoon session, both groups had free access to water for 30 min to maintain hydration levels. Finally, on Day 4 after the afternoon session, all the animals were weighed again to calculate the volume of LiCl that was to be injected during the conditioning phase.

On the following 4 days (Days 5–8), the rats received two conditioning trials (Days 5 and 7) and two recovery days, respectively (Days 6 and 8). In each conditioning day, the rats had access to 10 ml of Y for 30 min, immediately followed by an intraperitoneal injection of LiCl. The rats had free access to water for 30 min in the morning sessions on the recovery days. During the next four test days (Days 9–12), the rats received free access to compound AY for 30 min in the morning session.

Statistical Analysis

Statistical analyses were carried out on the consumption measure. General linear model null hypothesis testing analyses were conducted, adopting a rejection level of $p < .05$, and Greenhouse–Geisser corrections were used when needed. Partial eta squared (η_p^2) and Cohen's *d* were used to report effect sizes. Within-group factors were analyzed using repeated-measures analysis of variance (ANOVA), with Group as a between-subjects factor and Trial as the within-subjects factor. Interactions between these factors were explored using independent samples *t*-tests. Outlier analyses were based on Tukey's rule (Tukey, 1977), where outliers are values more than 1.5 times the interquartile range (IQR) from the quartiles, that is, either below Q1 − 1.5 IQR**[AQ6]**, or above Q3 + 1.5 IQR. The SPSS**[AQ7]** statistical program was used to carry out all analyses.

Transparency and Openness

This study was not preregistered. The raw data on which study conclusions are based are available in the APA's**[AQ8]** repository on the Open Science Framework (OSF (de Brugada, 2022), https://mfr.osf.io/render?url=https://osf.io/u6qfp/?direct%26mode=render%26action=download%26mode=render.

Results and Discussion

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes. Subjects in groups INT and BLK consumed an average of 4.84 and 4.79 ml, respectively, of the AX solution and 4.62 and 4. 8 ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX), Group (INT and BLK), and Batch (1 and 2) as variables showed no significant effects or interactions among these variables—largest, $F(1, 27) = .82$, $p = .37$, $\eta_p^2 = .03$, mean square error (*MSE*) = .8 for Group × Stimulus interaction.

In the conditioning phase, the consumption of Y decreased over the two trials (Figure 1). Unexpectedly, one rat drank an unusually small amount on the first day of conditioning. The outlier analysis revealed significant differences from all other rats, and this subject was withdrawn from the experiment after that first conditioning trial. A repeated-measures ANOVA with Trial, Group, and Batch as factors showed differences across trials, $F(1, 27) = 57$, $MSE = 1.7$, $p < .05$, $\eta_p^2 = .68$, and differences between batches, $F(1, 27) = 6.2$, $MSE = 2.04$, $p < .05$, $\eta_p^2 = .19$. Neither the Group factor nor interactions were significant—largest effect TrialxBatch, $F(1, 27) = 1.26$, $MSE = 1.7$, $p > .05$, $\eta_p^2 = .04$.

Figure 2 shows the consumption of AY across the four test days in Experiment 1. The INT group consumed more of this flavor than the BLK group on all the tests. A repeated-measures ANOVA with Trial, Group, and Batch as factors confirmed these impressions, showing a significant effect of Trial, $F(3, 81) = 88.6$, $MSE = 2.53$, $p < .05$, $\eta_p^2 = .77$; significant effect of Group, $F(1, 27) = 4.36$, $MSE = 11.28$, $p < .05$, $\eta_p^2 = .14$; and interaction TrialxBatch, $F(3, 81) = 3.7$, $MSE = 2.53$, $p < .05$, $\eta_p^2 = .12$. Neither Batch factor nor interactions were significant (all Fs < 1). The TrialxBatch interaction was analyzed using an independent samples *t*-test, which showed significant differences between batches on Test 1, $t(29) = 2.2$, $p < .05$ and $d = .8$. The differences between batches in the conditioning and test phase reflect the fact that rats from Batch 1 had a higher baseline consumption level than those from Batch 2, likely because the former were older and heavier than the latter.

As in Recio et al. (2018), the INT group showed a weaker aversion to AY than the BLK group. These results can be explained in terms of better unitization of the unique element A after intermixed exposure to the flavor compounds AX and BX. If A is well unitized, the perception of one element will retrieve the others, and A will be more likely to interfere with the response governed by a separately conditioned Y stimulus on the AY test (Recio et al., 2018).

Using a very similar external inhibition procedure but with a long interval between presentations of two similar stimuli (several hours), Blair and Hall (2003) found the same results, that is, the aversion to Y was more strongly impaired by the presence of A after intermixed exposure than blocked exposure (see also Rodríguez et al., 2008). These authors interpreted their results in terms of the greater salience of the unique element A after intermixed exposure than blocked exposure, increasing its ability to produce external inhibition (Hall, 2003).

While these two theoretical alternatives predict better discrimination after intermixed than blocked exposure (the standard perceptual learning effect), they differ in their prediction about the effective salience of the unique elements after intermixed exposure. Hall's (2003) account predicts that intermixed exposure with a long ISI, by allowing associative activation of the unique elements in their absence, keeps their effective salience high. In contrast, with a short ISI, Recio et al. (2018) predict that an element that receives more processing resources (and is therefore well unitized) will see its effective salience diminish, suffering a greater degree of latent inhibition (McLaren & Mackintosh, 2000).

In order to test the unitization hypothesis proposed by Recio et al. (2018) to explain the perceptual learning effect after rapid alternating exposure, in Experiment 2 we measured effective salience directly by conditioning the unique element A after intermixed exposure to AX and BX with a short interval between them.

Experiments 2a and 2b

In Experiments 2a and 2b, we assessed the associability of the unique element A after intermixed or blocked exposure with a short ISI. Following preexposure, all animals received conditioning trials to A followed by an i.p. injection of LiCl. A final test with unreinforced presentations of the unique element A was given to observe the course of extinction of the conditioned response. The design of these experiments is shown in Table 1. Following the results of Experiment 2a, we decided to conduct Experiment 2b, which aimed to increase the sensitivity of our procedure to detect differences in conditioning. This was achieved by halving the LiCl dose and extending the preexposure phase to 10 days.

