Mechanisms underlying the process of Comparison in Perceptual Learning

Mecanismos subyacentes al proceso de Comparación en el Aprendizaje Perceptivo

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THESIS PUBLICATIONS

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RESUMEN

El objeto de esta tesis es el estudio de los mecanismos subyacentes al proceso de comparación en el aprendizaje perceptivo, así como los cambios que la experiencia produce en las representaciones de los estímulos que permiten mejorar su discriminación. Además, se examina la generalidad de este proceso entre especies y es contrastado con otros mecanismos asociativos no basados en la comparación directa.

En el *Capítulo IV*, se presentan experimentos llevados a cabo con animales utilizando un procedimiento de exposición a estímulos semejante al que se utiliza con humanos, en el que se presentan sucesivamente compuestos de sabores similares de forma intercalada, facilitando su comparación, o en bloques separados. Con este procedimiento encontramos que la exposición intercalada favorece la formación de asociaciones entre los elementos únicos de los estímulos. Este proceso de precondicionamiento sensorial favorece su generalización posterior e impide que se manifieste el aprendizaje perceptivo. No obstante, cuando estas asociaciones son obstaculizadas al introducir una pequeña cantidad de agua entre las presentaciones, los animales que tienen la oportunidad de comparar muestran una mejor discriminación de los sabores. Estos resultados sugieren que, cuando se controla el efecto del precondicionamiento sensorial, los animales también pueden beneficiarse de la comparación.

A continuación, en el *Capítulo V*, replicamos el efecto de aprendizaje perceptivo en animales con este procedimiento de exposición rápida. Posteriormente, con el mismo procedimiento, evaluamos la asociabilidad y saliencia de los elementos únicos de los estímulos y encontramos que tras exposición intercalada estas propiedades se ven reducidas en comparación con las resultantes de una exposición en bloques. Estos resultados sugieren que este tipo de exposición, de rápida sucesión alterna entre

compuestos, lleva a un sesgo de procesamiento de los elementos únicos de los estímulos que consecuentemente resultan mejor representados en memoria. Estas características mejor representadas serían más discriminables pero asimismo verían reducida su saliencia y asociabilidad.

Complementariamente, en el *Capítulo VI,* se presentan una serie de experimentos con los mismos procedimientos anteriores, pero esta vez para evaluar los cambios que producen en las propiedades de los elementos comunes. Los resultados muestran que tras presentar los estímulos similares de forma rápida e intercalada, la saliencia y discrimnabilidad de sus elementos comunes se ve reducida, sin embargo no encontramos cambios en su nivel de asociabilidad. En este punto, las teorías del aprendizaje perceptivo no son claras respecto al impacto que tendría la comparación en los elementos comunes, aun así, se discuten distintas propuestas teóricas que podrían explicar los resultados hallados.

En el *Capítulo VII*, contrastamos el mecanismo de comparación propuesto con otros mecanismos del aprendizaje perceptivo basados en la presentación espaciada de los estímulos que conlleva a la activación asociativa de sus elementos únicos. Utilizando nuestro procedimiento rápido, observamos que la presentación del elemento común de forma espaciada también mejora la discriminación posterior de estímulos similares, pero además, que la presentación de los estímulos de forma intercalada y espaciada incrementa la asociabilidad de sus elementos únicos, al contrario que la exposición rápida. Estos resultados respaldan los dos tipos de mecanismos propuestos para el aprendizaje perceptivo y refuerza la idea de que es un fenómeno flexible que dependiendo de las demandas del entorno puede poner en marcha uno u otro.

Por último, en el *Capítulo VIII*, presentamos una serie de experimentos en humanos, con un procedimiento de rápida sucesión y estímulos visuales, con la intención de replicar los resultados hallados en animales. En primer lugar, encontramos que los estímulos presentados de forma rápida e intercalada son mejor reconocidos en una prueba con distractores que aquellos que se presentaron en bloques separados. Posteriormente, observamos que estos estímulos presentan más dificultades para predecir una consecuencia en una siguiente fase de condicionamiento. Estos resultados, semejantes a los obtenidos con animales, sugieren un mecanismo de aprendizaje perceptivo común entre especies.

Finalmente, las implicaciones teóricas de los resultados presentados en esta tesis son discutidas. También analizamos la importancia de la comparación y sus mecanismos en ámbitos como la nutrición, trabajos que requieren una discriminación fina, o su posible implementación en inteligencia artificial.

ABSTRACT

The aim of this thesis is to study the mechanisms underlying the process of comparison in perceptual learning, as well as the changes that experience produces in the representations of stimuli which enable an improvement in their discrimination. Furthermore, the generality of this process is examined across species and it is contrasted with other associative mechanisms not based on direct comparison.

In *Chapter IV*, we present experiments conducted with animals using a stimulus exposure procedure similar to that used with humans, in which similar flavor compounds are presented in succession, either intermixed, facilitating their comparison, or in separate blocks. With this procedure, we found that intermixed exposure promotes the formation of associations between the unique elements of the stimuli. This process of sensory preconditioning favors their subsequent generalization and prevents perceptual learning from appearing. However, when these associations are hindered by introducing a small amount of water between presentations, animals given the opportunity to compare show improved discrimination of flavors. These results suggest that, when the effect of sensory preconditioning is controlled, animals may benefit from comparison as well.

Following this, in *Chapter V*, we replicated the perceptual learning effect in animals with this rapid exposure procedure. Subsequently, with the same procedure, we evaluate the associability and salience of the unique elements of the stimuli and find that after intermixed exposure these properties become reduced compared to those resulting from a block exposure. These results suggest that this type of exposure, of rapid alternating succession between compounds, leads to a processing bias of the unique elements of the stimuli that are consequently better represented in memory. These better

represented features would be more discriminable but would also be reduced in salience and associability.

Complementing this, in *Chapter VI*, we present a series of experiments with the same procedures as above, but this time to evaluate the changes they produce in the properties of the common elements. The results show that after presenting similar stimuli quickly and intermixed, the salience and discriminability of their common elements is reduced, but there is no change in their level of associability. At this point, perceptual learning theories are not clear about the impact of comparison on common elements, however, different theoretical proposals are discussed that could explain the results found.

In *Chapter VII*, we contrast the proposed comparison mechanism with other perceptual learning mechanisms based on the spaced presentation of stimuli that leads to the associative activation of their unique elements. Using our rapid procedure, we observe that the presentation of the common element in a spaced manner also enhances the subsequent discrimination of similar stimuli, but in addition, that the presentation of the stimuli in an intermixed and spaced manner increases the associability of their unique elements, contrary to rapid exposure. These results support the two types of mechanisms proposed for perceptual learning and reinforce the idea that it is a flexible phenomenon that, depending on the demands of the environment, can trigger one or the other.

Finally, in *Chapter VIII*, we present a series of experiments in humans, using a rapid succession procedure and visual stimuli, with the intention of replicating the results found in animals. First, we find that stimuli presented in a rapid intermixed manner are better recognized in a test with distractors than those presented in separate blocks. Subsequently, we observed that these stimuli are more difficult to predict a consequence in a following conditioning phase. These results, similar to those obtained with animals, suggest a perceptual learning mechanism common to all species.

At last, the theoretical implications of the results presented in this thesis are discussed. We also analyze the importance of comparison and its mechanisms in areas such as nutrition, jobs requiring fine discrimination, or its possible implementation in artificial intelligence.

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PART I:

INTRODUCTION

CHAPTER I – CONTEXTUALIZATION AND HISTORICAL BACKGROUND

Perceptual learning refers to the process by which repeated exposure to similar stimuli enhances an individual's ability to discriminate between those stimuli in the future. This kind of learning becomes adaptive, as prior experiences help us to respond differently to stimuli that, because of their similarity, initially would provoke a generalized response. For instance, an experienced doctor examining the results of a brain MRI should be capable of distinguishing between a brain tumour and healthy brain tissue for the sake of the patient. This phenomenon is also observable in various professional domains, such as wine tasters discerning between a wide array of vintages or air traffic controllers differentiating between simultaneous signals on their radar. However, perceptual learning is also evident in our daily routines when we recognize familiar faces among similar ones, correctly identify a traffic signal, or simply while eating different foods.

A brief historical context for perceptual learning can be traced back to the philosophers of the 17th century. The nativist thinking of the time held that ideas were innate, so that experience with stimulation was irrelevant since perceptions were just perfect ideas from God. In contrast, empiricists such as John Locke postulated in 1690 that the experience from past sensations was necessary to form the ideas about how we perceive the world and introduced the concept of discrimination. In the midst of the nativist-empirist conflict, the associationism emerged to integrate the experience of sensations into particular representations of the stimuli (Berkeley, 1709).

Subsequently, enrichment theories were developed to explain how experience shapes these representations in an accumulative way. These theories claimed that representations of the stimuli tend to change with experience due to associative addition of sensations, becoming more complex and richer. For Helmholtz (1867), the enrichment of a stimulus representation should be elaborated by unconscious inferences which, following a rule of causality, add sensations from past experiences.

Titchener's theory (1909) assumed that representations of stimuli are made more distinct by the addition of previously associated features which the context retrieves.

More familiar is William James' (1890; Miller & Dollard, 1941) theory of acquired distinctiveness of the cues, which suggests an increase in discrimination between representations of similar stimuli not in terms of inferences or associations with past events, but in terms of practice and reinforcement. According to this theory, responses learned to the stimuli add response-produced cues to that stimuli representation which improve its discrimination with those sharing some similarities. Observation of two stimuli, A' and 'A, could develop representations with similar meanings, however when each of them is associated with a different outcome, for example Y and Z, the two compounds A'Y and 'AZ become better differentiated. Conversely, William James added the acquired equivalence of cues, that is when two stimuli are associated with the same outcome, for example A and B predict X, they become more similar to each other, i.e. AX and BX, and discrimination becomes more difficult.

James' theory finds support from discriminative learning experiments. Perception can be trained to discriminate between similar stimuli in bases of differential reinforcement. When Pavlov (1927) conditioned their dogs by presenting a circle (A') followed by food, they tended to salivate at the mere presence of the circle itself. However, he found that the dogs also tended to salivate if they were presented with an ellipse ('A), which is quite similar to the circle. This is an example of conditioned response generalization, whereby similar conditioned stimuli (CS) that are not well discriminated also evoke similar responses. Consequently, Pavlov trained his dogs with differential reinforcement, the circle was followed by food (A'+) but the ellipse was not ('A-). After that training, the dogs discriminated better between both stimuli and only tended to salivate at the circle. We can assume from the beginning that the dogs shared the same undifferentiated representation about the circle and the ellipse, for example percept "A" that means rounded, and their response was the same to both.

However, during differential training they added new features to the A percept splitting it into two separated ones, A’Y and ‘AZ more differentiated, were Y is food and Z is no food.

On the other hand, Gibson (1969) made a case against these enrichment theories. She argued that, over time, perception will become increasingly unspecific with respect to reality, as the construction of the percept would be based on the subjective associations made by the individual distancing itself from the physical target stimulus. It is true that Pavlov's dogs must have associated discriminative responses to different features of the stimuli, closed curves (’) signalled reinforcement while open curves (‘) did not, but to get this far they must have differentiated these features in the first place. For Gibson and Gibson’s (1955) theory of differentiation, perceptual learning was an increase in an organism's ability to get differential information from the similar stimuli as a result of mere repeated experience with them. The change in perceptual learning does not come from acquiring a new response to stimulus variables that were previously responded to (Y and Z), but rather from responding in a discovering way to stimulus variables that were previously undetected (’ and ‘). As they become differentiated, the representations of the stimuli increase in correspondence with reality (A’ and ‘A), contrary to enrichment theories that simply add content (A’Y and ‘AZ).

An illustrative example of perceptual learning might be that of professional beer tasters (Peron & Allen, 1988). These experts have developed with practice a greater ability to distinguish between very similar beers. Enrichment theories would explain that with each repeated exposure beer tasters add a stored reference feature to the representation of that specific beer. However, these additions would have no real specificity for that particular beer, but could be arbitrarily added to a wide range of beers. Thus, the end result would be generic representations of different beers, but to which we have learned to respond distinctly. On the other hand, differentiation theory would explain that repeated exposure allows these experts to discover various characteristics from the total stream of stimulation and experience them separately as specific to that particular beer. Prolonged practice with different beers allows these beer tasters to detect many features of the stimulus that a non-regular beer drinker might miss. The end result is a wide variety of representations of different beers that are specific to those experienced. There are more examples in our daily lives of how experience with similar stimuli improves subsequent discrimination: chicken sexers can recognise a chick's genitalia at a glance, air traffic controllers can identify simultaneously different radar signals, doctors save lives by detecting anomalies on x-rays which are not present on healthy samples etc...(Biederman & Shiffrar, 1987).

The difference between these theories explaining perceptual learning is that, while enrichment theories rely on active associations between features to elaborate a representation, theories of differentiation by mere exposure extend the representation of the stimuli discovering new features. Therefore, some experimental approaches have been developed to test whether simple exposure to similar stimuli actually improves their discrimination (perceptive learning) or if associative learning between stimuli and other cues is necessary (discriminative learning). In these studies, experimental subjects are first exposed to similar stimuli so that, according to Gibson and Gibson (1955), they have the opportunity to learn to differentiate them. In a second phase this perceptual learning is evaluated, subjects must respond differentially to each stimulus. If subject responds differentially, we consider that they have learned to discriminate them, if on the other hand they have not been previously discriminated, there would be a generalization in the response and the subject would perform poorly. Two processes that help discrimination must therefore be distinguished. First, perceptual learning: mere exposure without the need of differential reinforces and second, discriminative learning: acquired distinctiveness as a function of differential reinforces. For the case we are interested in, we will be evaluating the perceptual learning.

1.1 PREDIFFERENTIATION EXPERIMENTS

The best example of perceptual learning is the Gibson and Walk (1956) experiments with rats. A group of young rats was reared with geometrical figures on the home cages, these were circles and triangles. On the other side, control group of young rats was reared in the absence of such figures. When the rats were mature, all of them were pre-trained on the test apparatus to teach them that pressing any button would open the door device with food inside. In the final stage, the animals were placed back in the test apparatus with the difference that now each door was marked by a circle or a triangle, only one of which would lead to the food. Gibson and Walk (1956) found that rats reared in the experimental cages with the geometric figures learned to discriminate which figure signalled the food at a much faster rate than control rats with no prior exposure to the figures (see Figure 1).These results were stunning, as pre-training and discrimination training were equal for both groups, perceptual learning should have occurred during the mere exposure to the stimuli phase in the experimental group, and not during the acquisition of reinforcement.

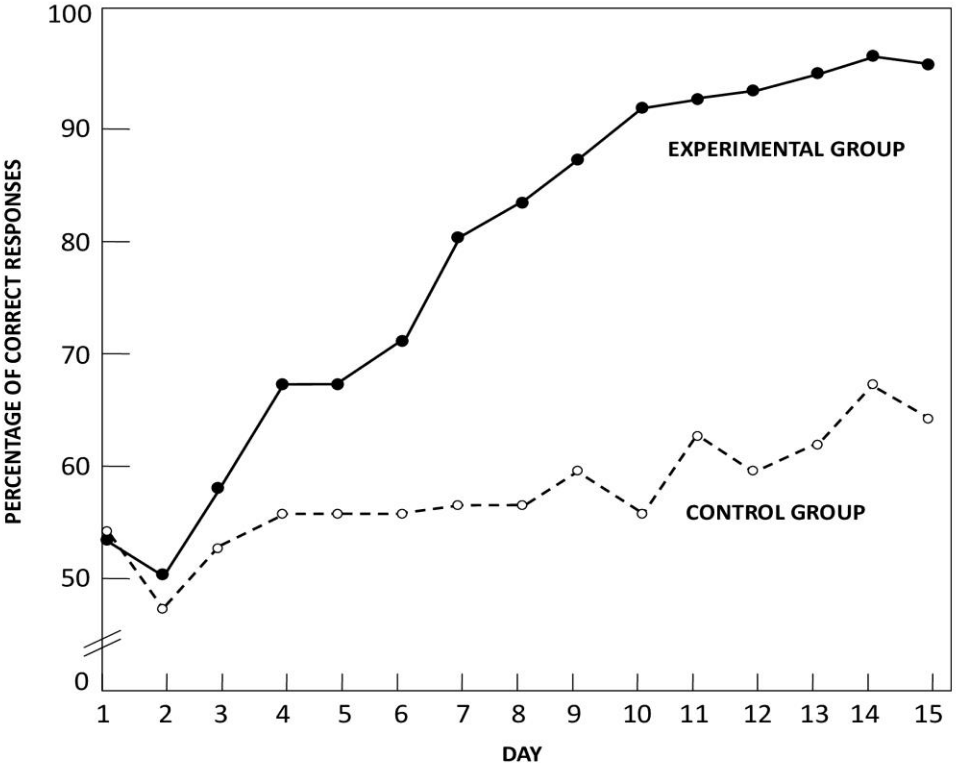

Figure 1. Adapted figure showing the learning from experimental and control groups of rats in Gibson and Walk (1956).

Following the novel work of Gibson and Walk (1956), further evidence of this mere exposure effect was found. For example, Honey, Horn and Bateson (1993) found better discrimimation in domesticated chicks with geometric figures as stimuli (namely A, B and C). Chicks in the experimental group were initially exposed to figure B and those in the control group to figure C, which were projected on the wall at the end of the experimental cabinet. This early exposure produced a filial imprinting effect, which promoted the subjects to approach the initially exposed stimulus. In the next phase, chicks from both groups were placed in a low-temperature experimental room, where stimuli A and B were projected at opposite ends of the cabinet. If the subject approached stimulus A, a stream of hot air was delivered (+); if it approached stimulus B, no hot air was delivered (-). In two experiments, the

Experimental group that had been preexposed to stimulus B acquired discrimination more quickly than group C, which had not been preexposed to it. This finding is also significant, since imprinting to B should have impaired approach learning to A, yet the group C for which both stimuli were novel actually showed more difficulty in acquiring this learning. Again, mere exposure but not acquisition training seems to have led to improved discrimination between A and B, which is perceptual learning (see also Kovach, Fabricius, & Falt, 1966 for a similar result with lights as stimuli).