If, during short ISI intermixed exposure to two similar stimuli, the unique elements of these stimuli are better processed, this should result in more unitized subunits. The associations among the unique features of each stimulus could be responsible for a decrease in the effective salience of the unique elements by reducing the discrepancy between external and internal inputs (McLaren et al., 1989; McLaren & Mackintosh, 2000). This being the case, one would expect that the conditioning of the unique element A should be less effective after intermixed than blocked exposure.

Experiment 2a

Method

Subjects and Apparatus

The subjects were 32 naïve male Wistar rats with a mean ad libitum weight of 239 g (range: 213–264 g). The maintenance of the animals and the apparatus used were the same as those in the previous experiment.

Procedure

Rats were divided into two groups (INT and BLK) of 16 with equivalent weight and consumption (mean INT weight: 242 and BLK: 236 g). The general procedure was essentially the same as in Experiment 1, but with some procedural changes. First, subjects were given two baseline days instead of three. Second, there were four conditioning trials with 10 ml of the element A (Days 5–12). This was followed by four test trials (Days 13–16), on which the rats were presented with 30 ml of A for 30 min. Any other detail not mentioned here was the same as in Experiment 1.

Results and Discussion

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes. Subjects in groups INT and BLK consumed an average of 4.97 and 5.1 ml, respectively, of the AX solution and 5.15 and 5.07 ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) yielded no significant effects or interaction between these variables—largest, $F(1, 30) = 0.52$, $p = .48$, $\eta_p^2 = .02$, $MSE = 1.33$ for Stimulus × Group interaction.

Figure 3a shows consumption during the conditioning phase. Decrease in consumption of A developed slowly from Trials 1 to 4, probably because prior exposure generated some latent inhibition to A. A repeated-measures ANOVA with Trial and Group as factors showed that this decrease in consumption was significant, with an effect of Trial, $F(2, 59.5) = 16.46$, $MSE = 5.74$, $p < .05$, $\eta_p^2 = .35$. Neither the Group factor nor the interaction were significant—largest, $F(1, 30) = 1.62$, $p > .05$, $MSE = 6.34$, $\eta_p^2 = .05$.

Figure 4a shows the consumption of A during the four test days, where the INT group showed higher consumption than the BLK group until the fourth trial. A repeated-measures ANOVA with Trial and Group as factors revealed a significant effect of Trial, $F(2.1, 63.9) = 15.86$, $MSE = 6.51$, $p < .05$, $\eta_p^2 = .35$. Again neither the Group factor nor the interaction were significant—largest effect for Group factor, $F(2.1, 63.9) = 1.63$, $p > .05$, $MSE = 6.51$, $\eta_p^2 = .05$.

The results from Experiment 2a show the same level of conditioning to A for the INT group and the BLK group. One possible explanation for this lack of a difference is that our procedure is not sensitive enough to detect differences in conditioning to a previously exposed stimulus. In view of this possibility, we decided to carry out Experiment 2b, introducing some slight changes from the procedure used in Experiment 2a.

Experiment 2b

Recent findings from Recio et al. (2019) and Ballesta et al. (2021) have shown that perceptual learning is boosted when the preexposure is lengthened, and in Experiment 2b we therefore decided to extend preexposure from 4 days to 10 with the aim of producing a more marked effect on the unique elements. In a similar attempt to increase the differences in conditioning of the unique elements, Blair & Hall et al. (2003 **[AQ9]**) used a weaker dose of LiCl and found differences in acquisition of the aversion during the conditioning phase. Therefore, the conditioning phase of Experiment 2b was extended by 1 day, where the A element was presented ad libitum during this phase, and half the dose of lithium was used. We expected these procedural changes to be enough to find differences between the preexposure groups either during conditioning or on test.

Method

Subjects and Apparatus

Subjects were 34 male Wistar rats that had had experience with saccharin, soya, and vanilla odor in a previous sensory-specific satiety experiment. The experiment was carried out in two consecutive batches with 16 and 18 subjects, respectively, due to the availability of rats. For the first batch, the mean ad libitum weight was 337 g (range: 310–380 g), while the weight of the second batch was somewhat higher, 455 g (range: 400–550 g). The maintenance of the animals and the apparatus used were the same as those in previous experiments except for the conditioning phase where 0.075M intraperitoneal injections of LiCl were administered at 1% of the subject's body weight.

Procedure

Rats from the first batch were divided into two groups (INT and BLK) of eight with equivalent weight and consumption (mean INT weight: 336 g and BLK: 338), while those from the second batch were divided into two groups (INT and BLK) of nine, also with equivalent weight and consumption (mean INT weight: 456 g and BLK: 453 g).

The general procedure was essentially the same as in Experiment 2, but with some procedural changes. The number of conditioning trials was increased to five (Days 11–13–15–17–19) and the dose of LiCl was decreased by half (0.075M intraperitoneal injections of LiCl at 1% of the subject's body weight). On each conditioning day, the rats received 30 ml of A for 30 min followed by a recovery day. With these changes, we might expect a more powerful effect of preexposure since a slower and more sensitive conditioning phase would allow us to observe differences between groups throughout the acquisition of the aversion. Conditioning was followed by four test trials (Days 21–22–23–24), on which the rats were presented with 30 ml of A for 30 min. Any other detail not mentioned here was the same as in Experiment 2.

Results and Discussion

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes. Subjects in groups INT and BLK consumed an average of 4.68 and 4.46 ml, respectively, of the AX solution and 4.47 and 4.48 ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX), Group (INT and BLK), and Batch (1 and 2) yielded no significant effects or interactions between these variables—largest, $F(1, 30) = 1.52$, $p = .23$, $\eta_p^2 = .05$, $MSE = 1.29$ for Stimulus × Group interaction.

Figure 3b shows consumption during the conditioning phase. An increase in the consumption of A was observed from the first to the second trial, after which it progressively decreased to minimum levels by the fifth trial. A repeated-measures ANOVA with Trial, Group, and Batch as factors showed that this decrease in consumption was significant, with an effect of Trial, $F(2.1, 62.8) = 22.73$, $p < .05$, $MSE = 8.77$, $\eta_p^2 = .43$. Neither the single factors nor interactions were significant—largest effect TrialxGroupxBatch, $F(2.1, 62.8) = 1.66$, $p > .05$, $MSE = 8.77$, $\eta_p^2 = .05$.