Also, human experiments have found improved discrimination after mere exposure to similar visual stimuli. Robinson (1955) tested the acquired distinctiveness and equivalence of cues (Miller & Dollard, 1941) by exposing participants in three groups to similar fingerprints. During preexposure phase, Group Distinctiveness should associate each fingerprint to a different name, Group Equivalence should associate half of the fingerprints to a category and half to the opposite, and Group S-D just have to say if each presented fingerprint was the same or different as the previous. Later, in a discriminative test all groups had to say if the fingerprints presented in pairs were the same or different. There weren't any difference in discrimination between the three groups, however all these performed much better than a fourth group which hadn't have any preexposure at all. These results showed that addition of a cue to the stimuli didn't help or hinder discrimination, but simple exposure, as in group S-D, is enough for discriminate. Indeed, subjects showed during discrimination task an improvement in detection of the distinctive features of the fingerprints. As the trials progressed, they spontaneously learned to name the features of the fingerprints that differentiated them (see also Gibson & Gibson, 1955 for a similar result with Scribbles).

Alongside these experiments, there is a wide variety of studies that have also found an improvement in discrimination between similar stimuli after simple exposure to them, with a great diversity of subjects and procedures. Hall (1979) replicated Gibson and Walk's (1956) experiment with both young and mature rats. Honey and Hall (1989) found that preexposure to two flavored solutions improved subsequent discrimination more than preexposure to a single flavored solution, but also this was superior to that of a non-preexposed group. Gibson, Walk, Pick and Tighe (1958) found that preexposure to a circle and a triangle also facilitated later discrimination between ellipse-isosceles triangle, but not between very different stimuli (rocks-stripes). Oswalt (1972) found that only difficult discriminations as triangle-circle could benefit from preexposure, but other easier as discrimination between vertical or horizontal lines are equally well discriminated by preexposed and non-preexposed groups.

The results of these experiments provide evidence of perceptual learning, how mere prior exposure to similar stimuli subsequently favors their discrimination, and demonstrate that differential reinforcement, as the used in discriminative learning, is neither necessary nor sufficient to explain this phenomenon (see for a review with a nonhuman animals Hall, 2001; and with human and nonhuman animals Mitchell & Hall, 2014). Consequently, all the data presented so far supported Gibson and Gibson's (1955) theory of differentiation, and add evidence against enrichment theories, as cue addition cannot support the improved discrimination after mere exposure. Indeed, Gibson (1969) added that the opportunity to compare between similar stimuli would maximise their differentiation, which occurs best during an exposure phase, although she did not propose any mechanism for this comparison process. As a result, a series of research was initiated from the associative framework, initially with non-human animals, aimed at studying how perceptual learning occurs during exposure and proposing a number of mechanisms to explain it.

CHAPTER II – PHENOMENA & MODELS OF PERCEPTUAL LEARNING

2.1 – DIFFERENTIAL LATENT INHIBITION AND UNITIZATION

2.1.1 McLAREN, KAYE AND MACKINTOSH MODEL (1989)

According to stimulus sampling theory (Atkinson & Estes, 1963; Estes 1950), a single stimulus (e.g., a triangle) is composed from a set of several sub-elements (e.g., corners, angles, brightness, etc.), that due to the limited processing system of the subject (for example, SOP in Wagner, 1981) only a little subset of these can be sampled on each trial. For an instance, in a conditioning trial the sampled subset of elements from a CS will be activated, and then enter into excitatory associations with the activated elements of the US (e.g., Rescorla & Wagner, 1972; Wagner, 1981). In the case of similar stimuli, namely AX and BX, their elements are composed of unique subsets, A and B, and common subsets, X, and the degree of similarity is related to the amount of the latter (see Figure 2). Therefore during a conditioning trial (AX+), if the activated subset of elements from the CS contains those that are common, the conditioned response could then generalize between both similar stimuli when one is presented in test (BX). This could exemplify a case of poor performance in experiments where similar stimuli are not well discriminated.

Based on these associations, McLaren, Kaye and Mackintosh (1989) proposed an associative model to explain the enhancement of discrimination between similar stimuli in perceptual learning. During exposure phase the sub-elements activated will establish associations within the stimulus itself, that is the unique sub-elements with themselves (a^1-a^2), the common sub-elements with themselves (x^1-x^2); and both sub sets with each other (a^1-x^2 & x^1-a^2); this process is called unitization. According to McLaren et al. (1989), these intrastimulus associations would in fact generate latent inhibition, as they would also occur among the sampled sub-elements of the context, and paradoxically impair future learning (Lubow, Schnur & Rifkin, 1976). Critically, given that in perceptual learning there are twice as many common sub-elements (e.g., AX and BX in a trial), these would be the first and most unitized of all. This bias would increase the latent inhibition of the common elements, reducing the source of generalization between similar stimuli and leaving the unique elements relatively more effective for learning. This is not to say that the unique elements do not unitize during exposure, but rather that the differential latent inhibition favor the discrimination.

This model may explain the results of experiments such as that of Gibson and Walk (1956). Preexposure to the triangle and circle resulted in a double sampling of their elements in common, which should lead to an increase in unitization and latent inhibition. Later, in the discrimination task, these elements should be less effective at establishing the association with the food, but the unique ones would be more receptive for it. Then, the experimental rats could easily have learned which unique element of the figures was followed by food and which was not, unlike the control rats, for whom the relatively more effective common element would also acquire food reinforcement, generalizing the conditioned response among the stimuli.

This proposal by McLaren et al. (1989) is ground-breaking, as it easily accommodates the fact that mere exposure hinders future learning (by generating latent inhibition), and also employs associative models like those used by enrichment theories to explain the posterior discrimination. The unitization process explains how the formation of intracompound associations during exposure reduces our learning about common elements and increases it towards the unique ones, favoring subsequent discrimination. It is worth noting, that a better intrastimulus association would also favor a greater activation of the whole stimulus pattern of characteristics, whose representation will be then more accurate to reality. Mclaren et al. (1989), however, often overlook this last fact when explaining perceptual learning. So far, differential latent inhibition is sufficient to reflect Gibson's (1969) process of differentiation, in which the differential features are abstracted during exposure, contrasting with the neglected common features, resulting in improved discrimination.

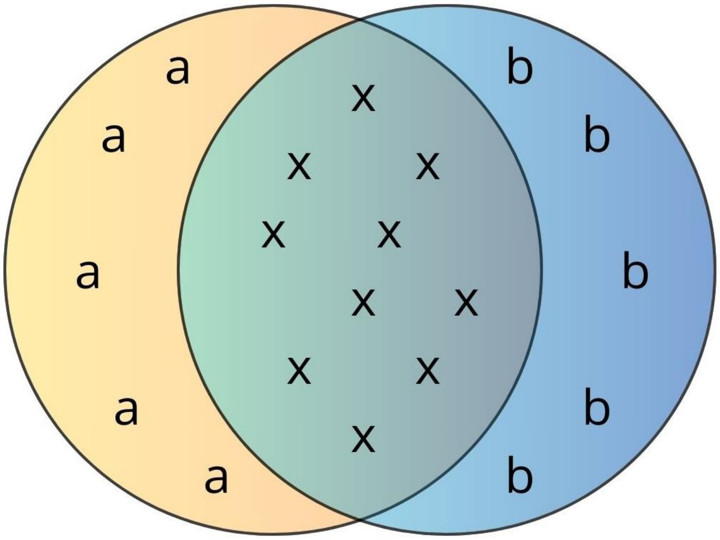

Figure 2. Schematic representation of two similar stimuli (AX and BX), showing their unique elements (A and B) and their overlapping common elements (X).

2.1.2 DIFFERENTIAL LATENT INHIBITION EXPERIMENTS

In order to test this differential latent inhibition, Mackintosh, Kaye and Bennett (1991) conducted a series of experiments with rats based on Honey and Hall (1989) flavor aversion procedures. Since this procedure is the one most commonly used to study perceptual learning in nonhuman animals, and the one mainly used in the experimental part of this thesis, it will be explained here in detail (see also Domjan, 1975; Nachman, 1963 for earlier versions of this procedure).

In their Experiment 1, Mackintosh et al. (1991) preexposed an Experimental group of rats to drink on alternated days a sucrose-lemon solution (AX) and a saline-lemon solution (BX), in contrast to a Control group without that preexposure. After this phase, all the animals were allowed to drink BX on conditioning trials, which were followed by an intraperitoneal injection of lithium chloride (LiCl, 15 M, at 1% of subjects' body weight). This injection generates digestive sickness which is strongly associated with any stimulus previously consumed by the animal, and hereafter will avoid its consumption in the future. That is, animals will avoid the consumption of BX, but also, of AX if they are not well discriminated. Finally at test phase, AX and BX were simultaneously presented and their consumptions were measured. Mackintosh et al. (1991) expected that previous exposure to both solutions in the Experimental group should have increased the lemon (X) latent inhibition during conditioning to BX reducing the generalization to AX. Results showed that the Experimental group significantly consumed more from the non-conditioned AX than from BX, but Control group consumed equal from both. The addition of the common element increased the generalization between compounds for the non-preexposed group, but it facilitated the discrimination for the preexposed group.

Using the same procedure, Symonds and Hall (1995, Experiment 1) gave different groups of rats a preexposure to two similar compounds (AX-BX), to one or the other (AX or BX), or to neither. The BX compound was then aversively conditioned and the generalization of the aversion to the AX compound was tested. Results showed higher consumption for the group preexposed to both compounds, followed by the groups only preexposed to one of them, and finally the group without preexposure. Symonds and Hall (1995) explained this difference because the common element (X) was presented twice in the groups preexposed to both stimuli than in the groups only preexposed to one of them, developing a double latent inhibition, and therefore impairing the generalization of aversion to greater extent.

Reasonably, Mackintosh et al. (1991) concluded that exposure to X alone would increase latent inhibition to a greater extent than exposure to it the same number of times in compound, as unitization for the common sub-elements would be enhanced in isolated presentations. Using the same previous procedures they preexposed three groups of rats in Experiment 2: Compound group (AX-BX), Unique group (A-B), and Common group (X). Results showed that groups preexposed to compounds and to common element alone were able to discriminate between the aversely conditioned BX and the non conditioned AX better than Unique group (see also Bennett, Wills, Wells & Mackintosh, 1994). However, the same level of discrimination from groups AX-BX and X was not expected. Preexposure to X alone would increase its latent inhibition; therefore during conditioning the unique element B should have acquired most part of the aversion. On the other hand, exposure to compounds should have generated also latent inhibition to the unique elements, and then the aversion acquired should be more distributed between the unique and the common elements in conditioning. Comparing these two deductions, group X should have showed less generalized aversion than the AX-BX group.

To investigate this further, Experiment 3 (Mackintosh et al., 1991) preexposed a Compound group to both stimuli (AX-BX) and an Elemental group to the same amount of their separated elements (A-B-X), so that latent inhibition should be equal for both all. The results showed, however, that exposure to the compounds improved their subsequent discrimination significantly more than exposure to all three elements alone; therefore, some interaction between the elements of the compounds during preexposure must be enhancing discrimination. Although the differential latent inhibition of the common elements is able to explain some of the results found in perceptual learning, it seems that is not sufficient mechanism to explain the improved discrimination when both stimuli are preexposed.

2.2 - THE INTERMIXED/BLOCKED EFFECT

Gibson (1969) suggested that the opportunity to compare between similar stimuli enhances perceptual learning, so that groups preexposed to both stimuli would have an advantage over groups preexposed only to their isolated elements, even though the latent inhibition would be equal for both groups. However, for the McLaren et al. (1989) model, the combination of stimulus presentation should be irrelevant, since all that matters is how many times X has been experienced, and the differential latent inhibition obtained with respect to the unique elements.

To test both propositions, Symonds and Hall (1995) rearranged the schedule of presentation of the two similar stimuli so that two groups had equal opportunities to experience X, but that one could compare and the other could not. In their Experiment 2 they divided the rats into three preexposure groups: the Intermixed group was preexposed to AX and BX in alternating sessions, the Blocked group was preexposed to AX for the first half of the preexposure and to BX for the remaining half, and the Control group had no preexposure. The BX stimulus was then aversively conditioned and AX was presented in the test phase. With this design, the latent inhibition of X should be the same for the Intermixed and Blocked groups, but only the Intermixed would be able to compare. Interestingly, the test results showed that the Intermixed group consumed significantly more AX than the Blocked and Control groups, while the latter two groups did not even differ significantly from each other. In fact, Experiment 3 used these same preexposure groups while omitting the common element X throughout the procedure, and yet the same pattern of results was also obtained, better discrimination of the Intermixed group than the Blocked group.

This was called the Intermixed/Blocked effect, a robust phenomenon that have been replicated numerous times in multiple species and with different kind of stimuli, for example: with visual stimuli in humans (Dwyer, Mundy, & Honey, 2011; Lavis, Kadib, Mitchell & Hall, 2011; Mitchell, Kadib, Nash, Lavis

& Hall, 2008a; Mundy, Honey & Dwyer, 2007; Recio, Iliescu, Mingorance, Bergés, Hall & de Brugada, 2016), visual stimuli in chicks (Honey & Bateson, 1996; Honey, Bateson & Horn, 1994; Honey et al., 1993), visual stimuli in rats (Prados, Artigas & Sansa, 2007), flavored stimuli in humans (Dwyer, Hodder & Honey, 2004; Mundy, Dwyer & Honey, 2006), flavored stimuli in rats (Artigas & Prados, 2014; Prados, Artigas & Sansa, 2007; Recio, Iliescu & de Brugada, 2018, 2019; Recio, Iliescu, Honey & de Brugada, 2016; Sánchez, Dwyer, Honey & de Brugada, 2022; Sánchez, González & de Brugada, 2023) and auditory stimuli in rats (Artigas & Prados, 2017; Ballesta, Gordón, Prados & Artigas, 2021; Mondragón & Murphy, 2010). In closing, this effect (I/B effect) has been considered evidence that the opportunity to compare between similar stimuli improves their subsequent discrimination as suggested by Gibson (1969).

2.2.1 McLAREN AND MACKINTOSH MODEL (2000): INHIBITORY LINKS

The differential latent inhibition proposed by McLaren et al. (1989) could not support the I/B effect, as both the Intermixed and Blocked groups experience the common elements the same number of times. Therefore, Mclaren and Mackintosh (2000) reformulated their model by introducing an additional mechanism whereby the unique elements will tend to inhibit each other after Intermixed exposure.

As their previous model (McLaren et al. 1989) assumed, during exposure to a similar stimulus, the coactivation of the unique and common sub-elements will form intra-compound associations between the common and the unique element (Rescorla & Cunningham, 1978; Rescorla & Durlach, 1981). Consequently, when the common element is presented in subsequent trials, its sampled sub-elements would associatively activate the previously associated sub-elements from the unique one. That is, after Intermixed exposure (AX/BX/AX/BX...), when BX is presented the unique element A would be associatively activated by X, and the same occurs on alternate trials when AX is presented and B is associatively activated by X as well. This associative activation is less likely in Blocked exposure

(AX/AX...BX/BX...), since only the second block of trials would associatively activate the first preexposed unique element and with subsequent repeated exposure this intracompound association will eventually extinguish.

Therefore, and in accordance with elementary models of associative learning (e.g., Wagner, 1981), in an AX trial when element B is associatively activated by X, inhibitory links will develop from the present element A to the associatively activated element B, i.e. A signals the absence of B. Conversely, in BX trials, B develops inhibitory links towards the associatively activated A. Thus after Intermixed exposure, when BX is conditioned and then AX is tested, element A will inhibit the associative activation of B (by X) and prevent part of the generalization of the conditioned response from the associative chain: X-B-US. Because these inhibitory links result weaker in the Blocked schedule, B could be associatively activated on AX test, but not inhibited, and then generalize the conditioned response.

With the addition of this inhibitory mechanism the new model of McLaren and Mackintosh (2000) can explain the lower generalization after Intermixed exposure in contrast to Blocked exposure, which differential latent inhibition couldn’t accommodate. This was the first time that the development of inhibitory links between neutral stimuli was stipulated, and thus several studies have attempted to prove that Intermixed exposure to AX and BX effectively establishes inhibitory links between A and B.

2.2.2 INHIBITORY LINKS EXPERIMENTS

The clearest evidence of these inhibitory links comes from a series of experiments conducted by Espinet, Iraola, Bennett and Mackintosh (1995). In their Experiment 1 they found after Intermixed exposure to AX and BX that final conditioning to B was retarded if previously A had been paired with the same US. This retardation effect reflected that B was established as inhibitor for A, as the conditioned response was also inhibited during conditioning retarding the acquisition of the associated response. In Experiment 2 after Intermixed exposure, the A element and a new Y element were aversely conditioned in separated sessions. In a final summation test it was found that if B accompanied the element Y the aversion was attenuated, reflecting again that B inhibits the conditioned response to A. This is known as the Espinet effect, the evidence that inhibitory links can be formed between neutral stimuli.

In addition, these authors included further evidence of these inhibitory links in their experiments 3 and 4. In Experiment 3 the retardation effect was eliminated when the common element was eliminated, which is congruent if the intracompound associations mediate the establishment of the inhibitory links, and in Experiment 4 they found that the summation effect was less effective after short preexposure (4 days) than after long (12 days). Since inhibitory links take longer to develop than excitatory links, it stands to reason that a short preexposure will be less effective in establishing B as an inhibitor of A.

There is also some evidence for these inhibitory links with the use of fixed sequences of stimulus presentation. Bennett, Scahill, Griffiths and Mackintosh (1999, Experiment 2) used the Forward sequence (AX->BX), the Backward sequence (BX->AX) and Blocked exposure (AX_BX), to find that discrimination is only improved in the backward case. In Backward sequence the inhibitory link is established from A towards B (since B is gone once A arrives), then, when aversion is established to BX and then generalization tested in AX, A would stop the aversive strength brought by the chain X-B-US. Finally, using the summation and retardation tests from Espinet et al. (1995), Bennett et al. (1999, Experiment 3) found that Intermixed and Backward preexposure were more effective establishing inhibitory links from A towards B than Forward and Blocked exposure.

To test these inhibitory links, Dwyer, Bennett and Mackintosh (2001) used a sodium depletion procedure, which increases the motivation for consume saline solutions and other tastes associated with salt (Rescorla & Durlach, 1981). Dwyer et al (2001) rats were preexposed in Intermixed or Blocked fashion to salt-lemon (AX) and sucrose-lemon compounds (BX), after what received a session with the compound salt-sucrose (AB), then received a Furo-Doca[1] injection and subsequently sucrose (B) consumption was measured in test. Experiment 1 results showed increased consumption of sucrose in the Blocked group in contrast to the Intermixed group. Therefore, association between salt and sucrose (A-B) should have been established readily in Blocked group presumably because for Intermixed group they were reciprocal inhibitors.

Still, this mechanism implies, as Espinet et al. (1995) pointed out, that prolonged exposure is needed to develop inhibitory links, but, intriguingly, some of the experiments reporting the I/B effect actually used brief stimuli preexposure. For example, Symonds and Hall (1995) only needed 4 days of preexposure to find the I/B effect, but given the same amount of Intermixed exposure in Espinet et al. (1995) did not reflect inhibition in the summation and retardation tests (although 12 days of exposure was sufficient to find it). Also, Prados, Hall and Leonard (2004) found no evidence of inhibitory links after prolonged Intermixed or Blocked preexposure when using retardation (Experiment 1) and summation (Experiment 2) tests, but using the same preexposure in Experiment 3, led them to find the I/B effect with the generalization test.

The most devastating evidence comes from Blair and Hall's (2003a) Experiment 5, that used an intrasubject design in which the latent inhibition of X should be equal for all stimuli, but also precluded the necessity for inhibition in the final test. These authors exposed their rats to Intermixed presentations of AX and BX, along with a separate block of CX. Then, they aversively conditioned a novel Y element and assessed the generalization to the BY and CY compounds during test. The results showed lower generalization of the Y aversion to the BY compound compared to the CY, a parallel result to the classic I/B effect. However, inhibitory links between A and B could not explain the reduced aversion to BY, as the A element was not aversive nor associated to Y. This, along with the brief preexposure results,

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[1] Since this treatment consists of a subcutaneous injection of a mixture of furosemide (furo) and deoxycorticosterone acetate (doca), we will refer to it hereafter as Furo-Doca (Fudim, 1978 and Symonds, Hall & Bailey, 2002).

demonstrates that the development of inhibitory links during Intermixed exposure can explain some, but not all, cases of perceptual learning. Importantly, Blair and Hall (2003a) proposed that Intermixed exposure to AX and BX would in fact increase the ability of B to reduce generalization.

2.2.3 HALL'S MODEL (2003): SALIENCE MODULATION

Following these latest results, a new analysis of perceptual learning was needed to address the Intermixed/Blocked effect. Hall (2003) and McLaren and Mackintosh (2000) proposed two models, which do not deny the formation of inhibitory links during Intermixed preexposure, but additionally suggest that associative activation of unique elements may itself increase their perceptual effectiveness, promoting discrimination as well.

For example, Hall's (2003) model assumes that repeated exposure leads to habituation of all elements of the stimulus resulting in a decrease in the subject's response and attention (e.g., Groves & Thompson, 1970). However, during Intermixed preexposure, associative activation of the unique absent element will partially reverse this habituation, restoring its perceptual effectiveness or, as Mondragón and Hall (2002) call it, its salience. This is because the subject has experienced the common element in the company of the unique one previously, establishing an expectation that they will be presented physically together in the future. In contrast, during intermingled exposure, the common element constantly changes companion and, breaking the expectation, associatively activates the unique element, which, in turn, increases its salience for future encounters (Hall, Prados & Sansa, 2005; Pearce & Hall, 1980). Meanwhile, the common element is always present and undergoes constant habituation; consequently, differential salience between unique and common elements in the Intermixed condition promotes the detection of unique ones enhancing discrimination. On the other hand, Blocked preexposure reduces the salience of all stimulus elements equally in general terms, leading to greater generalization between them (see Figure 3).

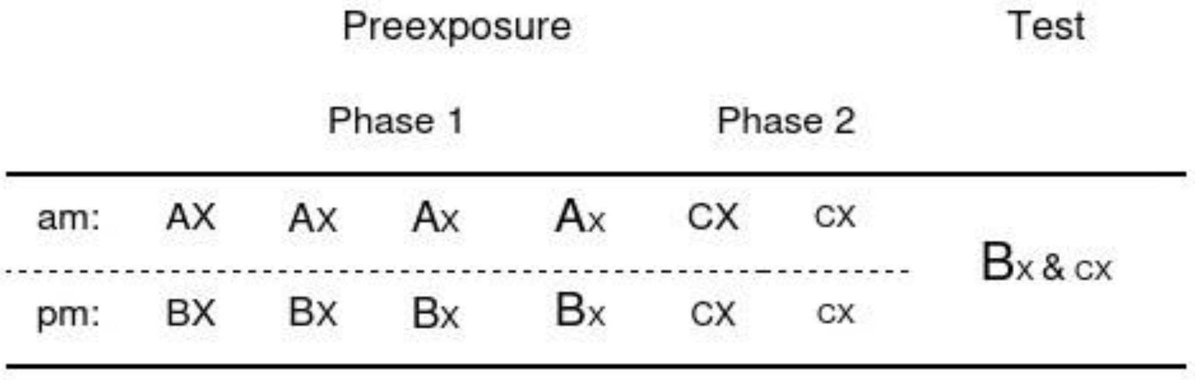

Figure 1. Schematic representation from Hall's (2003) model. It depicts AX and BX being exposed in Intermixed fashion and CX exposed in an isolated block, while presenting the assumed changes in effectiveness experienced by the different components of similar stimuli until the test phase.

Aside, McLaren and Mackintosh (2000) model make another assumption, along with inhibitory links, that associative activation of unique elements would decrease the stimulus unitization and reverse latent inhibition. Again, it is assumed that during exposure (of AX for example), unitization proceed among the unique (A) and common (X) sub-elements sampled but also with the context (A-X-CTX) (see Figure 4), which increase the stimulus latent inhibition. However, during Intermixed preexposure the associative activation of the unique element that is absent will weaken these unitized associations among the sub-elements and the context. Therefore, this process would lead to a “deunitization” (de Zilva & Mitchell, 2012) of the unique element that will decrease its latent inhibition and conversely increase its associability. As the common element is always presented, its latent inhibition is preserved in contrast to that of the unique elements after Intermixed preexposure, which would facilitate learning about the stimulus discrimination later on.

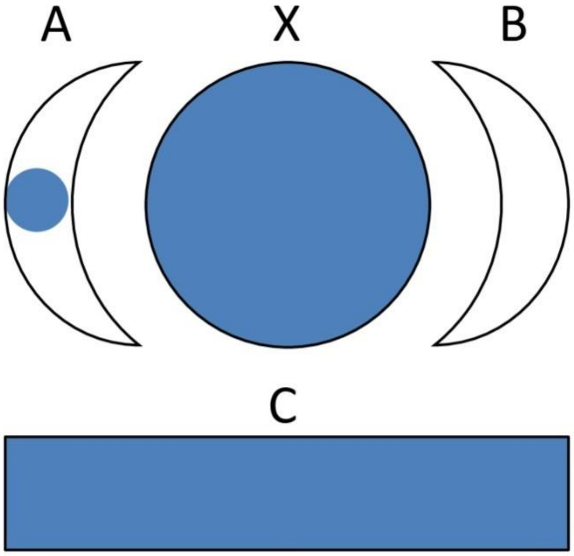

Figure 4. Diagram adapted from McLaren and Mackintosh (2000) showing how the different subsets of elements and the context are sampled during exposure to AX.

Although both theories rely on the associative activation of unique elements to explain the improved discrimination after Intermixed exposure, some clarifications are necessary. Hall (2003) declared that associative activation of the unique element reduces its habituation and increases its salience, on the other hand, McLaren and Mackintosh (2000) stated that associative activation reduces the unitization of the stimuli and reverse the latent inhibition of their unique elements, which increase their associability. Classical models of associative learning (Mackintosh, 1975; Pearce & Hall, 1980) describe salience as a parameter (S) related to the intensity of the stimulus, while latent inhibition is a reduction in the associability parameter (α). This is not to say that only one mechanism is correct, but rather that they both could be two sides of the same coin which helps discrimination. No further, some authors included that the salience of a stimulus, apart from reflect intensity, determines the speed of associability (Blair & Hall, 2003a; Mondragón & Hall, 2002) and that latent inhibition also reflects a reduction in the ability of the stimulus to attract attention for establish new learnings (Hall & Rodríguez, 2010; Pearce & Hall, 1980). Then by the moment, and in accordance with the general terms that have been used over the years, we are going to treat both qualities as equivalent and, positively, evidence from both salience models is found over huge variety of research.

2.2.4 SALIENCE MODULATION EXPERIMENTS

Firstly, assuming that a salient stimulus is also very associable, many investigations have focused on the capacity of the unique elements to acquire a conditioned response after different preexposures. For example, Mondragón and Hall (2002, Experiment 3) exposed their rats to flavored compounds in Intermixed or Blocked schedule, followed by aversive conditioning of AX, and subsequently; the acquisition of the aversion was tested presenting A alone. In Experiment 4, element A was directly conditioned after each preexposure condition, and the conditioned response was measured in extinction trials of A. Both experiments demonstrated a stronger conditioned aversion for the A element after Intermixed preexposure compared to Blocked preexposure; presumably, because the Intermixed schedule increased A salience enhancing its associability (see also Blair, Wilkinson & Hall, 2004 for a similar result).

It is assumed as well, that a very salient element would also divert attention from other present stimuli. Blair and Hall (2003a) assessed after preexposure the capacity of the unique elements to interfere with the conditioned response of other present stimuli. In Experiment 4 they presented AX and BX compound solutions in Intermixed fashion while CX was presented in Blocked, then aversive conditioning proceeded with AY compound, made of a unique preexposed and a novel element. In separated generalization tests, consumption of the compound BY was found superior to that of CY, reflecting less generalization of the aversion, presumably because B resulted more interfering than C after preexposure. In their Experiment 5a (Blair & Hall, 2003a), after the same within subject preexposure, element X was aversely conditioned and tested later in two compounds with B and C. Results again showed less aversion in the compounds were the Intermixed element B was presented than in those with C (see also Blair & Hall, 2003b; Hall, Blair & Artigas, 2006; Rodríguez & Alonso, 2004 for similar results). This evidence reflects that any conditioned aversion to another stimulus can be disrupted to a greater extent by the increased salience of a unique element after Intermixed preexposure than after Blocked.

There is also evidence of this increased salience after Intermixed preexposure with appetitive procedures. Blair and Hall (2003b, Experiment 2) used salt as common element (X) and after preexposure conducted a salt depletion procedure (Furo-Doca). In a two bottle preference test results showed increased consumption for the CX compound than the BX, showing that the unique Intermixed element interfered to greater extent with the conditioned salt motivation. Blair et al. (2004) used two within-subject groups for which, salt was A for Intermixed group and C for Blocked. Then salt was paired with a new element Y (compounds were AY and CY respectively) and Furo-Doca technique was carried out. In final test with Y alone results showed increased consumption of Y in the groups where compound AY was presented rather than CY, meaning that salt resulted more associable after Intermixed exposure than Blocked (se also Artigas, Sansa, Blair, Hall & Prados, 2006 for a similar result).

Nevertheless, not all perceptual learning studies have found increased salience of the unique elements after Intermixed exposure. Dwyer and Honey (2007) exposed AX and BY in Intermixed fashion, after what the element Y was presented in Blocked. The Y block should associative activate B and increase its salience. After exposure, the compound AB was aversely conditioned and finally a test with A or B was conducted. The results showed equal consumption for both elements, which led the authors to conclude that presentations of Y were ineffective to restore B salience, that actually was equal to A salience. In Experiment 2 rats received Intermixed presentations between BY and Y, and a block with AX, the rest of the procedure was the same. Conversely, results showed more aversion to the element A, suggesting the opposite to Hall's model (2003), that B after Intermixed exposure between BY and Y had reduced its salience comparing to A after Blocked exposure in compound with X.

Indeed, experiments from Contel, Sansa, Artigas and Prados (2011) showed reduced salience of the unique elements after Intermixed long exposure. In Experiment 1 all rats where preexposed to AX and BX Intermixed and to CX in Blocked, but this phase lasted 4 days for half of the subjects and 8 days for the remained, after which half of the rats were aversely conditioned with AX and tested with AN, and the other half with CX and CN respectively. Short preexposure groups showed more aversion to AN than to CN, confirming that element A resulted more salient and associable after Intermixed than after Blocked exposure, but no differences were found between long preexposure groups. Experiment 2 and 3 replicated this pattern of results, suggesting that initially associative activation in Intermixed preexposure can restore the unique elements salience, but with more prolongued exposure habituation could accrue equally for Blocked and Intermixed elements. It is possible that in prolonged exposure tasks the mechanism operating to improve discrimination is the development of inhibitory links between the unique elements (McLaren & Mackintosh, 2000).

2.3 – COMPARISON PROCESS

In general terms, salience models seem to reflect quite well the differentiation process described by Gibson (1969). Intermixed exposure offers the opportunity to compare stimuli which increase the distinctiveness of their unique elements and promote the discrimination. However, this last assumption is somewhat at odds with the procedures reviewed above, since the standard preexposure used usually takes intervals of several hours between the stimulus presentations (e.g., 5 hours in Symonds & Hall, 1995). Based on the common notion that one must have the active representations (by self-presentation or associative activation) of the stimuli at the same time in order to compare, a gap of several hours between the presentations doesn't sound as an optimal arrange for comparison. Gibson (1969) stated that the best the opportunity to compare, the better the discrimination, reasonable, reducing the inter-stimulus interval (ISI) during Intermixed preexposure should improve perceptual learning over longer ISI preexposures.

In any case, salience models don't seem able to account for a comparison mechanism which implies close presentation of the stimuli, mainly because the associative activation of the unique elements previously needs those elements to become inactivated. In Wagner terms (1981, see Figure 5), when AX is presented in Intermixed schedule its elements (A and X) are activated in a maximum processing state (a1 state in Wagner, 1981), and once the stimulus is retired will decay into a marginal processing state (a2 state in Wagner, 1981). During an extended ISI those elements will fall into inactivation (I state in Wagner, 1981), and then, presentation of BX would allow the element X to associatively activate the element A back at a2 and restore its salience. In Intermixed preexposure with short or null ISI, the representations of the unique elements would never turn inactive; their representation will be always active by physical presence in a1 or by decay in a2. Unfortunately, evidence for a supposed mechanism that allows close comparison to improve discrimination is scarce or even inconsistent within the animal kingdom.

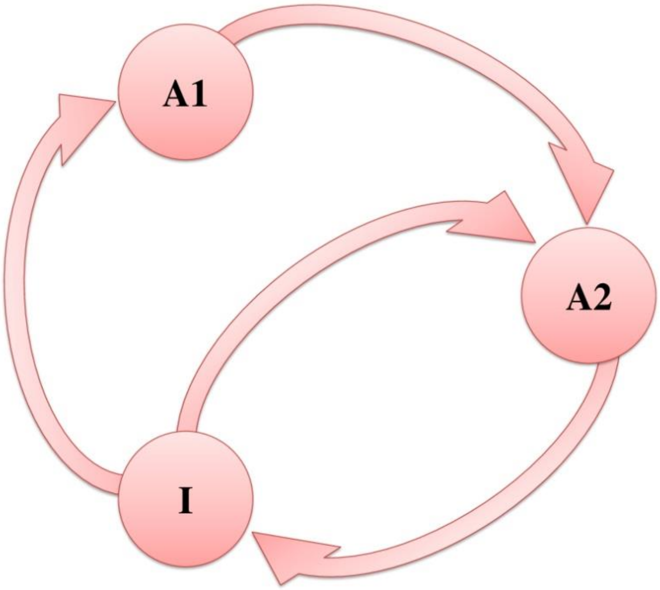

Figure 5. Diagram showing stimulus activation states and flow according to Wagner (1981, adapted from Brandon, Vogel & Wagner, 2003).

2.3.1 COMPARISON IN NONHUMAN ANIMALS

The first approach to this close comparison mechanism was made by Honey et al. (1994), who used a 7-second ISI during preexposure with domestic chicks. Following the same imprinting procedure as in Honey et al. (1993), they presented chicks violet circles and triangles in Intermixed or Blocked fashion. Parallel, in other Intermixed and Blocked groups, the circle and triangle also differed in color (scarlet and violet). After preexposure, Honey et al. (1994) placed subjects on the running wheel in a cold experimental room with the stimuli projected each on opposite sides. Running towards one of them was reinforced by a stream of warm air and the other was not. Congruently, results showed that groups preexposed to stimuli differing only in took longer to acquire the discriminative learning than groups preexposed to stimuli that also differed in color (the more similar the stimuli, the more difficult it is to discriminate). More interesting was that chicks preexposed to stimuli differing only in shape showed the classic I/B effect, but the reverse was found for chicks preexposed to stimuli differing also in color.