Figure 4b shows the consumption of A during the four test days, where the INT group showed higher consumption than the BLK group on all the tests. A repeated-measures ANOVA with Trial, Group, and Batch as factors confirmed these impressions, revealing a significant effect of Trial, $F(3,90) = 22.74$, $p < .05$, $MSE = 2.02$, $\eta_p^2 = .43$; Group, $F(1, 30) = 5.49$, $p < .05$, $MSE = 31.05$, $\eta_p^2 = .15$; and Batch, $F(1, 30) = 9.26$, $p < .05$, $MSE = 31.05$, $\eta_p^2 = .24$. The interaction between Trial and Group was also significant, $F(3, 90) = 3$, $p < .05$, $MSE = 2.02$, $\eta_p^2 = .09$. This interaction was explored using a simple effects analysis, which showed significant differences between the groups on Test 2, $t(32) = 2.47$, $p < .05$, $d = .85$; Test 3, $t(32) = 2.59$, $p < .05$, $d = 0.89$; Test 4, $t(32) = 2.02$, $p = .05$, $d = .69$. No other interactions were significant—largest effect GroupxBatch, $F(1, 30) = 2.07$, $MSE = 31.05$, $p > .05$, $\eta_p^2 = .06$.

The differences observed between the batches were due to a higher level of consumption of the second batch than the first; this was confirmed by a repeated-measures ANOVA introducing Batch and Trial as the main factors where we found a significant effect of Trial, $F(3, 96) = 21.58$, $p < .05$, $MSE = 2.13$, $\eta_p^2 = .4$, and Batch, $F(1, 32) = 7.81$, $p < .05$, $MSE = 36.86$, $\eta_p^2 = .2$. The interaction between these two factors was not significant ($F < 1$). These results can be explained by age differences between the two batches of rats since subjects from the second batch were older and thus showed higher consumption levels than the younger rats from the first batch.

The results from Experiment 2b showed a similar conditioning rate for the INT group and BLK group. Conversely, during extinction, the intermixed subjects showed a progressively higher rate of consumption than those from the blocked group. These differences between Experiment 2a and Experiment 2b were expected on the basis of the increased amount of preexposure given. The latter results reflect a weaker association between the unconditioned stimulus (US) **[AQ10]** and the unique element as a consequence of the intermixed schedule. This is consistent with the idea of unitization of the unique elements after short ISI intermixed preexposure, since a unitized unique element would be lower in salience and will suffer greater latent inhibition than after blocked preexposure (McLaren & Mackintosh, 2000; Wagner, 1981).

However, the absence of differences during the acquisition phase still allows salience models (Hall, 2003) to explain the results of Experiment 2b and, ultimately, those from Experiment 1. It is known that a salient stimulus has higher associability; therefore, the faster extinction of the conditioned response on the test could be observed due to the development of associations between the unique element and "no consequences" across the test trials, resulting in higher—rather than lower—associability of this element in the intermixed group (Mondragón & Hall, 2002). Owing to this possibility, we will use a different test in Experiment 3 to assess the salience of the unique elements, that is, we will measure the ability of A to overshadow Y when conditioned as a compound. We expect that the unique elements resulting from the intermixed preexposure will overshadow conditioning to Y to a lesser extent, and thus, Y will be more aversive on test than after blocked preexposure. Fortunately, this overshadowing procedure has been found to be more sensitive than direct conditioning when it comes to assessing salience (e.g., Mondragón & Murphy, 2010 **[AQ11]** used this procedure to evaluate the salience of common elements).

Experiment 3

The design of this experiment is shown in Table 1. After intermixed or blocked preexposure a conditioned aversion was established to the compound AY, where Y was a novel element and A the preexposed unique element, after which the aversion to Y alone was measured in the test phase. Experiment 3 is analogous to Experiment 1. In both cases, after the preexposure phase, the unique element is presented in compound with a non preexposed element, Y, to either measure the degree of interference of the unique element in the aversion acquired by Y (Experiment 1) or to assess its ability to compete for associative strength during compound conditioning (Experiment 3). For this reason, we decided to use the same preexposure procedure in this experiment as in Experiment 1.

We expect that the unique intermixed element, being less salient than that presented during blocked exposure, will compete to a lesser extent for associative strength during AY conditioning, and therefore the intermixed group would show a greater aversion to Y in the test phase. In contrast, if the unique element is more salient, it will compete more strongly for associative strength during conditioning, restricting the aversion developed to Y, resulting in higher consumption on the test.

Method

Subjects and Apparatus

Subjects were 32 male Wistar rats that had received experience with sucrose and glutamate in previous experiments, where the effect of a novel stimulus presentation on a typical sensory-specific satiety procedure was examined. The mean ad libitum weight was 354 g (range 307–420 g). The maintenance of the animals and the apparatus used were the same as those described in Experiment 1 except that stimulus Y was a strawberry odor at 0.05% of the total volume of the solution (Manuel Riesgo, Madrid, Spain).

Procedure

The subjects were divided into two groups (INT and BLK) of 16 with equivalent weights (mean INT weight: 357 g and BLK: 350 g). Following the same preexposure as in Experiment 1, all subjects received two conditioning trials (Days 5 and 7) where a 12-ml presentation of the AY solution was followed by an i.p. injection of 0.15M LiCl administered at 1% of the subject's body weight. Each conditioning day was followed by a recovery day (Days 6 and 8). Finally, the subjects received eight test trials (Days 9–16) with free access to the Y solution for 30 min. Other details not mentioned here were the same as in Experiment 1.

Results and Discussion

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes. Subjects in groups INT and BLK consumed an average of 4.47 and 4.63 ml, respectively, of the AX solution and 4.6 and 4.75 ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) as variables showed no significant effects or interactions between these variables—largest, $F(1, 30) = .45$, $p = .51$, $\eta_p^2 = .02$, $MSE = 2.04$ for stimulus factor.

As Figure 5 shows, AY consumption decreased throughout the two conditioning trials. A repeated-measures ANOVA with Trial and Group as factors confirmed that this decrease in consumption was significant, $F(1, 30) = 29.33$, $p < .05$, $MSE = 10.07$, $\eta_p^2 = .5$. Neither the Group factor nor the interaction Group × Trial was significant ($Fs < 1$)

Figure 6 presents the group mean scores for consumption of Y over four two-trial blocks of the test phase. Rats from the blocked group increased their consumption at a faster rate than those from the intermixed group. A repeated-measures ANOVA with Block and Group as factors revealed significant effects of Block, $F(2.2, 64.9) = 39.3$, $p < .05$, $MSE = 5.79$, $\eta_p^2 = .6$, and an interaction Block × Group, $F(2.2, 64.8) = 3.54$, $p < .05$, $MSE = 5.79$, $\eta_p^2 = .1$, but not effect of group, $F(1, 30) = 3.5$, $p > .05$, $MSE = 26.8$, $\eta_p^2 = .1$. This interaction was explored using independent samples t-tests, which showed significant differences between the groups on Block 4, $t(30) = 2.24$, $p < .05$, and $d = .79$.