Honey and Bateson (1996) explained this reversed perceptual learning effect in terms of sensory preconditioning (Brogden, 1939). Close presentation of two stimuli would favor the development of excitatory associations between them, and, after that, there is evidence that any conditioned response to one of them would generalize to the other via these associations (9 seconds ISI in Lavin, 1976). In Wagner's (1981) terms, it is possible that some sub-elements of the first stimulus were still active in a1 when the next stimulus arrived, thus establishing excitatory associations between them that would favor subsequent generalization. Because Honey et al. (1994) mean ISI was 7 sec, this is within the realm of possibility. In their Experiment 1, Honey and Bateson (1996), preexposed chicks again in Intermixed or Blocked fashion to similar fowls images with an ISI of 14 seconds. This time, the I/B effect was correctly found. Later, in Experiment 2, they contrasted an Intermixed group with 14 seconds of ISI with another Intermixed group with 28 seconds of ISI. Contrary to expectations, chicks in the longer ISI group learned the discriminative task faster than chicks in the short ISI group. It was argued that two opposing processes could operate during close-Intermixed exposure at the same time, comparison that enhances discrimination (Gibson, 1969) and excitatory associations that subsequently favor generalization (Brogden, 1939), and that both progress directly as a function of the ISI.

2.3.2 SHORT-TERM HABITUATION OF THE COMMON ELEMENT

Despite the problem of sensory preconditioning, Honey and Bateson (1996) proposed a rapid mechanism for which close comparison could improve discrimination. Based on Wagner’s model (1981, see Figure 5), when AX is presented its elements (A and X) are activated in a1, but once the stimulus is retired they will decay into a2 and, in rapid intermixed schedule, stimulus BX should be due to appear. Thus, in a subsequent BX trial, we have A and X elements decayed in a2, and the element B active alone in a1, because X (or any other stimulus) cannot return from a2 to a1 in Wagner's model (1981). Therefore, in this scenario, the unique element B (active in a1, the maximum state of processing) would benefit from an augmented amount of processing resources, improving the production of its representation in memory. In simple terms, the rapid intermixed exposure would lead to a constant short-term habituation of the common elements in a2 because they are always present, and consequently, would produce a processing bias towards the unique elements that will encode good quality representations to help in subsequent discriminations. This mechanism should be also valid for simultaneous exposure, which according to Gibson (1969) is the most optimal opportunity for comparison, as the ISI length would be that necessary for the subject to shift between one stimulus to another (Mundy et al., 2007).

However, although this mechanism is well grounded in standard associative learning models (e.g., Wagner, 1981), the results found in non-human animal are not very encouraging. Bennett and Mackintosh (1999) exposed rats to flavored solutions (AX and BX) in Intermixed long ISI (4 hours), Intermixed short ISI (5 min) and Blocked fashion. After preexposure, AX was aversely conditioned and BX tested. The results showed better discrimination for the Intermixed groups over the Blocked groups, but the long ISI was significantly better than the short ISI. In Experiment 2 they contrasted the Intermixed long ISI group with a Simultaneous group, in which both stimuli were presented in two bottles at the same time. Results again showed that after conditioning the BX compound, AX was better discriminated by the Intermixed long ISI group than by Simultaneous group. Finally Experiment 3 compared the Simultaneous group with a short ISI Intermixed group (2 minutes ISI), but results one more time showed better discrimination for the group with longer interval between stimuli presentations. These experiments reflect a direct contrast between exposures that either allow or hinder a comparison, but no results obtained from them suggest that this opportunity enhances discrimination, as suggested by Gibson (1969).

Following in the footsteps of Bennett and Mackintosh (1999), Alonso and Hall (1999) replicated their procedure and surprisingly found better discrimination of the Blocked group over the Simultaneous group (Experiment 1), even when they gave extinction trials to A and B after preexposure to extinguish any possible excitatory association between them that might lead to sensory preconditioning (Experiment 2). Similarly, Rodríguez and Alonso (2008) preexposed their rats to AX and X alone solutions, an approach that would avoid the formation of A-B excitatory associations, then element X was aversely conditioned and AX tested. The results showed that an Intermixed spaced group discriminated better than Blocked, but sadly, again this latter discriminated better than the Simultaneous. So far, the evidence did not seem very encouraging to support that the opportunity to compare increases discrimination.

In a last-ditch attempt, Rodríguez, Blair and Hall (2008, Experiment 1) exposed their rats to two bottles of X and AX (Simultaneous Stimuli), and, on alternated rapid sessions, to two bottles of water and BX (Intermixed Stimuli), then aversion was established to X and generalization measured to AX and BX. Again, results showed more generalization to the simultaneous stimulus, AX, than to the Intermixed stimulus, BX. However, in their Experiment 2, they repeated the previous procedure and added a new element Y to be aversely conditioned, then test proceeded with the compounds AY and BY. This time, at least, they found no differences in consumption, suggesting that Simultaneous and Intermixed Stimuli should discriminate equally well. For Experiment 3, they used a between subjects design to present AX and X in three groups: group Simultaneous, group Intermixed and group Blocked; then element Y was aversely conditioned and generalization to AY measured in test. Finally, results showed improved and equal discrimination of the Simultaneous and Intermixed group over the Blocked one. This study represents one of the few pieces of evidence that animals can benefit from the opportunity to compare similar stimuli in order to discriminate between them afterwards.

Furthermore, it is possible to obtain indirect evidence of the short-term habituation mechanism, since it is assumed that the better the processing of the unique element, the more latent inhibition it will have and the lower its associability will be (McLaren et al., 1989). Artigas, Contel, Sansa and Prados (2012) preexposed AX and BX compounds in Forward (AX->BX) and Backward (BX->AX) sequences with 1 minute ISI. After preexposure, element A was aversely conditioned and its extinction measured in test trials. The processing bias would better encode the element A for group Backward than for group Forward, because X is previously presented in BX, and therefore would show more latent inhibition. Results confirmed this; they showed that A resulted less aversive in the Backward group than in the Forward. Experiment 2 contrasted again Forward and Backward rapid groups, after which an aversion was established to AX and then a compound NX was tested. With this procedure the level of salience of A would be measured by the aversion reflected by X on the NX test. Results showed less consumption in the Backward group, reflecting higher aversion acquired by X during the AX conditioning because A was too low on associability to acquire much conditioning (see also Artigas et al., 2012, Experiment 3).

Yet, in contrast to this salience measure, there are still some inconsistent results. Lombas, Alonso and Rodríguez (2008) preexposed two Intermixed groups to AX and BX with different ISI, 5 min or 24h. After that the element A was aversely conditioned and its extinction measured in test. This design allow directly compare the salience of the unique elements after two different mechanisms. While the associative activation of the unique elements restores their salience in spaced presentations, the better encoding of these elements in close exposure should lead to the reverse (Artigas et al., 2012). Unexpectedly, these authors didn't find differences in salience between the Intermixed unique elements resulted from both different ISI conditions.

In summary, contrary to Gibson's (1969) suggestion, the results found in animals have never indicated better discrimination of stimuli when the ISI have been short in intermixed schedule or simultaneous, if anything the opposite. It may be that the comparison mechanism is hindered by some effects such as sensory preconditioning, but still results have remained the same pattern when attempts to control this effect have been made. Eventually, this counter-evidence has led some authors to even claim that animals cannot benefit from the opportunity to compare (Mitchell & Hall, 2014, p. 294). Fortunately, clearer evidence comes from human animal studies.

2.3.3 COMPARISON IN HUMAN ANIMALS

Based on the associative models proposed to explain the I/B effect found in animals, a series of experiments were carried out in humans to test this phenomenon. Although with clearly different methods: a single session, short ISI and some water to remove the remnants of the previous stimulus; some studies were able to develop very similar procedures with human participants to those used previously on animals.

As an instance, Dwyer et al. (2004) preexposed human participants to lemon-sucrose (AX) and lemon-salt (BX) flavored compounds in Intermixed or Blocked exposure. They were asked to take a sip of each stimulus every 10 seconds and also a sip of water between trials to eliminate the remaining flavor (that could lead to sensory preconditioning). After this, participants' tasted BX with an added unpleasant taste (De Houwer, Thomas & Baeyens, 2001) to negatively condition this compound, and then performed a generalization test by rating a series of AX and BX trials on a liking scale. While doing so, they were also asked to judge whether or not the current stimulus was the same as the previously rated. The results didn't find a generalization effect, but a significant difference in the Same/Different test, where the Intermixed group showed higher accuracy in rating the compounds as different than the Blocked group. On "Same" trials all participants tend to be extremely accurate, as the presentation of a stimulus followed by itself again is clearly easy to discriminate (also with visual stimuli, e.g., Lavis & Mitchell, 2006). In Experiment 2a these results were replicated and finally, in Experiment 2b, with minimal changes in the procedure, significantly more generalized aversion of compound BX to AX was found in the Blocked group than in the Intermixed group (see also Mundy et al. 2006, Experiment 1 for a within subject procedure).

Interestingly, Mundy et al. Experiment 2 exposed all participants to the stimuli in two rapid sequences, namely Forward (AX->BX) and Backward (DY->CY), then conditioned AX and CY to finally test the generalization to BX and DY respectively. Results showed that compounds preexposed in Backward generalized the aversion more to DY than did those preexposed in Forward to BX. Mundy et al. (2006) explained these latter results in terms of inhibitory links between the unique elements, in the Forward group B would learn to inhibit A at test, but D couldn't inhibit C (McLaren & Mackintosh, 2000). However, short-term habituation of X is able to explain the latter results as well (Honey & Bateson, 1996). The Forward condition allowed the element X to habituate in the short term and thus better process element B, which after AX conditioning would improve discrimination. Indeed, A being less processed and hence more salient, should acquire more conditioning and X should generalize less aversion to BX, but also C would be better processed and less salient, so Y would acquire more aversion and generalize to more extent the dislike to DY.

However, in general, human experiments have mainly used visual stimuli and computer tasks to assess perceptual learning. For example, Lavis and Mitchell (2006) preexposed 3 pairs of similar checkerboards in which a pattern of squares formed the common background (X) and a few other squares formed the unique patterns (A, B, C, D, E and F). Two pairs of checkerboards were presented in separated Intermixed blocks (AX/BX & CX/DX) and another pair in pure Blocked fashion (FX_DX). Therefore, inhibitory links could develop between the unique elements within the same Intermixed pair, but not between Intermixed pairs. On the other hand, if short-term habituation of the common element improves unique elements encoding, all alternated stimuli should be equally differentiated. Results from the Same/Different test showed that Intermixed stimuli were better and equally discriminated in different trials than pure Blocked, suggesting that inhibitory links didn't play an important role here.

Similarly, Mitchell et al. (2008a, Experiment 3) exposed: a pair of checkerboards Intermixed (AX/BX), one checkerboard Blocked (DX) and a checkerboard Intermixed with the common background (CX/X). Element C could not establish inhibitory links towards any other element but alternation with the common one could increase its discrimination if X tends to habituate in short-term (Hall et al., 2006; Rodríguez & Alonso, 2004). Same/Different test contrasted the checkerboards against the common background and results showed a classic Intermixed/Blocked effect, better discrimination for AX and BX over DX, but also an improved discrimination of CX (same results in Experiment 4). These results gave some support to the suggestion that comparison improves discrimination (Gibson, 1969) and to the rapid comparison mechanism proposed by Honey and Bateson (1996).

Consequently, Mundy et al. (2007) reasoned that exposing stimuli simultaneously should habituate the common elements to greater extent than successive presentations, as the common element would be habituated faster and for both similar stimuli at the same time, improving even more the encoding of their unique elements. Mundy et al. (2007) Experiments 3 and 4 contrasted Simultaneous vs. Successive presentation of similar faces both in exposure phase and also in test phase. Results of Experiment 3 showed the best accuracies for the stimuli preexposed in Simultaneous than in Successive arrange, and additionally, Experiment 4 also showed that increasing Successive preexposure can improve discrimination but not Simultaneous (presumably because in Successive exposure there is still room for improvement).

Because the latter results were discussed to be face-specific (Dwyer, Mundy, Vladenau & Honey, 2009; Mundy, Honey, Downing, Wise, Graham & Dwyer, 2009b), Mundy, Honey and Dwyer (2009a) next experiments introduced checkerboards to replicate the simultaneous exposure effect. Experiment 2 showed that checkerboards from a Simultaneous group were better discriminated than those from a Successive group, and that the latter were better discriminated than the Non-Preexposed group. From these experiments they reasoned that, Simultaneous exposure should not allow the formation of inhibitory links (McLaren & Mackintosh, 2000), rather the opposite, because two stimuli active in a1 state should be more ready to form excitatory associations between them and therefore impair following discriminations. These authors concluded then that the most plausible mechanism would be the short-term habituation of the common elements and the processing bias towards the unique ones (Honey & Bateson, 1996).

In order to further assess this mechanism, Dwyer et al. (2011) introduced a distractor between the rapid presentations of the Intermixed stimuli, which should disrupt the common element short-term habituation and eliminate the processing bias, but wouldn't affect inhibitory links. For Experiment 1 participants were exposed to pairs of faces in Intermixed and Blocked fashion, and an unexposed pair was added later at test. Three distractor conditions were added to fill in the ISI between the Intermixed and Blocked exposures: a face, a checkerboard, or nothing. Same/Different test showed a classic Intermixed/Blocked effect for the control condition, for the checkerboard condition this effect was attenuated, but the face condition directly eliminated it. To corroborate these results Experiment 2 preexposed participants to three Intermixed sequences: Comparison sequence put the distractor between the stimuli, Masking sequence put the distractor before or after the stimuli and Control sequence didn't put any distractor. After each sequence, a Same/Different task was performed for the corresponding stimuli. Results showed high discrimination for the Control sequence, followed by the Masking sequence and finally the Comparison sequence obtained the worst accuracy. Dwyer et al. (2011) reported that the short-term habituation of X was disrupted by the distractor in the Comparison group, thereby eliminating the processing bias towards unique elements, thus impairing discrimination, which firmly supports the mechanism proposed by Honey and Bateson (1996) and discard that of inhibitory links (McLaren & Mackintosh, 2000), which shouldn't be affected by the distractors.

Parallel, from another perspective, two mechanisms based on memory processes were provided as well to explain the rapid perceptual learning effect found in humans. Mitchell, Nash and Hall (2008b) initially proposed that the I/B effect could be explained by the advantage of spaced over massed practice (Ebbinghaus, 1885), then Intermixed presentations would allow the consolidation in memory of the features of the stimuli rather than massive Blocked exposure (Wickelgren, 1972). To determine this, Mitchell et al. (2008b) contrasted the discrimination of a pair of similar checkerboards preexposed Intermixed (AX/BX) with another checkerboard Intermixed with a gap (CX/-, Experiment 1) or a non-similar stimulus (CX/DY, Experiment 2), ensuring all preexposures allow the same time interval for consolidation. However, only the first pair of stimuli, the similar Intermixed, was effectively discriminated.

In consequence, Mitchell et al. (2008b, see also Lavis et al., 2011) suggested another approach involving controlled memory processes. According to them, if a stimulus is remembered from one presentation to the next, its processing would be reduced, instead if it is forgotten, processing increases upon its reappearance (Jacoby, 1978). In this manner, intermixed presentations would facilitate the forgetting of unique elements on the alternated trials that are absent, favoring on the other hand the increased encoding in following presentations, whereas Blocked exposure will reduce its processing progressively within the same block. To check this and assess the encoding level of the unique elements, Mitchell et al. (2008a) preexposed Intermixed (AX/BX) and Blocked (CX_DX) checkerboards, followed by a same/different test with the unique elements in a different background (AY, BY, CY & DY). The results demonstrated superior discrimination for Intermixed elements, indicating that these were better encoded. After the same preexposure, Lavis et al. (2011) conducted a memory test in which participants should match the color of the unique elements with their form. The color-match test reflected better accuracy for the Intermixed unique elements than the Blocked ones, suggesting that both features of the unique element were better encoded in memory after intermixed rapid exposure.

In essence, this mechanism is similar to that proposed by Honey and Bateson (1996). Unfortunately, it encounters some problems in attentional terms. Lavis et al. (2011) found that additional exposure to the unique elements isolated also improved discrimination, but Recio et al. (2016) showed that this effect only appeared if the element was presented in the same place on the screen as it was during the stimulus presentation. Likely, participants learned to attend only the place where differences appeared, which is more frequently during Intermixed exposure, leading to a better encoding of these elements (see also Jones & Dwyer, 2013; Wang, Lavis, Hall & Mitchell, 2012). In addition, Recio et al. (2016) found that the classic I/B effect with checkerboards by Lavis and Mitchell (2006) was eliminated if instructions did not advise participants to look for differences, or even, if there were no instructions at all (see also Navarro, Arriola & Alonso, 2016). However, it is worth noting that Angulo, Alonso, Di Stasi and Catena (2019) managed to find the I/B effect using irrelevant instructions for the task, but notably the effect was more marked if the instructions encouraged participants to look for differences. Irrevocably, this tendency to look for differences could arouse genuinely from the participants, the fact that they detect differences on their own may reinforce intrinsically this tendency to keep looking for them (Mackintosh, 2009). These biases would rather lead to discriminative learning, as the detection of any difference would be reinforced (by the experiment or by oneself), which is contrary to the mere exposure used in perceptual learning.

In any case, nowadays some studies have attempted to adapt in animal experiments the procedures used in humans to demonstrate the role of short-term habituation and the processing bias, as these subjects can presumably avoid these methodological biases mentioned above. Paradoxically, this strategy brings us back to the starting point.

CHAPTER III – ACTUAL PERSPECTIVE

From the above reviewed experiments, one conclusion that emerges is that humans can benefit from close comparison to enhance discrimination, but non-human animals cannot (see for a review Mitchell & Hall, 2014). Animal experiments never showed better discrimination when similar stimuli were presented quickly over those presented spaced apart, and some have even shown the opposite (Alonso & Hall, 1999; Rodríguez & Alonso, 2008). In contrast, human experiments have definite evidence that Simultaneous exposure to stimuli is better than Successive, and this better than Blocked (e.g., Mundy et al., 2007).

Paradoxically, the I/B effect found in animals with spaced presentations can be easily explained by proposed models such as salience modulation or inhibitory links, but these have difficulties in explaining the human results, for one thing, the rapid presentations do not allow for the associative activation on which these models are based. On the other hand, Honey and Bateson's (1996) proposal, short-term habituation and processing bias, may explain the human results quite well, but the spaced procedures used with animals do not fit with this mechanism, since when the second stimulus is presented much later, the first one has decayed to an inactive state and the common element is no longer habituated. However, it is possible that the mechanisms of perceptual learning are in fact shared across species, but that depending on the different procedures, different mechanisms are activated. This assumption leaded our group to propose animal procedures more similar to human ones to study whether the mechanism of close comparison is possible in animals as well, and to defend shared mechanisms.

As an example of a classical perceptual learning procedure adapted from humans, Recio et al. (2019), preexposed their rats to similar flavored stimuli presented in rapid succession, but critically introduced a small water interval between stimuli (similar to Dwyer et al., 2004; Mundy et al., 2006). Amusingly, like previous animal experiments, they first observed a reverse I/B effect during the generalization test (Alonso & Hall, 1999; Rodríguez & Alonso, 2008) which, following Honey and Bateson (1996), explained in terms of sensory preconditioning as well (Brogden, 1939). In a final attempt, they extended the preexposure days in Experiment 2 (from 4 days to 12) and, this time, they found greater discrimination of the Intermixed group over the Blocked group. However, although this rapid procedure succeeded in finding better discrimination after intermixed presentation, it could not be firmly adduced to a comparative mechanism such as that proposed by Honey and Bateson (1996). The fact that a long (Experiment 2) but not a short (Experiment 1) preexposure led to the I/B effect tends to fit more comfortably into the model of inhibitory links, which are more likely to develop within long exposures.

In order to assess the close comparison mechanism, Recio et al. (2018) had previously developed another procedure that made use of an unorthodox generalization test, but which presumably would not be affected by sensory preconditioning, and therefore there would be no need to extend the preexposure days. After 4 days of rapid Intermixed or Blocked preexposure (featuring water during the ISI), they aversely conditioned a new element Y and then measured the generalization response to AY. Theoretically, these changes may reduce the influence of excitatory associations between A and B; in fact, the I/B effect has already been found using this procedure in animals with spaced (Blair & Hall, 2003a) and closed (Rodríguez et al., 2008) presentations, but also in humans (Mitchell et al., 2008a). Finally, the results of Recio et al. (2018) showed that Intermixed rats consumed more AY than rats in the Blocked group, reflecting less generalization between Y and AY in the former group and demonstrating that animals may benefit from the opportunity for comparison to discriminate.

With a view to contrast whether this I/B effect with rapid presentations was due to the mechanism proposed by Honey and Bateson (1969), Recio et al. (2018) adapted the Dwyer et al. (2011) distractor procedure with their animals. In Experiment 3, one Intermixed group of rats received a distractor (sugar) between stimulus presentations, while another Intermixed group received water in between and the distractor after stimulus presentations. As in the Dwyer et al. (2011) experiment, the distractor in between the stimuli was expected to disrupt short-term habituation of the common element, eliminating the processing bias towards unique elements and thereby impairing discrimination. Accordingly, results from Experiment 3 showed worst discrimination when the distractor was preexposed in between the stimuli than after them (see also Experiment 2), replicating the results from Dwyer et al. (2011) with humans.

The results from Recio et al. (2018) procedures supported the existence of a mechanism in animals analogous to the short-term habituation of common elements proposed by Honey and Bateson (1969). Importantly, Recio et al. (2018) contributed to this proposal by adding the feature that the processing bias could lead to better unitization of the unique elements, which will form a better representation of them and subsequently improve discrimination. In Wagner's (1981) terms, after rapid exposure to AX both elements would move to a2 by the time BX arrives, so that more sub-elements of B would be processed and associated together because the sub-elements of X would still be in a2. With repeated rapid Intermixed exposures, this unitization of the unique elements would create very complex, complete and accurate to reality representations of the distinctive features of similar stimuli, favoring their discriminability.

This thesis aims to evaluate the unitization process proposed by Recio et al. (2018) and to reinforce the universality of this mechanism among species. The main prediction that emerges from this is that if the I/B effect found in rapid comparison experiments is due to a increased unitization of unique elements, they will be better discriminated, but will also lose salience and associability. This conclusion is contrary to salience models classically proposed to explain perceptual learning in animal research (e.g., Hall, 2003). We will test these predictions in the following experimental chapters. First we will try to replicate the I/B effect with rapid exposure. Then we will study the responsible mechanism in terms of unitization, and therefore the studies would be aimed at assessing the level of salience and associability resulting from the unique and common elements after the rapid comparison. The next step is to manipulate the span of the intervals, in order to study the different mechanisms proposed as a function of the procedures (Salience Modulation vs. Short-Term Habituation). Finally, we will carry out a series of human studies to also evaluate this unitization proposal as a shared comparative mechanism across species.

PART II:

EXPERIMENTAL SECTION

CHAPTER IV –THE PROBLEM OF SENSORY PRECONDITIONING

Introduction

From the evidence reviewed so far, we can affirm that mere exposure to similar stimuli helps effectively the subject to discriminate between them in a following task. Furthermore, Gibson (1969) noted that this improvement in discrimination should be enhanced the better the subject's opportunity to compare between these stimuli, but in fact, she did not propose any mechanism by which this comparison might work. In the popular sense of the verb, we understand comparison as the process of contrasting (at least) two items to identify differences and/or similarities between them, so it is reasonable that they must be active at the same time in the subject's memory for any contrast to take place.

Human procedures have shown the I/B effect using short intervals (<1 sec ISI), which is consistent with a comparison process as the representation of the first stimulus presented can remain active until the next stimulus arrives. These results have been explained in terms of short-term habituation of the common element (Honey & Bateson, 1996). When similar stimuli are presented quickly, the elements they have in common become habituated because they have already been processed when the first stimulus appeared, subsequently freeing up resources to process oncoming unique elements. This processing bias should enhance the unitization of the unique elements favoring the subsequent discrimination (Recio et al. 2018). Moreover, it has been seen that the introduction of a distractor between the stimuli during preexposure can eliminate this I/B effect, reportedly because the distractor interrupt the short-term habituation of the common element disabling the processing bias (Dwyer et al., 2011).

As we have mentioned before, evidence of the existence of this short-term mechanism in species other than humans has been sparse (Rodríguez, Blair & Hall, 2008) or even opposing when the classic generalization test is carried out (Alonso & Hall, 1999; Honey & Bateson, 1996; Rodríguez & Alonso, 2008). Honey and Bateson (1996) found in domestic chicks that alternating geometric figures worsened discrimination the closer in time they were presented, and more recently Recio et al. (2019) found in rats that the discrimination of the Intermixed group was worse than that of the Blocked group when presented similar flavors in rapid succession (reversed I/B effect). Honey and Bateson (1996; Recio et al., 2019) proposed in animals that due to the close contiguity during rapid Intermixed exposure stimuli will tend to form excitatory associations with each other. Subsequently these associations will produce a sensory preconditioning effect (SPC), as conditioning of one of these stimuli will generalize the conditioned response to the other through these associations, impairing discrimination.

Sensory preconditioning occurs when two neutral stimuli are repeatedly presented in contiguity, so that later if one of these is conditioned to elicit a response by training, the other will elicit a similar conditioned response without the need for training because they have been associated together (Brodgen, 1939). An illustrative example is the experiment of Rizley and Rescorla, (1972), they presented a Light immediately followed by a Tone (L→T), after which the Tone was paired with a Shock (T→US). Then one group of rats had extinction unreinforced trials with the Tone (T→) while others did not, and finally the rate at which the Light was conditioned with the Shock was measured (L→US?). It was found that the extinction group acquired Light conditioning more slowly than the non-extinction group, which suggested that weakening the Tone-Shock link (T→US) in the associative chain impaired the Light to elicit the Shock (L→US). In the perceptual learning scenario, the Intermixed rapid exposure to similar stimuli will allow them to predict each other because this exposure is successive (AX→BX & BX→AX). When BX is presented some sub-elements of A are still active in a1 (and of B when AX is presented), allowing bidirectional excitatory associations between A and B to be established. Later on, conditioning phase will establish one of the stimulus as predictor for the US (BX→US), and finally, the presentation of the other stimulus at test (AX) will lead to the activation of the chain that predicts the US (A→B→US) (Rescorla, 1981), along with the activation of the X-US chain, resulting in greater generalization.

SPC with successive exposure is well established in the literature with visual or auditory stimuli and may explain the increase in generalization found in Honey and Bateson (1996; Honey, Bateson & Horn, 1994) as stimuli were presented closer together. However, evidence for this phenomenon with olfactory or palatable stimuli such as those commonly used in perceptual learning is scarce and limited (see for a review Holmes, Wong, Bouchekioua & Westbrook, 2022). One of the few examples is the experiment of Lavin (1976) with rats and flavors. He presented 1 ml of saccharin solution quickly followed by 1 ml of coffee solution, then the coffee was aversively conditioned and the generalized suppression in consumption was measured in the saccharin. Lavin (1976) found that saccharin resulted aversive only when the ISI between stimuli during preexposure was of 9 seconds or less (see also Lyn & Capaldi, 1994 for same results with conditioned preference).

Although the main explanation for the absence of the I/B effect with rapid comparison in animals has been in terms of SPC, according to Lavin's (1976) data it is only applicable to the case where the stimuli are presented almost simultaneously (e.g., Rodríguez & Alonso, 2008), but it is less clear in the other experiments where the interval is longer than 9 sec (e.g., Recio et al., 2019). However, it is possible that due to the nature of the stimuli typically used, odor and taste compounds, their effects remain after their presentation is over. In particular, it could be that during rapid preexposure the sampling of some gustatory or olfactory stimuli, some sub-elements remain in the subject's sensory receptors or the environment for when the next stimulus arrives, and thus the sub-elements of both are sampled together favoring the formation of excitatory associations and therefore SPC (Müller, Gerber, Hellstern, Hammer & Menzel, 2000). The reason why perceptual learning experiments produce an SPC effect with longer intervals (impairing the I/B effect) and Lavin does not find it beyond 9 sec may be due to the amount of stimulus used in this latter, as he only allowed rats to drink 1ml, a quantity much reduced to that normally used in animals for these perceptual learning procedures, which easily can be dissipated after more than 9 seconds of ISI.

Consistent with this assumption Recio et al. (2019) rapidly preexposed rats to similar odor and taste compounds, while introduced a 5-min ISI of water between presentations to try to remove the remnants of the first stimulus by the time the next arrived. However using the classical test they found the reverse I/B effect, and as Honey and Bateson (1996) they explained it in terms of SPC. Recio et al. (2019) claimed that could be that the water was not sufficient to dissipate the odors of the stimuli between trials resulting in a jointed association of the unique elements during Intermixed exposure which later would produce increased generalization at test. To try to find the I/B effect with a rapid succession procedure they proposed a different test which reduces the final influence of SPC. Following Blair and Hall (2003a) experiments, Recio et al. (2018) after preexposure conditioned a new element, Y, and tested it in compound with one of the preexposed unique elements, AY. In this case, the influence of the SPC would be reduced, as the possible association between A and B would not produce a generalization of the conditioned response. With this procedure, Recio et al. (2018) found that the group in which AX was preexposed Intermixed with BX discriminated better between Y and AY than the Blocked group, reflecting an unorthodox I/B effect (see also Blair & Hall, 2003a for same results with spaced ISI).

With the aim of studying the effect of SPC on perceptual learning with rapid exposure, and following the results of Recio et al. (2018; 2019), we will manipulate the sensory modality of the stimuli, whether or not the presentation of water between presentations can dissipate the persistence of these stimuli, and finally the kind of test used. Theoretically, if the unique elements used are tastes, water should be more effective in preventing the formation of excitatory associations between them than in the case of odors. Therefore, we expect with this manipulation to replicate the results of Recio et al. (2018) with the superposition test, conditioning Y and assessing discrimination to AY, but also to find the I/B effect with the classical BX and AX test, with which Recio et al. (2019) found the opposite effect. In addition, apart from measuring consumption, we will also measure the lick cluster size (a measure of hedonic reactions, see Dwyer, 2012), which is a measure never seen before in perceptual learning and may give some clues about the processes occurring during preexposure.

Experiment 1: Classic and Superimposition Test with taste compounds

Two groups of rats received Intermixed exposure to two taste compounds (without odorous components as in Recio et al., 2018) on each of the 4 days (INT groups) of preexposure phase, while the other two groups received a block of AX presentations on 2 days and a block of BX presentations on the other 2 days (BLK groups), the order of stimulus presentation being counterbalanced. Both groups received water in the 5-min interval between successive presentations on a given day. After the exposure stage, half of the rats in each condition received BX conditioning trials and were tested with AX (INT-AX and BLK-AX), and the rest received Y conditioning trials and were tested with AY (INT-AY and BLK-AY). The design for Experiments 1-3 is summarized in Table 1. After using a rapid preexposure procedure, and controlling for sensory preconditioning, we expect the INT-AX group to generalize less aversion to AX than the BLK-AX group, the classic I/B effect. Furthermore, the comparison between the INT-AY and BLK-AY groups allows us to assess whether the Recio et al. (2018) effect observed with odors can also be observed with tastes, that is, increased consumption of AY by the Intermixed group.

EXPERIMENT	Groups	Preexposure	Conditioning	Test	C.R. Test
1	INT-AX	AX/W/BX	BX+	AX?	
	BLK-AX	AX/W/AX			
	INT-AY	AX/W/BX	Y+	AY?	
	BLK-AY	AX/W/AX			
2	INT-W	AX/W/BX/N	BX+	AX?	
	BL	AX/W/AX/N			
	INT-N	AX/N/BX/W			
	BLK-N	AX/N/AX/W			
3	INT	A>B	B+	A?	B?
	BLK	A>A			

Table 1. INT refers to Intermixed preexposure, BLK refers to Blocked preexposure. W means water and N means no water. A and B were salt and sucrose for Exp1 and 2, and salt and lemon for Experiment 3, all counterbalanced. In Exp1 X and Y were lemon juice and quinine counterbalanced and in Exp2 X was quinine. The "+" indicates an intraperitoneal injection of LiCl. The "/" indicates rapid succession of stimuli within the same session, and ">" rapid succession in fixed order. Note: during preexposure INT group also experienced trials in which BX preceded AX, and BLK group experienced trials in which both tastes were BX (or B in Experiment 3).

Method

Subjects

Sixty naïve male Lister Hooded rats were used (supplied by Envigo, Blackthorn, U.K). The rats were housed in pairs in standard cages and maintained on 12-hr/12-hr light/dark cycle (lights on at 7 a.m.). Their mean ad libitum weight was 374g (range: 290-449g) when the water-deprivation regimen began, and they had continuous access food when they were in their home cages. Research was conducted in accordance with the Home Office regulations under the Animal (Scientific Procedures) Act 1986. There were 15 rats in each group because 4 rats from the original cohort of 64 were taken for use in a separate electrophysiology study. This sample size has proven adequate in the past to detect perceptual learning effects using a consumption measure and similar procedures and design (e.g., groups sizes were 8 in Recio et al., 2019, and either 8 or 16 in Symonds & Hall, 1995).

Apparatus

Rats received exposure, conditioning and test in 16 custom-made drinking chambers (supplied by Med Associated Inc., St Albans, VT; 32 × 15 × 12cm, L × W × H). The chambers had white acrylic walls, and wire mesh floors and ceilings. Access to fluids was via stainless-steel drinking spouts, attached to 50 ml tubes, which could be inserted through the left-hand or right-hand side of the mesh lid of the chamber. Here, the tubes were inserted in the left-hand side. A contact-sensitive lickometer registered the time of each lick to the closest 0.01 s, and the licks were recorded by a computer using MED-PC software (Med Associates Inc.). Consumption was measured by weighing the tubes before and after each fluid presentation. The stimuli were solutions of 2% sucrose and .9% salt (which served as A and B), and solutions of 2% lemon juice and 0.000015M quinine (which served as X and Y; all wt/wt). These solutions were combined to create three compounds (AX, BX and AY) in a way that maintained their concentrations.

Procedure

The water deprivation schedule began with rats receiving access to water for 30 min starting at 10:00 and 16:00 on each of the first 2 days. On the subsequent 4 days rats received exposure to AX and BX at 10:00 and 30-min access to water at 16:00. Solutions of sucrose and salt served as A and B, and solutions of lemon juice and quinine served as X and Y. The identities of the stimuli that served these roles were otherwise fully counterbalanced. Rats received successive periods of 10 min, 5 min and 10 min in which they received access to 10 ml, 8 ml and 10 ml of the designated solutions. For groups INT-AX and INT-AY, the designated solutions were respectively: AX, Water, BX, and BX, Water, AX, counterbalanced across subgroups, with the sequence alternating across days (e.g., AX, Water, BX, on days 1 and 3 of the exposure stage, and BX, Water, AX, on days 2 and 4). For groups BLK-AX and BLK-AY, the solutions were AX, W, AX, and BX, W, BX; with the order being counterbalanced across subgroups:

AX, Water, AX, on days 1 and 2, and BX, Water, BX, on days 3 and 4, for one subgroup; and BX, Water, BX, on days 1 and 2, and AX, Water, AX, on days 3 and 4, for the second subgroup.

Rats received conditioning trials on Days 5 and 7 and recovery days on Days 6 and 8. On conditioning trials, rats in groups INT-AX and BLK-AX received 30-min access to 15 ml of BX followed by an injection of 0.15 M LiCl at 10ml per kg bodyweight (1% of b.w.). Rats in groups INT-AY and BLK-AY received an identical conditioning treatment to their namesakes with the exception that access to Y was paired with LiCl. On the recovery days, rats received access to water for 30 min at 11:00. At 11:00 on day 9 rats in groups INT-AX and BLK-AX received access to AX for 30 min, whereas those in groups INT-AY and BLK-AY received access to AY. After this test, rats received water for 30 min in the afternoon, and we also assessed performance to AB. However, the results of this test were not informative and will not be reported here.