In Experiment 3, presentation of a compound stimulus (AY) with the unique preexposed element A and a novel element Y was followed by an injection of LiCl. No differences were observed during the conditioning phase; however, in subsequent tests with Y alone, the INT group showed a stronger aversion than the BLK group. These results indicate that element A had a lower capacity to restrict conditioning to Y after intermixed than blocked preexposure. Unitization of the unique elements increases their latent inhibition, reducing their ability to compete for associative strength, so that most of the associative strength was acquired by the Y element, resulting in a stronger aversion on the test. These results confirm those obtained in Experiment 2, showing a lower salience of the unique elements after a short ISI intermixed preexposure, thus supporting the notion that unitization is the mechanism that promotes better discrimination following rapid alternation of similar stimuli (Experiment 1).

General Discussion

Findings from studies with human and nonhuman subjects using a short interval between presentations of two similar stimuli have shown that intermixed presentation of the stimuli results in better discrimination than presentation in a series of blocks—the Intermixed/Blocked effect (Dwyer et al., 2011; Recio et al., 2018, 2019; Sanchez et al., 2022). This example of perceptual learning has been explained in terms of a processing bias of the unique elements due to a process of short-term habituation of common elements (Dwyer et al., 2011; see also Honey & Bateson, 1996; Mundy et al., 2007). Recio et al. (2018), based on McLaren and Mackintosh's (2000) model, propose that this processing bias of unique elements favors their unitization. Thus, after intermixed preexposure, the unique and distinctive elements of the stimuli will be better represented in memory and can therefore be better discriminated when later presented with similar stimuli. Furthermore, following the model of McLaren et al. (1989), Recio et al. (2018) predict a lower salience of these elements, making it more difficult for these elements to enter into new associations. In fact, we can suggest that perceptual learning is precisely that "It is easier to discriminate between familiar than between novel stimuli, even though it might be harder to learn about the former" (Recio, 2017, p.32). The experiments conducted here were aimed to evaluate the changes in discriminability and salience of the unique elements following intermixed preexposure with a short ISI, as proposed by Recio et al. (2018) with nonhuman animals.

Experiment 1 is a replication of Recio et al.'s (2018) Experiment 1 and confirms an I/B effect with an external inhibition test. After preexposure, an aversion was conditioned to a novel flavor, Y, after which subjects were tested with AY. The aversion to Y was more impaired by the presence of A after short ISI intermixed preexposure than after blocked exposure. A better memory representation of A due to processing bias during intermixed preexposure (Dwyer et al., 2011) would be more discriminable and, therefore, could be expected to interfere more with the processing of Y (McLaren & Mackintosh, 2000; Recio et al., 2018; Wagner, 2003). We might expect that a better-represented stimulus (more unitized) would not only become more discriminable but will also suffer a loss of effective salience (latent inhibition) (McLaren et al., 1989). In Experiment 2, after short ISI intermixed or blocked preexposure, an aversion was conditioned to A, and its consumption on test was measured. The results showed a weaker aversion to A after intermixed than after blocked preexposure, which indicates that the unique element A was less salient. Experiment 3 employed an overshadowing test; after preexposure, an aversion was conditioned to AY and consumption of Y was then assessed. We found a greater conditioned response to Y after intermixed than blocked exposure. This implies that A was less effective at overshadowing Y during conditioning, which is again compatible with the idea that A is less salient. Thus, like Experiment 2, this finding suggests that A is rendered less effective by the intermixed procedure. The results of Experiments 1–3 show a greater interference with the conditioned response to a novel stimulus as well as a reduction in effective salience of the unique elements after short ISI intermixed preexposure in comparison with blocked preexposure.

It should be noted that the results of Experiments 1 and 2 can be explained in alternative ways that need to be addressed. It has been suggested that very closely spaced presentations of AX and BX will allow the formation of a direct associative link between A and B, and this association could facilitate the generalization of the conditioned response on the test, thus obscuring the perceptual learning effect (Honey & Bateson, 1996). Indeed, Recio et al. (2019), using a procedure with short ISI preexposure and a generalization test (after preexposure, an aversion was established to AX, and the aversion to BX was then measured), found that the I/B effect was reversed (see also Alonso & Hall, 1999; Hall, 2021; Rodríguez & Alonso, 2008 for a review). Recio et al. (2019) explained this paradoxical result in terms of sensory preconditioning between A and B (see also Honey & Bateson, 1996). To decrease the possible influence of an A–B association on the test, and following Recio et al. (2018), we used an external inhibition test to assess perceptual learning in Experiment 1 (see also Blair & Hall, 2003). However, it should be noted that this type of test is not entirely free from the influence of such an association. In Experiment 1, we can assume that after intermixed preexposure the A–B association would allow for A to be a more effective external inhibitor precisely because it also activated a representation of B during the test with stimulus Y. That is, for Group Intermixed, the effective stimulus could be ABY rather than just AY in Group Blocked, resulting in greater interference with the conditioned response to Y in the former case. Similarly, in Experiment 2, the associative activation of B during conditioning to A could allow the formation of an association between the stimulus compound AB and LiCl, overshadowing the acquisition of the aversion by element A. This would explain the reduced learning about A without recourse to a salience reduction mechanism. However, this account has difficulty in explaining the results from Experiment 3. In that case, the activation of the element B during AY conditioning would hinder—rather than improve—the aversion acquired by Y in the intermixed group. Thus, the weaker overshadowing of Y observed in the intermixed group supports our salience reduction account.