Statistical Analysis

During the exposure stage, rats consumed the small quantities of AX and BX within the 10-min periods, which meant that a reliable analysis of lick microstructure was not possible. Therefore, the analysis that follows focuses on consumption and lick-cluster sizes during 30-min conditioning trials with BX or Y and the 30-min test with AX or AY. The analysis of lick microstructure during conditioning and testing followed reported protocols (e.g., Dwyer, 2012; Patitucci, Nelson, Dwyer & Honey, 2016). A cluster was defined as a set of licks, each separated by an inter-lick-interval of no more than 0.5 s, as most pauses greater than that are also greater than 1 s (e.g., Davis & Smith, 1992; Spector, Klumpp & Kaplan, 1998). General linear model null hypothesis testing analyses were conducted, assuming a rejection level of $p < 0.05$ for mixed factorial analysis of variance. Partial eta squared, and Cohen's d tests were used to measure effect sizes. The Greenhouse-Geisser correction was used when the sphericity assumption was violated. The JASP statistical program was used to carry out the analyses

(Love, Selker, Marsman, Jamil, Dropmann, Verhagen, Ly, Gronau, Šmíra, Epskamp, Matzke, Wild, Knight, Rouder, Morey & Wagenmakers, 2019).

Transparency and Openness

This study was not preregistered. All data from this study are available by emailing the corresponding authors.

Results

During the exposure phase, rats in groups INT-AX, BLK-AX, INT-AY and BLK-AY consumed 4.77, 4.75, 4.37, and 4.01ml, respectively, of the AX solution and 4.67, 4.79, 4.37, and 4.19ml, respectively, of the BX solution. ANOVA revealed no effect of Exposure Schedule (Intermixed or Blocked), Conditioned SStimulus (BX versus Y), or Solution (AX versus BX), and there were no significant interactions between these factors (all Fs < 1).

Table 2 shows consumption and lick clusters sizes during the BX and Y conditioning trials. Inspection of the table shows that consumption of BX (for group INT-AX and BLK-AX) and Y (for groups INT-AY and BLK-AY) declined between the two conditioning trials; and that consumption scores were generally higher for the familiar compound (BX) than for the novel stimulus (Y). There was also a reduction in lick cluster sizes in the four groups between the two trials, with lick cluster size being higher for BX than Y. An ANOVA conducted on the consumption scores, with Exposure Condition (Intermixed or Blocked), Conditioned Stimulus (BX or Y), and Trials (1 or 2) as factors, revealed an effect of Conditioned Stimulus, F(1, 56) = 205.31, p < .001, ηp2 = .786, MSE = 4.07, an effect of Trial, F(1, 56) = 205.31, p < .001, ηp2 = .786, MSE = 4.07, and an interaction between the three factors, F(1, 56) = 4.24, p = .044, ηp2 = .070, MSE = 7.36, there was no significant effect of exposure condition or other two-way interactions (largest F(1, 56) = 1.65, p = .204, ηp2 = .029, MSE = 4.07 for the Exposure Condition ×

Conditioned Stimulus interaction). Inspection of the descriptive statistics in Table 2 suggests that the significant 3-way interaction stems from the fact that, for the groups conditioned with BX there was a tendency for the Blocked exposure group to show a smaller decrease in consumption across conditioning than the alternating exposure group, while for the groups conditioned with Y, this was reversed. Despite these impressions, separate ANOVAs performed on each Conditioned Stimulus only showed main effect of Trial for BX, F(1, 28) = 14.20, p < .001, ηp2 = .336, MSE = 10.42, and for Y, F(1, 28) = 33.22, p < .001, ηp2 = .543, MSE = 4.30, the effect of Exposure Condition or Trial × Exposure Condition interaction were non-significant (largest F(1, 28) = 2.76, p = .108, ηp2 = .090, MSE = 3.26 for main effect of exposure condition in the groups conditioned with Y).

Group	**Trial 1**				**Trial 2**			
	Consumption		*Lick cluster size*		*Consumption*		*Lick cluster size*	
INT-AX	10.84	(0.14)	32.79	(2.41)	6.34	(0.64)	22.97	(2.12)
BLK-AX	9.31	(0.98)	27.17	(2.33)	7.53	(0.81)	22.55	(2.95)
INT-AY	4.04	(0.44)	16.51	(1.33)	1.63	(0.61)	9.35	(1.57)
BLK-AY	5.49	(0.53)	22.86	(2.54)	1.73	(0.40)	9.39	(1.00)

Table 2. Mean (+SEM) consumption and lick cluster size on the conditioning trials in Experiment 1. Note: Consumption is measured in ml and lick cluster size in licks per bout. For groups INT-AX and BLK-AX the 2 conditioning trials were with BX, while for groups INT-AY and BLK-AY they were with Y.

An equivalent ANOVA conducted on the lick cluster sizes revealed an effect of Conditioned Stimulus, F(1, 56) = 43.15, p < .001, ηp2 = .435, MSE = 97.54, an effect of Trial, F(1, 56) = 60.85, p < .001, ηp2 = .521, MSE = 37.87, and an interaction between the three factors F(1, 56) = 6.55, p = .013, ηp2 = .105, MSE = 37.87, again there was no significant effect of Exposure Condition or other two-way interactions (largest F(1, 56) = 2.97, p = .090, ηp2 = .050, MSE = 97.54 for the Exposure Condition × Conditioned Stimulus interaction). Inspection of the descriptive statistics in Table 2 suggests again that the significant 3-way interaction stems from the fact that for the groups conditioned with BX there was a tendency for the Blocked exposure group to show a smaller decrease in lick cluster size across conditioning than the Intermixed exposure group, while for the groups conditioned with Y this pattern was reversed. A separate ANOVA conducted on the groups conditioned with BX revealed only a significant main effect of trial, F(1,28) = 15.47, p < .001, ηp2 = .356, MSE = 50.55, and no significant effect of Exposure Condition or Trial × Exposure Condition interaction (largest F(1, 28) = 2.00, p = .168, ηp2 = .067, MSE = 50.55 for the Trial × Exposure Condition interaction), while the analysis performed on groups conditioned with Y revealed a main effect of Trial, F(1,28) = 63.29, p < .001, ηp2 = .693, MSE = 25.19, and a Trial × Exposure Condition interaction F(1,28) = 5.92, p = .022, ηp2 = .175, MSE = 25.19, but no significant main effect of Exposure Condition F(1,28) = 2.46, p = .128, ηp2 = .081, MSE = 62.47.

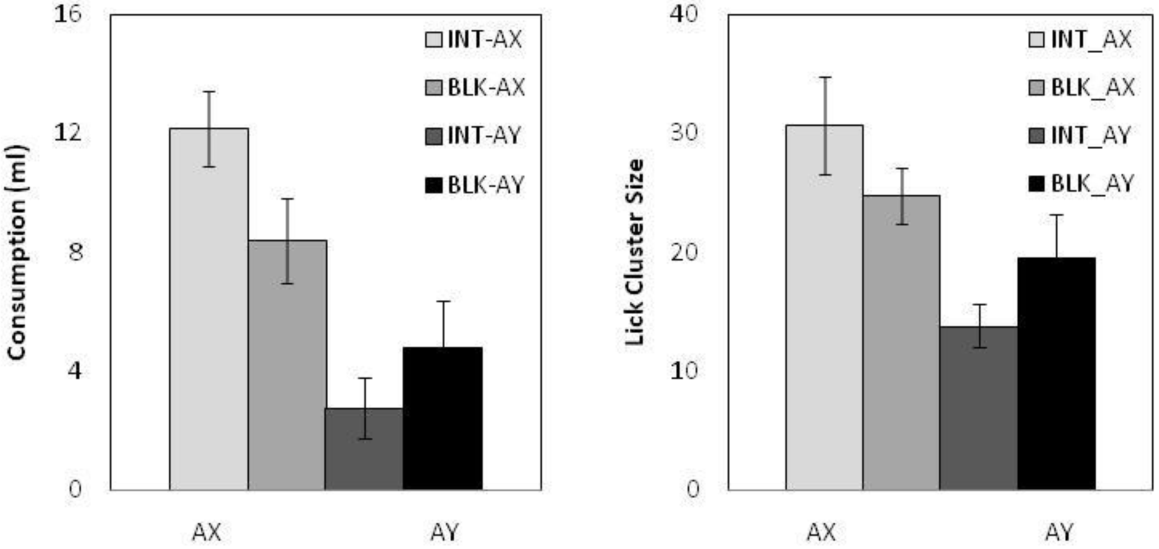

Figure 6. Experiment 1: Mean (±SEM) consumption (left-hand panel) and mean lick cluster size (right-hand panel) during test trials with AX and AY. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. AX groups received conditioning to BX compound and tested AX compound, while AY groups received conditioning to Y compound and tested AY compound.

Figure 6 depicts consumption and lick-cluster sizes for the test trial with AX and AY. Inspection of the left-hand panel shows that rats in group INT-AX consumed more AX than those in BLK-AX. There was, however, no difference in consumption to AY between groups INT-AY and BLK-AY; with consumption of AY being lower than AX. Inspection of the right-hand panel reveals that the lick-cluster sizes paralleled those for consumption, with these sizes being larger in group INT-AX than in group BLK-AX (and larger in group BLK-AY than INT-AY). As we shall see, however, the sole statistically significant effect involving lick cluster size was the nature of the test stimulus (AX versus AY).

ANOVA conducted on the consumption scores revealed an effect of Test Stimulus (AX or AY), F(1, 56) = 23.86, p < .001, ηp2 = .299, MSE = 26.51, an interaction between Exposure Condition and Test Stimulus, F(1, 56) = 4.78, p = .033, ηp2 = .079, MSE = 26.51, but no effect of Exposure Condition (Intermixed or Blocked), F(1, 56) = .42, p = .520, ηp2 = .007, MSE = 26.51. A t-test conducted on the AX consumption scores revealed significant differences between groups INT-AX and BLK-AX, t(28) = 1.99, p = .056, d = -0.73. There was no significant difference between the AY consumption scores in groups INT-AY and BLK-AY, t(28) = 1.09, p = .283, d = 0.4.

A parallel analysis of the lick-cluster scores revealed only a main effect of the Test Stimulus (AX versus AY), *F*(1, 56) = 12.36, *p* < .001, η_p^2 = .181, MSE = 148.83, with no effect of Exposure Condition (Intermixed or Blocked), *F*(1, 56) < 0.01, *p* = .970, η_p^2 < .001, *MSE* = 148.83, and no interaction between Exposure Condition and Test Stimulus, *F*(1, 56) = 3.42, *p* = .070, η_p^2 = .058, *MSE* = 148.83.

Discussion

Experiment 1 demonstrated that manipulating the arrangement in which compound tastes (AX and BX) are presented (rapid Intermixed or Blocked) can modulate the generalization of a conditioned aversion. When discrimination involved conditioning an aversion to BX and testing AX, Intermixed exposure reduced generalization to AX to a greater extent than Blocked exposure. However, when the procedure involved conditioning an aversion to Y and testing AY, we found no advantage of either group in discrimination. Furthermore, both measures, consumption and lick cluster size, showed effects of conditioned stimulus type (BX or Y) and trial, but only consumption showed the main effect of exposure type on generalization assessment. This latter finding may suggest that the two measures in fact reflect different processes (Parker, Limebeer & Rana, 2009). This dissociation will be further explored in the discussion of Experiment 2, where both measures of generalization will be used again.

We have found the I/B effect by using taste compounds and introducing a small amount of water during the ISI, in contrast to Recio et al. (2019) who obtained the reverse pattern of results when using odor/taste compounds. As stated by the latter authors, it is possible for odorous unique element to persist until the next one arrives, allowing an association between them, but when these stimuli are tastes the water in the middle of the trials can remove the remnants from the environment preventing the establishment these associations. Experiment 2 will directly test the latter hypothesis by changing the exposure conditions, with and without water during the ISI, while replicating the reliability of the pattern of results obtained in the INT-AX and BLK-AX groups.

Experiment 2: Classic Test with and without ISI water

In this experiment the INT-W and BLK-W groups received the same treatment as that of the INT-AX and BLK-AX groups in previous Experiment 1. We added two new groups that also received rapid Intermixed or Blocked exposure to AX and BX: INT-N and BLK-N, but they received the 5-min access to water immediately after the second taste compound of the day and nothing during the ISI. This design is summarized in Table 1. For groups INT-W and BLK-W we expect to replicate the results from Experiment 1, that rapid Intermixed preexposure will enhance discrimination between compound tastes after conditioning to BX. However, if water placement was critical in Experiment 1 to prevent the formation of associations between the unique elements, we might expect the INT-N group to generalize the conditioned aversion of BX to a greater extent during test (Dwyer, Burgess & Honey, 2012; Rescorla & Cunningham, 1978). Again, we used two measures of generalization, consumption and lick cluster size.

Method

Subjects and Apparatus

Sixty-four naïve male Lister Hooded rats were used (supplied by Envigo, Blackthorn, U.K). The rats were housed and maintained in the same way as Experiment 1. Their mean ad libitum weight was 296g (range: 260-325g) when the water-deprivation regimen began. The Apparatus was the same as that used in Experiment 1. The stimuli were solutions of 2% sucrose and .9% salt (which served as A and B counterbalanced), and 0.000015M quinine (which served as X). These tastes were combined to create the two compounds (AX and BX) in a way that maintained their concentrations.

Procedure

The rats were divided into 4 groups (ns = 16: INT-W, BLK-W, INT-N, and BLK-N). The 2-day water deprivation schedule was the same as in Experiment 1. On the subsequent 4 days rats received exposure to AX and BX at 10:00 and 30-min access to water at 16:00. Rats in groups INT-W and BLK-W received the same treatment as groups INT-AX and BLK-AX in Experiment 1. The INT-N and BLK-N groups receive the same training as their W-subscripted namesakes, with the exception that they did not receive water in the 5-min intervals between the flavor compound presentations on a given day, but rather in the 5-min period that immediately followed the second compound presentation on each day.

Rats received conditioning trials on Days 5 and 7 and recovery days on Days 6 and 8. On conditioning trials, rats received 30-min access to 15 ml of BX immediately followed by an injection of 0.15 M LiCl at 10ml 1% of b.w. On the recovery days, rats received access to water for 30 min at 11:00. At 11:00 on the next 6 days (Days 9-16), rats received access to AX for 30 min, and in the afternoon they received 30-min access to water. The analysis that follows again focuses on consumption and lick-cluster sizes during conditioning with BX and the tests with AX. The analysis of lick microstructure during conditioning and testing followed reported protocols (e.g., Dwyer, 2012; Patitucci et al., 2016).

Results

During the exposure phase, rats in groups INT-W, BLK-W, INT-N and BLK-N consumed 4.52, 4.34, 5.30, and 5.57ml, respectively, of the AX solution and 4.64, 4.39, 4.90, and 5.53ml, respectively, of the BX solution. ANOVA revealed an effect of Water Placement (W versus N), F(1, 60) = 18.11, p < .001, ηp2 = .232, MSE = 23.3, presumably because of the effect of water consumption prior to the second solution presented each day in the INT-W and BLK-W groups. As expected, there was no significant effect of Exposure Schedule (Intermixed or Blocked) or no effect of Solution (AX versus BX), nor any significant interactions (largest F(1, 60) = 2.75, p = .102, ηp2 = .044, MSE = 3.54, for the Exposure Condition × Water Placement interaction).

The levels of consumption and lick clusters sizes during the BX conditioning trials are shown in Table 3. Inspection of the table shows that the consumption of BX decreased between the two conditioning trials in the four groups, with some evidence that the reduction was somewhat greater in the groups given water between presentations than the groups that did not. There was also a reduction in lick cluster size between the two trials, with an indication that lich cluster size was smallest on the second trial in group INT-W. An ANOVA conducted on the consumption scores with Exposure Condition (Intermixed or Blocked), Water Placement (W or N), and Conditioning Trial (1 or 2) as factors revealed a main effect of Conditioning Trial, F(1, 60) = 35.43, p < .001, ηp2 = .371, MSE = 7.79, but no other significant main effects or interactions (largest F(1, 60) = 3.05, p = .086, ηp2 = .048, MSE = 7.79, for the Conditioning Trial × Water Placement interaction). A parallel analysis of the lick cluster size revealed main effects of Conditioning Trial, F(1, 60) = 14.94, p < .001, ηp2 = .199, MSE = 111.41, and Water Placement, F(1, 60) = 5.00, p = .029, ηp2 = .077, MSE = 148.68, but no other significant main effects or interactions (largest F(1, 60) = 3.77, p = .057, ηp2 = .059, MSE = 111.41, for the Conditioning Trial × Water Placement × Exposure Condition interaction).

Group	Trial 1				Trial 2			
	Consumption		Lick cluster size		Consumption		Lick cluster size	
INT-W	10.83	(0.25)	34.62	(2.93)	6.92	(0.75)	21.16	(1.80)
BLK-W	10.92	(0.30)	29.6	(1.76)	7.23	(0.97)	28.81	(3.17)
INT-N	10.01	(0.68)	34.3	(2.48)	8.36	(0.72)	27.92	(2.63)
BLK-N	11.08	(0.24)	39.73	(3.37)	8.58	(0.70)	31.51	(3.61)

Tabla 3. Mean (+SEM) consumption and lick cluster size on the conditioning trials in Experiment 1. Note: Consumption is measured in ml and lick cluster size in licks per bout. Conditioning trials for all groups were with BX.

Figure 7 shows the results of principal interest from Experiment 2. This figure shows the consumption scores (left-hand panel) and lick-cluster sizes (right-hand panel) for AX across three, 2-test blocks. Inspection of the left-hand panel shows that rats in group INT-W consumed more than those in BLK-W, and it also suggests that – if anything – the opposite difference is evident in groups INT-N and BLK-N. In contrast, inspection of the right-hand panel reveals that there no marked or consistent differences in lick-cluster sizes between the groups.