An alternative explanation for the findings of Experiment 1 can be proposed in terms of generalization decrement during

intermixed preexposure. When a stimulus is presented repeatedly, it can be experienced slightly different across trials, and the properties attributed to it can then be reset (Wheeler et al., 2006). If we assume that during alternating exposure the unique elements are perceived as different, their salience could remain high rather than undergoing the accumulative effects of habituation resulting from repeated exposure. However, several perceptual learning experiments have demonstrated that after intermixed preexposure these stimuli and their elements are better recognized than nonpreexposed or blocked stimuli/elements (for stimuli, see Honey & Bateson, 1996, and for elements, see De Zilva & Mitchell, 2012), implying that subjects perceived the preexposure and test stimuli as essentially the same items. Even so, this account can only explain the results from Experiment 1 where high salience of the unique intermixed element could interfere with the conditioned response to Y. In Experiments 2 and 3, we found that the unique elements after intermixed short ISI preexposure were lower in salience and not higher, as this hypothesis would suggest.

The results of Experiment 1 run counter to those reported by Ballesta et al. (2021, Experiment 3) showing that a unique element preexposed in an intermixed fashion was less able to interfere with the conditioned response to a novel stimulus Y than a unique element preexposed in blocks. To address this issue, we will consider what we take to be an important difference between the procedure of Ballesta et al. (2021) and ours, which concerns the nature of the stimuli. Specifically, while tones do not relate to hunger, liquids are important for thirst. Regarding our procedure, first, the stimuli could be positively reinforced during preexposure by reducing thirst; second, the Y element is aversively conditioned to reduce consumption, and finally, on the AY test opposing effects are in operation. The better unitization of the unique elements during intermixed preexposure should better establish a reduction in thirst than blocked preexposure, resulting in more interference with the conditioned aversion to Y. In contrast, although in the study by Ballesta et al. (2021) the intermixed unique elements are also well unitized, these tones were not reinforced to modulate hunger during preexposure, so when presented in compound with the conditioned Y tone on test, they did not affect the reinforced positive response of eating and hunger reduction. In fact, one reason why after the blocked preexposure given by Ballesta et al. (2021) the unique elements might interfere more with the CR is that these elements are less well recognized, and therefore, animal subjects tend to react cautiously when considering intake behavior. The same could apply to our test; a less recognized flavor A after blocked preexposure should be an unreliable indicator of safety during drinking, thus leading the animal to further reject AY. It seems, therefore, that biologically relevant behaviors such as ingestion can be modulated by the perceptual properties of stimuli.

The results presented here are not compatible with previous models such as Hall's salience modulation model (2003), for which the I/B effect depends on the associative activation of the unique elements in their absence. A rapid succession preexposure such as the one used here is unlikely to provide an opportunity for the activation of the representation of the unique features of the two stimuli in their absence. In fact, Hall's model would have problems explaining the distractor effects reported by Dwyer et al. (2011) and Recio et al. (2018) with short ISI preexposure. They showed that when a new irrelevant element is introduced between the pairs of stimuli during intermixed preexposure, the improved discrimination effect is eliminated. According to salience modulation theories (Hall, 2003), the opposite would be expected, that is, introducing a distractor would interrupt the habituation of the stimuli and increase their salience, which would improve rather than hinder discrimination. Moreover, the distractor should displace the unique element representation to an inactivate state, and the common element would be able to activate it associatively on the next trial, increasing its salience. However, the results of Dwyer et al. (2011) and Recio et al. (2018) support the opposite, suggesting that the distractor disrupts the short-term habituation of stimulus elements and thus eliminates any processing bias, giving common and unique elements equal access to processing resources. It might therefore be worthwhile to test the possibility that a distractor could increase the salience of unique elements during short ISI preexposure.

To conclude, it seems that better discrimination after exposure to similar stimuli may be due to at least two different mechanisms, and the key factor in triggering one discrimination process or the other is the interval between stimuli (ISI). With a rapid succession procedure such as the one used here, a mechanism in terms of better processing of the unique elements could operate (e.g., Mitchell et al., 2008; Mundy et al., 2007). This mechanism results in highly unitized and well-represented unique elements in memory, facilitating their subsequent discrimination while making it more difficult for them to enter into new associations. This process is vulnerable to the presence of a distractor. However, procedures in which a long interval occurs between AX and BX are more likely to involve a mechanism based on the associative activation of the absent stimulus (e.g., Hall, 2003; McLaren & Mackintosh, 2000). This results in unique elements that maintain a high level of salience, facilitating both their later discrimination and the acquisition of new learning. Importantly, this process would not be disrupted by a distractor. The data support this theoretical proposal, showing a perceptual learning effect with both a short ISI exposure procedure (using a generalization test, see Recio et al., 2019; Sánchez et al., 2022; for an external inhibition test, see Recio et al., 2018; our Experiment 1) and with a long ISI exposure procedure (generalization test, e.g.,

Symonds & Hall, 1995; external inhibition test, e.g., Blair & Hall, 2003). Moreover, some studies have reported lower effective salience of the unique elements after intermixed exposure with a short ISI (e.g., Experiment 2;Ballesta et al., 2021) and a higher effective salience of these elements after intermixed exposure with a long ISI (Blair et al., 2004). Perceptual learning is thus a complex and flexible form of learning that can activate several mechanisms to guide behavior depending on the environment or demands of the task.

References

Alonso, G., & Hall, G. (1999). Stimulus comparison and stimulus association processes in the perceptual learning effect. *Behavioural Processes*, **48**(1–2), 11–23. 10.1016/S0376-6357(99)00067-4

Artigas, A. A., Contel, D. M., Sansa, J., & Prados, J. (2012). Salience modulation in serial preexposure: Implications for perceptual learning. *Journal of Experimental Psychology: Animal Behavior Processes*, **38**(1), 66–73. 10.1037/a0026399

Artigas, A. A., Sansa, J., Blair, C. A. J., Hall, G., & Prados, J. (2006). Enhanced discrimination between flavor stimuli: Roles of salience modulation and inhibition. *Journal of Experimental Psychology: Animal Behavior Processes*, **32**(2), 173–177. 10.1037/0097-7403.32.2.173

Ballesta, S., Gordón, C., Prados, J., & Artigas, A. A. (2021). Mechanisms of perceptual learning: Prolonged intermixed preexposure reduces the effectiveness of the unique and the common elements. *Journal of Experimental Psychology: Animal Learning and Cognition*, **47**(1), 36–47. 10.1037/xan0000279

Blair, C. A., & Hall, G. (2003). Perceptual learning in flavor aversion: Evidence for learned changes in stimulus effectiveness. *Journal of Experimental Psychology: Animal Behavior Processes*, **29**(1), 39–48. 10.1037/0097-7403.29.1.39

Blair, C. A., Wilkinson, A., & Hall, G. (2004). Assessments of changes in the effective salience of stimulus elements as a result of stimulus preexposure. *Journal of Experimental Psychology: Animal Behavior Processes*, **30**(4), 317–324. 10.1037/0097-7403.30.4.317

De Brugada, I. (2022, November 7). *Isabel de Brugada's quick files*. https://osf.io/s3f96**[AQ12]**

De Zilva, D., & Mitchell, C. J. (2012). Effects of exposure on discrimination of similar stimuli and on memory for their unique and common features. *Quarterly Journal of Experimental Psychology*, **65**(6), 1123–1138. 10.1080/17470218.2011.64430

Dwyer, D. M., Mundy, M. E., & Honey, R. C. (2011). The role of stimulus comparison in human perceptual learning: Effects of distractor placement. *Journal of Experimental Psychology: Animal Behavior Processes*, **37**(3), 300–307. 10.1037/a0023078

Estes, W. K.. (1959). *The statistical approach to learning theory. En S. Koch (Ed.): Psychology: A study of a science. Vol. 2. New York: McGraw-Hill.*.**[AQ13]**

Gibson, E. J. (1963). Perceptual learning. *Annual Review of Psychology*, **14**(1), 29–56. 10.1146/annurev.ps.14.020163.000333

Gibson, E. J. (1969). *Principles of perceptual learning and development*. Appleton-Century-Crofts.

Hall, G. (2003). Learned changes in the sensitivity of stimulus representations: Associative and non-associative mechanisms. *The Quarterly Journal of Experimental Psychology: Section B*, **56**(1b), 43–55. 10.1080/02724990244000151

Hall, G. (2021). Some unresolved issues in perceptual learning. *Journal of Experimental Psychology: Animal Learning and Cognition*, **47**(1), 4–13. 10.1037/xan0000276

Honey, R. C., & Bateson, P. (1996). Stimulus comparison and perceptual learning: Further evidence and evaluation from an imprinting procedure. *The Quarterly Journal of Experimental Psychology: Section B*, **49**(3b), 259–269. 10.1080/713932631

Honey, R. C., & Hall, G. (1989). Acquired equivalence and distinctiveness of cues. *Journal of Experimental Psychology: Animal Behavior Processes*, **15**(4), 338–346. 10.1037/0097-7403.15.4.338

Lavis, Y., Kadib, R., Mitchell, C., & Hall, G. (2011). Memory for, and salience of, the unique features of similar stimuli in perceptual learning. *Journal of Experimental Psychology: Animal BehaviorProcesses*, **37**(2), 211–219. 10.1037/a0021888

McLaren, I. P., Kaye, H., & Mackintosh, N. J. (1989). An associative theory of the representation of stimuli: Applications to perceptual learning and latent inhibition. In **R. G. M. Morris** (Ed.), *Parallel distributed processing: Implications for psychology and neurobiology* (pp. 102–130). Clarendon Press/Oxford University Press.

McLaren, I. P., & Mackintosh, N. J. (2000). An elemental model of associative learning: I. Latent inhibition and perceptual learning. *Animal Learning & Behavior*, **28**(3), 211–246. 10.3758/BF03200258

Mitchell, C., & Hall, G. (2014). Can theories of animal discrimination explain perceptual learning in humans? *Psychological*

Bulletin, **140**(1), 283–307. 10.1037/a0032765

Mitchell, C., Kadib, R., Nash, S., Lavis, Y., & Hall, G. (2008). Analysis of the role of associative inhibition in perceptual learning by means of the same-different task. *Journal of Experimental Psychology: Animal BehaviorProcesses*, **34**(4), 475–485. 10.1037/0097-7403.34.4.475

Mondragón, E., & Hall, G. (2002). Analysis of the perceptual learning effect in flavor aversion learning: Evidence for stimulus differentiation. *The Quarterly Journal of Experimental Psychology Section B*, **55**(2b), 153–169. 10.1080/02724990143000225

Mondragón, E., & Murphy, R. A. (2010). Perceptual learning in an appetitive Pavlovian procedure: Analysis of the effectiveness of the common element. *Behavioural Processes*, **83**(3), 247–256. 10.1016/j.beproc.2009.12.007

Mundy, M. E., Honey, R. C., & Dwyer, D. M. (2007). Simultaneous presentation of similar stimuli produces perceptual learning in human picture processing. *Journal of Experimental Psychology: Animal Behavior Processes*, **33**(2), 124–138. 10.1037/0097-7403.33.2.124

Prados, J., Artigas, A. A., & Sansa, J. (2007). Preexposure effects in the spatial domain: Dissociation between latent inhibition and perceptual learning. *Journal of Experimental Psychology: Animal BehaviorProcesses*, **33**(2), 115–123. 10.1037/0097-7403.33.2.115

Recio, S. A. (2017). *The role of comparison in perceptual learning* [Doctoral thesis]. Universidad de Granada.

Recio, S. A., Iliescu, A. F., & de Brugada, I. (2018). The role of stimulus comparison in animal perceptual learning: Effects of a distractor placement. *Quarterly Journal of Experimental Psychology*, **71**(12), 2488–2496. 10.1177/1747021818757101

Recio, S. A., Iliescu, A. F., & de Brugada, I. (2019). The amount of exposure determines generalization in animal perceptual learning using short inter-stimulus intervals. *Behavioural Processes*, **166**, Article 103900. 10.1016/j.beproc.2019.103900**[AQ14]**

Recio, S. A., Iliescu, A. F., Honey, R. C., & de Brugada, I. (2016). Perceptual learning in flavor preference conditioning: Restricting generalization of acquired preferences between flavors. *Learning and Motivation*, **56**(Suppl. 1), 31–37. 10.1016/j.lmot.2016.09.001

Rodríguez, G., & Alonso, G. (2008). Stimulus comparison in perceptual learning: Roles of sensory preconditioning and latent inhibition. *Behavioural Processes*, **77**(3), 400–404. 10.1016/j.beproc.2007.06.010

Rodríguez, G., Blair, C. A. J., & Hall, G. (2008). The role of comparison in perceptual learning: Effects of concurrent exposure to similar stimuli on the perceptual effectiveness of their unique features. *Learning & Behavior*, **36**(2), 75–81. 10.3758/LB.36.2.75

Sánchez, J., Dwyer, D. M., Honey, R. C., & de Brugada, I. (2022). Perceptual learning after rapidly alternating exposure to taste compounds: Assessment with different indices of generalization. *Journal of Experimental Psychology: Animal Learning and Cognition*, **48**(3), 169–178. 10.1037/xan0000333

Symonds, M., & Hall, G. (1995). Perceptual learning in flavor aversion conditioning: Roles of stimulus comparison and latent inhibition of common stimulus elements. *Learning and Motivation*, **26**(2), 203–219. 10.1016/0023-9690(95)90005-5

Tukey, J. W. (1977). *Exploratory data analysis*. Addison-Wesely.