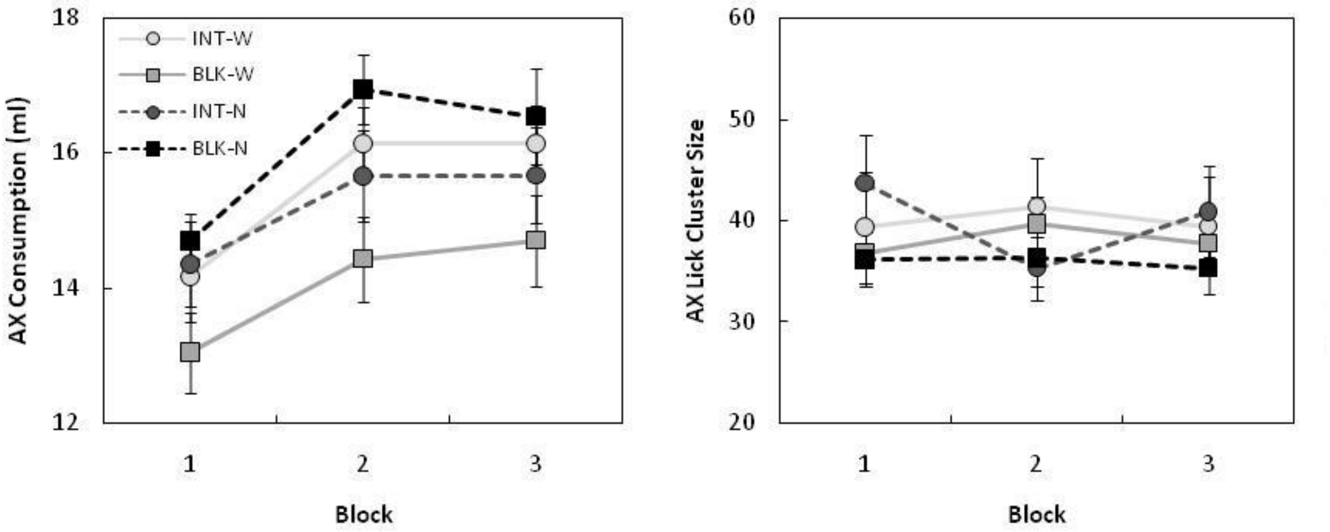

Figure 7. Experiment 1: Mean (±SEM) consumption (left-hand panel) and mean lick cluster size (right-hand panel) during test trials with AX. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. W groups received water between the stimuli presentation while N groups received water after the stimuli presentation.

ANOVA conducted on the consumption scores revealed main effect of Test block (1-3), F(2, 120) = 22.14, p < .001, ηp2 = .27, MSE = 2.82, and critically, an interaction between Exposure Condition and Water Placement, F(1, 60) = 4.80, p = .032, ηp2 = .074, MSE = 12.66; but no significant effects of Exposure Condition (Intermixed or Blocked), F(1, 60) = 0.33, p = .565, ηp2 =.006, MSE = 12.66, Water Placement (W or N), F(1, 60) = 2.85, p = .097, ηp2 = .045, MSE = 12.66, or other interactions (Test block × Water Placement, F(2, 120) = 0.16, p = .849, ηp2 = .003, MSE = 2.82; Test block × Exposure Condition, F(2, 120) = 0.04, p = .959, ηp2 < .001, MSE = 2.82; Test block × Water Placement × Exposure Condition, F(2, 120) = 0.80, p = .450, ηp2 = .0013, MSE = 2.82). Separate ANOVAs were conducted with the W and N groups to follow up the Exposure Condition and Water Placement interaction. For the W groups, the ANOVA revealed a main effect of Exposure Condition F(1, 30) = 4.33, p = .046, ηp2 = .126, MSE = 11.21, confirming greater consumption in INT-W than BLK-W. The main effect of Test block was also significant, F(2, 60) = 9.29, p < .001, ηp2 = .236, MSE = 3.50, but the Test block × Exposure Condition interaction was not F(2, 60) = 0.19, p = .825, ηp2 = .006, MSE = 3.50). For the N groups, the ANOVA revealed a main effect of Test block, F(2, 60) = 14.21, p < .001, ηp2 = .236, MSE = 2.14, but no main effect Exposure Condition, F(1, 30) = 1.17, p = .289, ηp2 = .037, MSE = 14.10, or Test block × Exposure Condition interaction, F(2, 60) = 0.80, p = .454, ηp2 = .026, MSE = 2.14).

A parallel ANOVA conducted on the lick-cluster-size scores (summarized in the right-hand panel of Figure 7) revealed an interaction between Water Placement and Test block, F(2, 120) = 3.46, p = .035, ηp2 = .055, MSE = 51.92, but no effects of Exposure Condition (Alternating or Blocked), F(1, 60) = 0.76, p = .398, ηp2 =.012, MSE = 593.51, Water Placement (W or N), F(1, 60) = 0.10, p = .748, ηp2 = .002, MSE = 593.51, or Test block (1-3), F(2, 120) = 0.238, p = .789, ηp2 = .004, MSE = 51.92, and other interactions were non-significant (Test block × Exposure condition, F(2, 120) = 1.76, p = .176, ηp2 = .029, MSE = 51.92; Water Placement × Exposure Condition, F(1, 60) = 0.09, p = .770, ηp2 = .001, MSE = 593.51; Test block × Water Placement × Exposure Condition, F(2, 120) = 1.34, p = .266, ηp2 = .0022, MSE = 51.92).

Discussion

Experiment 2 replicated the discriminative effect found in Experiment 1, where rapid Intermixed exposure to AX and BX reduced later generalization between AX and BX in contrast to Blocked exposure. However, this effect was only observed when subjects had access to water during the 5 minutes between stimulus presentations. The fact that this effect was eliminated when access to water was delayed after AX and BX presentations is consistent with the assumption that the remaining taste of the former compound tends to establish associations with the latter; and that it promotes increased generalization from BX to AX through the bias of A (and X) to activate B during the test (e.g., Dwyer et al., 2012; Rescorla & Cunningham, 1978). The perceptual learning effect obtained with rapid Intermixed exposure when water was present between presentations reinforces the results found in Experiment 1 (cf. Recio et al., 2018); and the finding that this effect was only evident on one generalization measure (consumption) but not another (lick cluster size; cf. Dwyer et al., 2012) also reinforces the same pattern of results observed in Experiment 1.

Aversive conditioning of a solution has been shown to produce a reduction in both consumption and licking patterns, but when this aversion is associatively activated the behavior is only reduced in the case of consumption (Dwyer et al., 2012). Applying this observation to our results might suggest that any conditioned aversion that was associatively activated in our tests was not susceptible to being measured by licking cluster size, resulting in null differences between groups whether they discriminated or not. However, it is also possible that rapid comparison promotes an associative process during the test that enhances discrimination, which is not observable through lick-cluster size but it is evident through the direct measure of consumption. This associative process could represent the associative activation pattern of unique sub-elements that arise when the subject samples a unitized element during the test, nevertheless, we will elaborate further on this unitization mechanism and how it aids discrimination in the following chapters.

Returning to the SPC problem, we have accepted that the introduction of water between taste compounds is capable of eliminating the possible associations (through residual remnants) between them, allowing perceptual learning to be reflected. However, we have not yet directly measured these suspected associations between stimuli. This chapter final experiment will preexpose only taste elements rapidly in an Intermixed or Blocked fashion, followed by conditioning aversion to one of them and measuring its generalization to the other. We expect that the absence of water between trials would promote associations between the elements in Intermixed exposure, reflecting more aversion at the non conditioned element in test. Because unfortunately, the lick-cluster size is not able to show evidence of sensory preconditioning, we will dispense with this measure in this experiment.

Experiment 3: Taste measure of Sensory Preconditioning

The design for Experiments 3 is summarized in Table 1. We are going to present taste stimuli in rapid succession, after which one of them is going to be aversively conditioned and the other tested. For this procedure the ISI was changed to presumably 0 and a fixed order was used to induce a direct association from A to B. After conditioning to B, it was carried out a consumption test with A, and the next day a conditioned response test with B, to evaluate the efficacy of aversion establishment. We expect that rapid Intermixed exposure to tastes A and B, rather than Blocked, would allow the formation of excitatory associations between them, so the aversive conditioning to B will reflect a decrease in consumption in A as well, showing the typical sensory preconditioning effect.

Method

Subjects and Apparatus

The subjects were 16 male Wistar rats with a mean ad libitum weight of 534 g (range 482 g – 620 g). They had had previous experience with tastes and aromas but these were different from those used in this experiment. This time rats were individually housed and also tested in transparent plastic boxes measuring 35x22x18 cm, with sawdust for the bedding. They were kept on a 12-h light/dark cycle that began at 8:00 a.m. The stimuli were solutions of 2% lemon juice and .9% salt which served as A and B counterbalanced.

Procedure

The subjects were divided into two groups (INT and BLK) each of eight rats of equivalent weight (INT mean: 532g; BLK mean: 535g). On the subsequent 4 days rats received exposure to A and B at 11:00 and 30-min access to water at 16:00. The presentation of one stimulus lasted 5 min immediately followed by the second stimulus which also lasted 5 min, with no water or gap between them. In the INT group the A presentations always preceded the B presentations, and for the BLK group the A stimulus block always preceded the B stimulus block. Rats received conditioning trials on Days 5 and 7 and recovery days on Days 6 and 8. On conditioning trials, rats received 30-min access to 12 ml of B immediately followed by an injection of 0.2M LiCl at 1.2% of the subject's bodyweight. At 11:00 on the next day 9 rats received access to A for 30 min, and in the final day 10 they received 30-min access to B. The latter B test was conducted to assess whether the aversive treatment had been effective and actually there existed an aversion to generalize. Results from this test showed that two rats (one INT and one BLK), which tested positive for outliers analysis, were unable to establish the aversion, and then they were removed from further analysis of the data. Here and in following experiments we only used consumption as measure of generalization, other details no commented were the same as in Experiment 1.

Results

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes; this was true for both tastes, A and B. In the conditioning phase the consumption of B decreased from the first to the second trial in both groups, consistent with the development of a conditioned aversion. The INT group consumed a mean of 10.4 ml on the first trial and of 5.6 ml on the second. For the BLK group the scores were 10.3 ml and 6.9 ml. A repeated measures ANOVA with Trial and Group as variables showed that the decrease in consumption across trials was significant, $F(1, 12) = 24.23$, $p < .05$, $\eta 2p = 0.67$ and $MSE = 4.82$; neither the Group factor nor the interaction of Group x Trial were significant ($Fs < 1$).

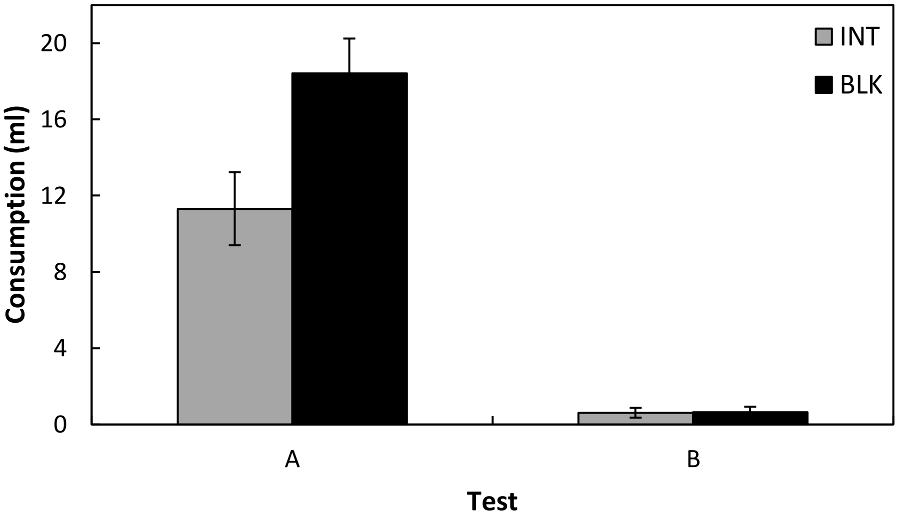

Figure 8. Experiment 3: Mean (±SEM) consumption on separated test trials with A and B. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 8 shows the consumption of A on a first test trial and B on a subsequent conditioned response test. Consumption was less suppressed in the BLK group than in the INT group on the A test, while it was totally and equally suppressed for both groups on the B test. A one factor ANOVA with Group as variable confirmed these impressions showing a significant effect of Group in the A test F(1, 12) = 7.26, $p < .05$, η2p = 0.38, MSE = 24.4, but not in the B test, F(1,12) < 0.01, $p > .05$, η2p < 0.01, MSE = 0.55. The same analysis carried out on difference scores resulting from subtracting the consumption of B from the consumption of A also showed differences between groups, F(1, 12) = 6.35, $p < .05$, η2p = 0.35, MSE = 27.79.

Discussion

In this Experiment 3 we changed the ISI to presumably 0 sec, implying no water between stimuli, in order to directly assess the establishment of possible excitatory associations between taste unique elements that may influence perceptual learning via the SPC. After a rapid Intermixed or Blocked exposure to two stimuli, taste B was aversively conditioned and the generalization of aversion was measured in the test of A, finally the level of aversion to B was assessed. Results showed more suppression in the consumption of A for the Intermixed group than for the Blocked, but respectively both groups showed the same level of aversion to B. Therefore, we can reason that Intermixed rapid preexposure have promoted the establishment of associations between taste stimuli, leading afterwards to great generalization of the B aversion to A through these associations, reflecting a sensory preconditioning effect. Finally, we can conclude that sensory preconditioning may influence the development of perceptual learning, in particular if the exposure is rapid and alternating, and the stimuli tastes. However, if the SPC is controlled, for example by introducing water or some cleaner of the remnants of the previous stimulus, the perceptual learning effect may emerge.

General Discusion

Contrary to results in humans, procedures with rapid exposure to similar stimuli have generally found that animals discriminate worse after Intermixed presentations, which allow close comparison, than after Blocked presentations. The absence of perceptual learning in animals when rapid comparison is promoted has been explained by sensory preconditioning. This effect promotes the generalization of responses between previously associated neutral stimuli. In the case of rapid exposure procedures, the rapid alternation between similar stimuli will facilitate their association, so that when one is conditioned, the other will also generate the respective conditioned response.

This has been clearly seen in procedures with visual stimuli, but is less clear in those with sapid stimuli. For example, Lavin (1976) found no sensory preconditioning when the interval between stimuli was less than 9 seconds, yet many of the perceptual learning experiments " failed by SPC" use longer intervals (e.g., Recio et al. 2019). In this chapter we have proposed that the rapid succession of these stimuli could leave flavor traces in the environment that make it possible for subjects to sample the incoming stimuli as a whole, facilitating the formation of excitatory associations between them and subsequently impairing the discrimination.

In Experiments 1 and 2 we have used the same designs as Recio et al. (2018; 2019) changing the use of odors as unique elements to tastes. In this case, the introduction of water in the middle of the rapid stimulus presentation was effective in eliminating taste remnants and presumably prevented excitatory associations between the unique elements. Thus, in Experiment 1 using the classical test we obtained better discrimination between BX and AX after rapid Intermixed than Blocked exposure, although we found no difference when using the AY superimposition test. In Experiment 2, we repeated the classical test procedure, but this time we added two new INT and BLK groups without water between trials. The I/B effect was replicated again when water was placed in the middle of the stimuli, but it was eliminated when there was absence of ISI water. These results endorse the idea that taste stimuli form excitatory associations between them during rapid Intermixed exposure, unless there is water between trials to eliminate the remnants from the environment. Furthermore, Experiment 3 directly assessed the existence of these excitatory associations, presenting successively taste elements without ISI water. After rapid Intermixed or Blocked exposure, taste A was aversely conditioned and then consumption of B taste tested. Results showed that A consumption was more suppressed after Intermixed preexposure than after Blocked, supporting that actually this exposure leaded to the establishment of excitatory associations between both through which the conditioned aversion was generalized.

Moreover, in Experiment 1 and 2 we additionally used a lick cluster size measure of aversion. This measure has been used previously for sensory preconditioning analysis (Dwyer et al., 2012), but this is the first time it has been carried out in a perceptual learning procedure. Interestingly, our results have shown that when rats received pairings of BX with LiCl during conditioning, two changes occurred: subsequent presentations of BX resulted in reduced consumption and reduced lick cluster size (the same occurred in Experiment 1 with Y). However, the differences in discrimination found by the consumption measure were not significant in the analysis of lick cluster size, even though as related measures they followed the same pattern. There is some evidence that these different behaviors in aversive conditioning are dissociable. For example, if rats receive a sensory preconditioning procedure in which BX is first exposed and then X is paired with LiCl, the reduction in consumption of X generalizes to B, but the reduction in lick cluster size does not (Dwyer et al., 2012). Again, this is interesting because it suggests (cf., Rescorla, 1988) the need for models of Pavlovian conditioning and higher-order conditioning to provide a more sophisticated analysis of the translation of (associative) learning into different forms of conditioned behaviors (see Honey et al., 2020; Honey & Dwyer, 2021; 2022).

Ultimately, the question remains why we could not replicate the I/B effect obtained by Recio et al. (2018) with the superimposition test. It could simply be that our procedure was not sensitive enough to find differences between groups, or even that this type of test is more effective with compound stimuli with different sensory modalities (e.g., see Westbrook, Homewood, Horn, & Clarke, 1983 for an example of the odor-taste potentation effect). Another possibility is that water was not effective in removing the odorous unique elements in the Intermixed group of Recio et al. (2018), so A and B got associated and activated later at test. Therefore, A could activate associatively B during the AY test and that might interfere to a greater extent with the aversion activated by Y. In any case, we will replicate the Recio et al. (2018) superimposition procedure with odor/taste compounds in the next chapter, and discuss these possibilities in the General discussion section. The next chapters will focus on the mechanism underlying the close comparison process, the short-term habituation of the common elements and the processing bias towards the unique elements, and their effect on the properties of the stimuli which improves discrimination.

CHAPTER V - UNIQUE ELEMENTS

Introduction

Perceptual learning refers to the improvement in discrimination between similar stimuli that occurs because of mere exposure to them. Furthermore, Gibson (1969) suggested that the opportunity to compare these stimuli would enhance this process and, accordingly, a wide range of experiments has been conducted to assess the role of comparison in perceptual learning. What has been found is that similar stimuli exposed in an Intermixed manner are better discriminated later than the same stimuli exposed in separate blocks. This is known as the Intermixed/Blocked (I/B) effect, which has been consistently demonstrated in animal studies using procedures with widely spaced stimulus presentations (e.g., Symonds and Hall, 1995).