Wagner, A. R. (1981). SOP: A model of automatic memory processing in animal behavior. In **N. E. Spear & R. R. Miller** (Eds.), *Information processing in animals: Memory mechanisms* (pp. 95–128). Erlbaum.

Wagner, A. R. (2003). Context-sensitive elemental theory. *The Quarterly Journal of Experimental Psychology: Section B*, **56**(1b), 7–29. 10.1080/02724990244000133

Wheeler, D. S., Amundson, J. C., & Miller, R. R. (2006). Generalization decrement in human contingency learning. *The Quarterly Journal of Experimental Psychology*, **59**(7), 1212–1223. 10.1080/17470210600576342

Experiment	Group	Preexposure	Conditioning	Test
		AX/W/BX		
	INT			
		BX/W/AX		
Experiment 1			Y+	AY?
		AX/W/AX		
	BLK			
		BX/W/BX		
		AX/W/BX		
	INT			
		BX/W/AX		
Experiments 2a and 2b			A+	A?
		AX/W/AX		
	BLK			
		BX/W/BX		
		AX/W/BX		
	INT			
		BX/W/AX		
Experiment 3			AY+	Y?
		AX/W/AX		
	BLK			
		BX/W/BX		

Note. INT refers to intermixed preexposure. BLK refers to blocked preexposure. A and B are hazelnut and caramel (counterbalanced) odors. X is a saline solution, and W is water. Y was a citric acid solution for Experiment 1 and a strawberry odor for Experiment 3. The symbol "+" indicat**[AQ16]**es an i.p. injection of LiCl, and "/" indicates that the stimuli are presented in rapid succession within the same session.

Figure 1

Experiment 1. Mean Direct Consumption (±*SEM*) of Y During the Conditioning Phase

Note. INT refers to the group given intermixed preexposure, and BLK refers to the group given blocked preexposure. *SEM* = Standard error of the mean~~XXXX~~.

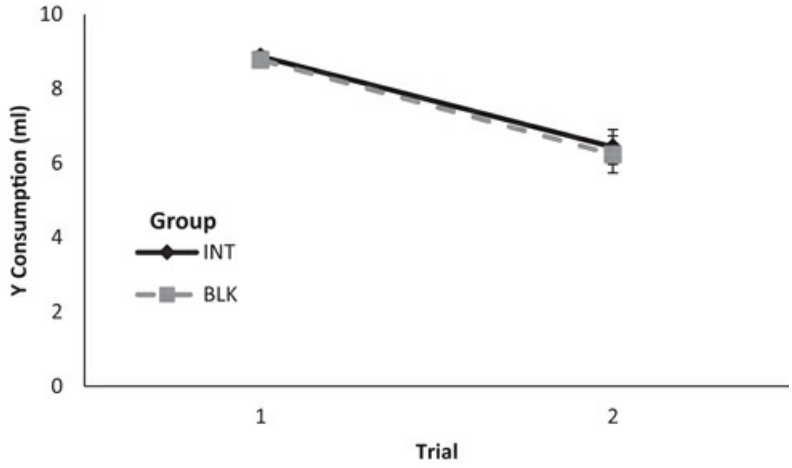

Figure 2

Experiment 1. Mean Direct Consumption (±*SEM*) of AY During the Test Phase

Note. INT refers to the group that received intermixed exposure, and BLK refers to the group that received blocked exposure. *SEM* = Standard error of the mean~~XXXX~~.

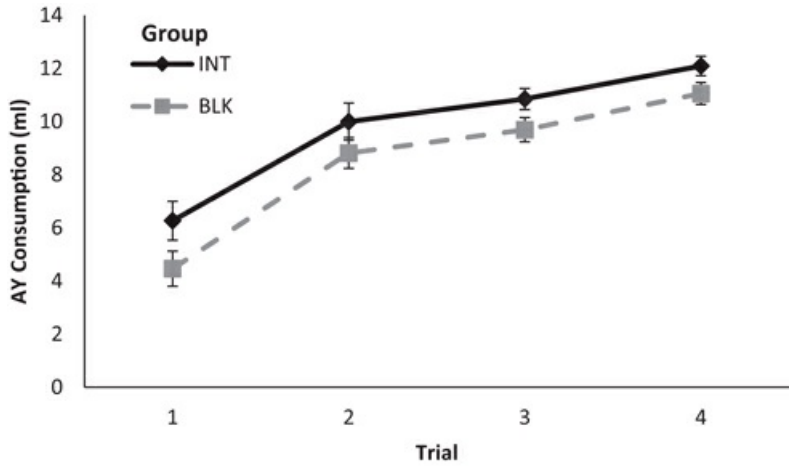

Figure 3

(a) Experiment 2a and (b) Experiment 2b. Mean Direct Consumption (±*SEM*) of A During the Conditioning Phase

Note. INT refers to the group given intermixed preexposure, and BLK refers to the group given blocked preexposure. *SEM* = Standard error of the mean~~XXXX~~.

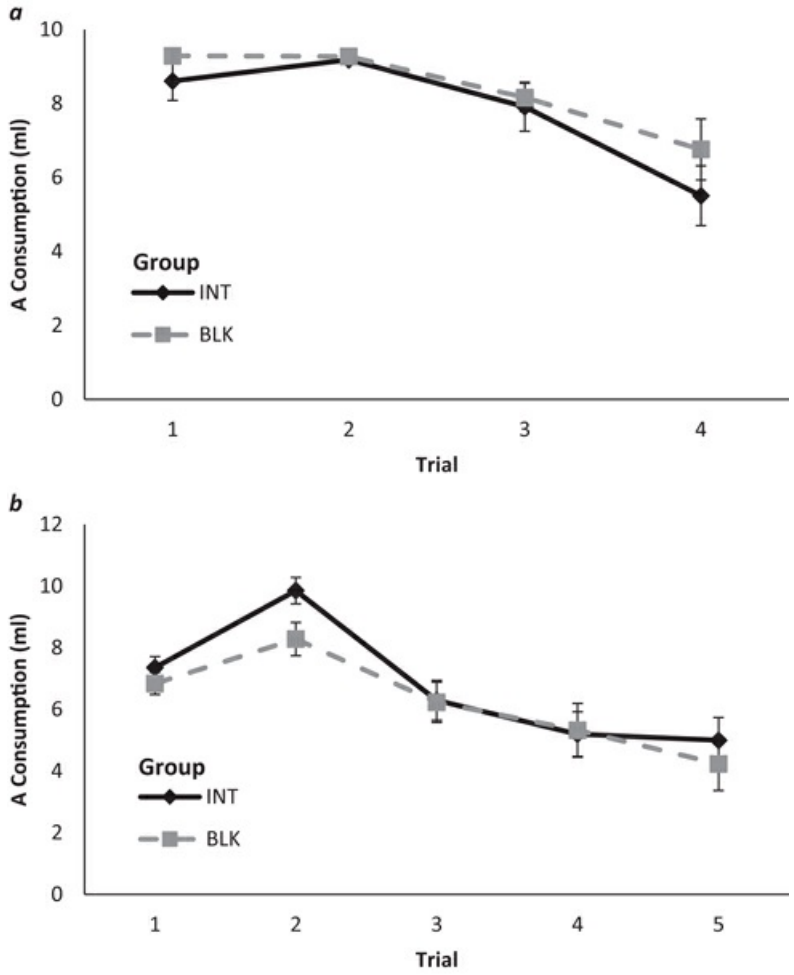

Figure 4

(a) Experiment 2a and (b) Experiment 2b. Mean Direct Consumption (±*SEM*) of A During the Test Phase

Note. INT refers to the group that received intermixed exposure, and BLK refers to the group that received blocked exposure. *SEM* = Standard error of the mean~~XXXX~~.

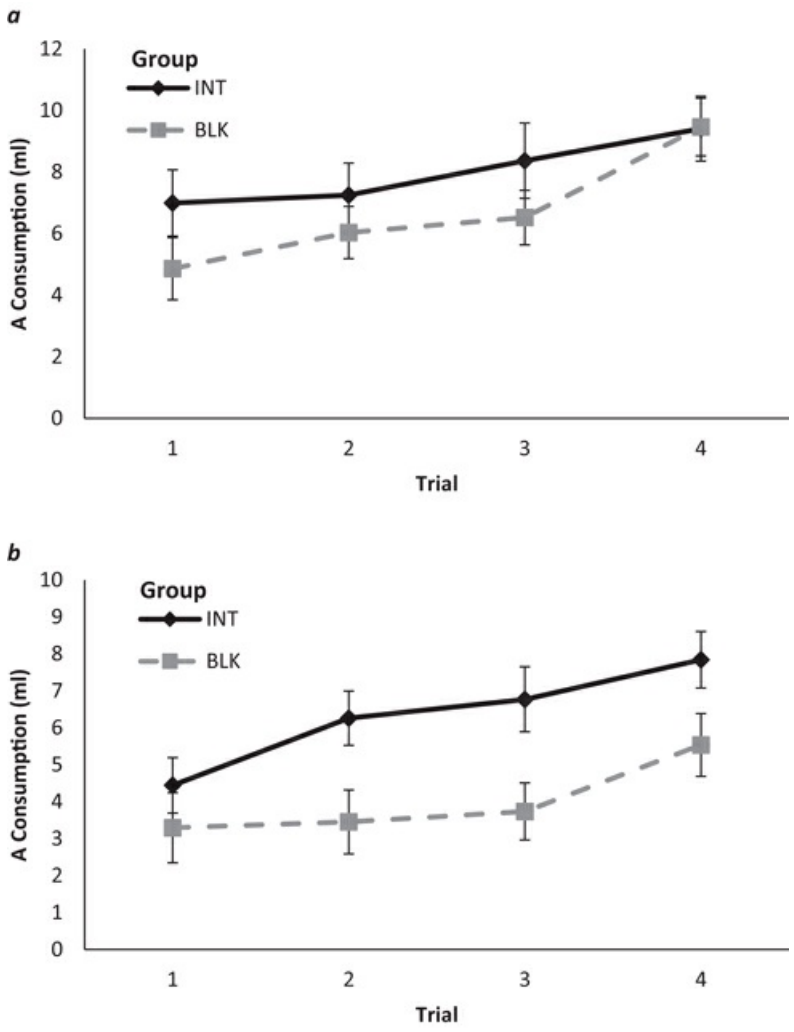

Figure 5

Experiment 3: Mean Direct Consumption (±*SEM*) of AY During the Conditioning Phase

Note. INT refers to the group given intermixed preexposure, and BLK refers to the group given blocked preexposure. *SEM* = Standard error of the mean~~XXXX~~.

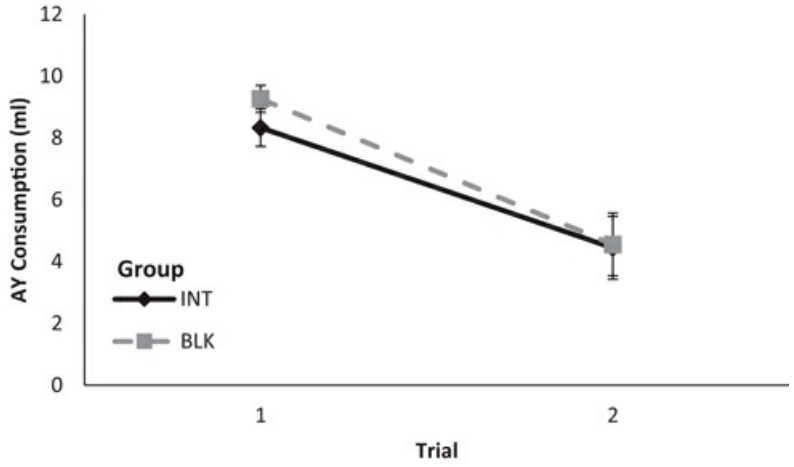

Figure 6

Experiment 3: Mean Direct Consumption (±*SEM*) of Y During the Test Phase

Note. INT refers to the group that received intermixed exposure, and BLK refers to the group that received blocked exposure. *SEM* = Standard error of the mean~~XXXX~~ **[AQ15]**.