One of the first proposals to explain this effect was introduced by McLaren and Mackintosh's model (2000). Initially, these authors explained that simple exposure to similar stimuli, e.g. AX and BX, would promote the formation of intra-compound excitatory connections (A-X and B-X) (McLaren, et al. 1989), but additionally, in the McLaren & Mackintosh model (2000), they added that Intermixed exposure would also develop reciprocal inhibitory connections between the unique elements of the stimuli (A B and B A). That is, when AX is present, the common element X will associatively activate through the intra-compound connections the absent unique element B, promoting to the formation of an inhibitory association from A towards B, as A element signals the absence of B (and vice versa on BX trials). As a result, less generalization of the conditioned response is expected in the test after Intermixed than Blocked preexposure, as one unique element inhibits the other.

Years later, Hall's (2003) model takes the associative activation of the unique elements from another perspective to explain the spaced I/B effect. First, this model assumes that repeated exposure, such as during the preexposure phase, leads to a habituation of all stimuli and their elements, resulting in a reduction of their effective salience. However, the Intermixed exposure changes the unique element on each trial, inducing uncertainty in the subject, which through associative activation increases the perceived salience of this element for subsequent presentations, counteracting habituation. Consequently, Intermixed exposure maintains the salience of unique elements relatively higher compared to that of the common ones, which reduces the generalization between the similar stimuli in posterior discrimination tests.

These two models are successful, because they are able to explain most of the results observed in non-human animal studies (see for a review Mitchell & Hall, 2014), they are not incompatible with each other (Artigas et al., 2006) and both are based on the associative activation of the unique elements in their absence. The next step was to assess the generality of these models, for which a series of studies with humans as subjects were initiated. For example, Mundy et al. (2007) preexposed their participants to Intermixed or Blocked pairs of similar faces with a short ISI (1-2 seconds), 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 faces were discriminated more accurately than the Blocked faces, obtaining the typical I/B effect. Similar to this finding by Mundy et al. (2007), there is ample evidence that humans can also benefit from Intermixed presentations (e.g., Lavis et al., 2011 with checkerboards as stimuli).

However, although human rapid discriminative enhancement resembles the comparison process suggested by Gibson (1969), it is complex to fit it into the theories used to explain the I/B effect in animals. The fact that exposure in human experiments occurs rapidly, with seconds of ISI, avoids the possibility that unique elements become inactivated and may return in the next trial by associative activation. Therefore, and based on Honey and Bateson's (1996) mechanism, Mundy et al. (2007)

explained that the rapid Intermixed presentation of similar stimuli causes their common elements to undergo short-term habituation and thus processing resources are biased in favor of the unique elements. This bias encodes well-defined representations of the unique elements in memory, which when retrieved on the test will facilitate their discrimination. Supporting this, Dwyer et al. (2011) found that the introduction of a distractor between stimuli reduced the discriminative advantage of Intermixed over Blocked exposure, as, they explained, this presentation disrupted the short-term habituation and eliminate the processing bias.

The introduction of a rapid comparison mechanism in humans and the fact that animals had demonstrated poor performance with rapid preexposures (see Chapter 1 - The problem with Sensory Preconditioning) led some authors to claim that only humans could benefit from comparison, and even that perceptual learning develops different mechanisms depending on the species (Mitchell & Hall, 2014). To assess whether this idea of comparison was uniquely human, Recio et al. (2018) developed a rapid procedure similar to that of Dwyer et al. (2011) to assess perceptual learning in animals. As mentioned previously, this procedure exposed similar tastes in a rapid fashion to rats, after which a novel element, Y, was aversively conditioned, and the generalization of this aversion to a compound, AY, was measured in a test. This type of test had been used in other animal studies with spaced procedures before, and it has been shown able to evidence differences in discrimination between preexposure groups (Blair & Hall, 2003a). In the case of Recio et al. (2018) rapid procedure, they not only obtained the basic I/B effect, but also they found that this was eliminated with the introduction of a distractor between the preexposed stimuli, replicating the results found by Dwyer et al. (2011) in humans.

Following the previous authors, Recio et al. (2018) explained their animal results as well in terms of short-term habituation of the common element, and proposed that the consequent bias of processing towards the unique elements also increase their unitization (McLaren & Mackintosh, 2000). According to

Recio et al. (2018) the processing bias on Intermixed exposure would increase the likelihood that a greater number of subelements, which, for example, form the unique element A on AX trials, could be sampled together, increasing the formation of excitatory associations between them. These associations increase the unitization of the unique element A, developing a complete well-defined representation of this element in memory. As a consequence, any sampled subelement of A on the discrimination test will associatively prime the rest of its representation and reduce the generalization to other similar stimuli.

It must be acknowledged that, paradoxically, while this unitization mechanism is expected to increase the discrimination between similar stimuli, it will also decrease the effective salience of the unique elements as well, which is the opposite that salience models propose with spaced procedures. The classic model of McLaren et al. (1989) explains that a unitized element forms strong connections between its sub-elements, but also forms them in parallel with the context, which generates latent inhibition and reduced the associability of the element. Recently, in line with McLaren et al. (1989) but using terms from Hall's model (2003), Ballesta et al. (2021) suggested that the active representation of a unitized element would resemble so closely the actual presented element, in other words, the internal input coincides with the external input, that the value of the subjects' discrepancy would approach zero and, consequently, the perceived salience of this element would decrease. Few experiments have found evidence of this unitization mechanism in animals, and have shown reduced salience and associability of unique elements after Intermixed exposure with short ISI (see for taste aversion preparations Artigas et al., 2012; and for appetitive preparations Ballesta et al., 2021).

Our following experiments are aimed to expand the evidence in animals of the mechanism of unitization of the unique elements after rapid Intermixed exposure, which resembles the comparison process suggested by Gibson (1969). To assess this, we conducted three experiments with rats using a preexposure procedure involving short interstimulus intervals (ISI) and odorous/taste stimuli.

Experiment 1 aimed to assess the discriminability of the unique elements with the superimposition test and replicate the I/B effect obtained by Recio et al. (2018, Experiment 1). The remaining two experiments were designed to measure the effectiveness of the unique elements, either directly by measuring their subsequent associability with a conditioned aversion (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 or interfering with a conditioning 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).

Experiment 1: Superimposition Test

This experiment is a replication of Experiment 1 of the study by Recio et al. (2018), the design of which is summarized in Table 4. In this study, we used a short ISI preexposure procedure and an external inhibition test to measure the I/B effect (see also Blair & Hall, 2003a). 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 two 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).

EXPERIMENT	Group	Preexposure	PC	Conditioning	Test
1	INT	AX/W/BX	—	Y+	AY?
	BLK	AX/W/AX			
2a & 2b	INT	AX/W/BX	—	AY+	A?
	BLK	AX/W/AX			
3	INT	AX/W/BX	—	AY+	Y?
	BLK	AX/W/AX			

Table 4. INT refers to Intermixed preexposure, BLK refers to Blocked preexposure. W means water. A and B are hazelnut and caramel aromas (counterbalanced). X is salt solution. Y was acid for Experiment 1 and strawberry aroma for Experiment 2-3. The "+" indicates an intraperitoneal injection of LiCl; "/" indicates rapid succession of stimuli within the same session. Note: during preexposure INT group also experienced trials in which BX preceded AX, and BLK group experienced trials in which both flavors were BX.

On the basis of previous findings, we expected to find less generalization of the aversion in the Intermixed group, i.e. a higher consumption of AY than the Blocked group in the test phase. After rapid Intermixed exposure the unique element A would be highly unitized, thus, sampling any subunit of A on the test will associatively prime the rest and easily activate this well-defined representation, reducing its similarity with Y and hence interfering to some extent with the conditioned response.

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 332g (range 300g-370g), while the mean ad libitum weight of the second batch was somewhat lower, 304 g (range 283g-345g). The rats were housed individually in transparent plastic boxes measuring 35x22x18 with sawdust for the bedding. They were maintained on a 12h 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 (9g / 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 / L solution of citric acid. For conditioning, 0.15M intraperitoneal injections of LiCl were administered at 1% of the subject's body weight.

Procedure

All the procedures used were approved by the Ethical Committee for Animal Experimentation (CEEA) of the University of Granada, number 06/06/2019/099, and were 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 8 rats with equivalent weight and consumption (mean INT weight: 330g and BLK: 333g), while rats from the second batch were divided into two groups (INT and BLK) of 8 rats, also with equivalent weight and consumption (mean INT weight: 301g and BLK: 307g). Access to water was restricted for all rats, and they could only drink on two 30-minute 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 four 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 two days and the other compound on the last two days. The order of presentation of the stimuli was counterbalanced for both groups during the four 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 four 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. When this measure was lost due to emptying of the tubes or blockage of the nozzle, the group mean was used to replace this data. General linear model null hypothesis testing analyses were conducted, adopting a rejection level of $p < 0.05$, and Greenhouse-Geisser corrections were used when needed. Partial eta squared (η2p) and Cohen's d were used to report effect sizes. Within-group factors were analyzed using repeated-measures 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, where outliers are values more than 1.5 times the interquartile range from the quartiles, that is, either below $Q1 - 1.5$ IQR, or above $Q3 + 1.5$IQR. The JASP 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 repository on the Open Science Framework (OSF). https://mfr.osf.io/render?url=https://osf.io/u6qfp/?direct%26mode=render%26action=download%26mode=render

Results

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes, both the flavored compounds and water. In the conditioning phase, the consumption decreased for the INT group from 8.69ml to 6.12ml, and for the BLK group from 8.77ml to 6.23ml. 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. A repeated-measures ANOVA with Trial, Group, and Batch as factors showed differences across trials, $F(1, 27) = 57$, MSE = 1.7, $p < .05$ and η2p = .68 and differences between batches $F(1, 27) = 6.2$, MSE = 2.04, $p < .05$ and η2p = .19. Neither the Group factor nor interactions were significant (largest effect Trial x Batch, $F(1, 27) = 1.26$, MSE = 1.7, $p > .05$ and η2p = .04).

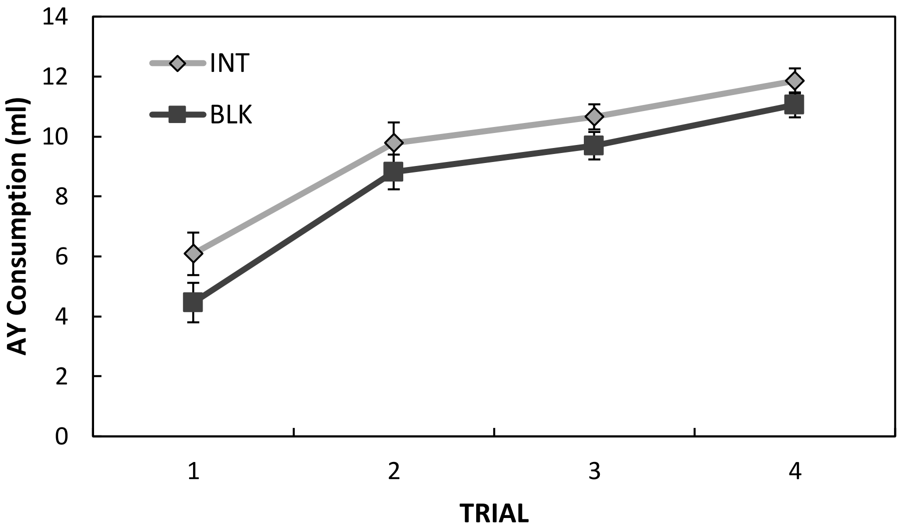

Figure 9. Experiment 1: Average direct consumption (±SEM) of AY in test phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 9 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 and η2p = .77, significant effect of Group*, F*(1,27) = 4.36, MSE = 11.28, *p* < .05 and η2p = .14 and interaction Trial x Batch *F*(3,81) = 3.7, MSE = 2.53, *p* < .05 and η2p = .12. Neither Batch factor nor interactions were significant (All *F*s. < 1). The Trial x Batch 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.

Discussion

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 subelement will retrieve the others, and A will be more likely to interfere with the response elicited by the separately conditioned Y stimulus on the AY test (Recio et al., 2018).

In parallel, using a very similar external inhibition procedure but with a long interval between presentations of two similar stimuli (several hours), Blair and Hall (2003a) 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). Contrary, 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. Conversely, 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 and 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 obtained after rapid comparison, we will measure the effective salience of the unique element A after rapid Intermixed and Blocked exposure to AX and BX in the following experiments. As it is assumed that a salient stimulus also implies high associability, we will directly condition element A after the preexposure phase in Experiment 2 to assess its level of associability, and thus its salience.

Experiments 2a & 2b: Direct Conditioning Assessment

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 4. In Experiment 2b, we aimed to increase the sensitivity of our procedure for detecting differences in conditioning.

Rapidly Intermixed exposure of two similar stimuli should habituate in the short term the elements they have in common and free up resources to better process those that are unique. This bias should result in more unique sub-elements sampled and associated together, i.e. greater unitization of the unique element. As a consequence, this should decrease the element salience, by reducing the discrepancy between external and internal inputs, and increase its latent inhibition due to the unitization with the context as well (McLaren et al., 1989; McLaren & Mackintosh, 2000). In this case, we expect that the unique element A conditioning would be less effective following rapid 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 213g-264g). 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: 242g and BLK: 236g). 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 10ml 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. Figure 10 shows consumption during the conditioning phase. Decrease in consumption of A developed slowly from Trial 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 and η2p = .35. Neither the Group factor nor the interaction were significant (largest *F*(1, 30) = 1.62, *p* > .05, MSE = 6.34 and η2p = .05).

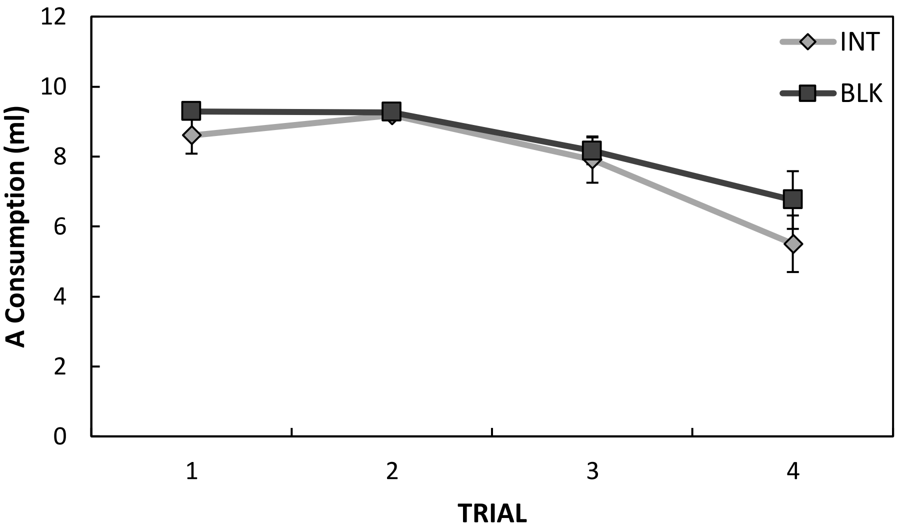

Figure 10. Experiment 2a: Average consumption (±SEM) of A in conditioning phase trials. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 11 shows the consumption of A during the four test days, where the INT group showed higher consumption than the BLK group until the 4th 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 and η2p = .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 and η2p =.05).

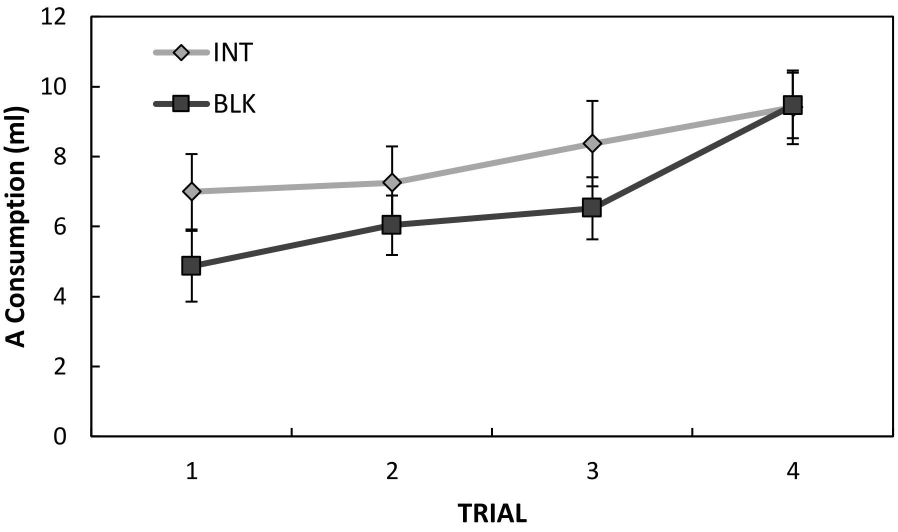

Figure 11. Experiment 2a: Average consumption (±SEM) of A in test phase during extinction trials. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure

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. 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 we therefore decided to extend preexposure from 4 days to 10 with the aim of producing a more marked effect on the unique elements. Moreover, to increase the sensitive, the conditioning phase was extended by one day, the element A was presented ad libitum during this phase, and half the dose of lithium was used.

Experiment 2b

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 310g-380g), while the weight of the second batch was somewhat higher, 455 g (range 400g-550g). 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 8 with equivalent weight and consumption (mean INT weight: 336g and BLK: 338), while those from the second batch were divided into two groups (INT and BLK) of 9, also with equivalent weight and consumption (mean INT weight: 456g and BLK: 453g).

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. Figure 12 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 and η2p =.43. Neither the single factors nor interactions were significant (largest effect Trial x Group x Batch *F(*2.1, 62.8) = 1.66, *p* > .05, MSE = 8.77 and η2p =.05).

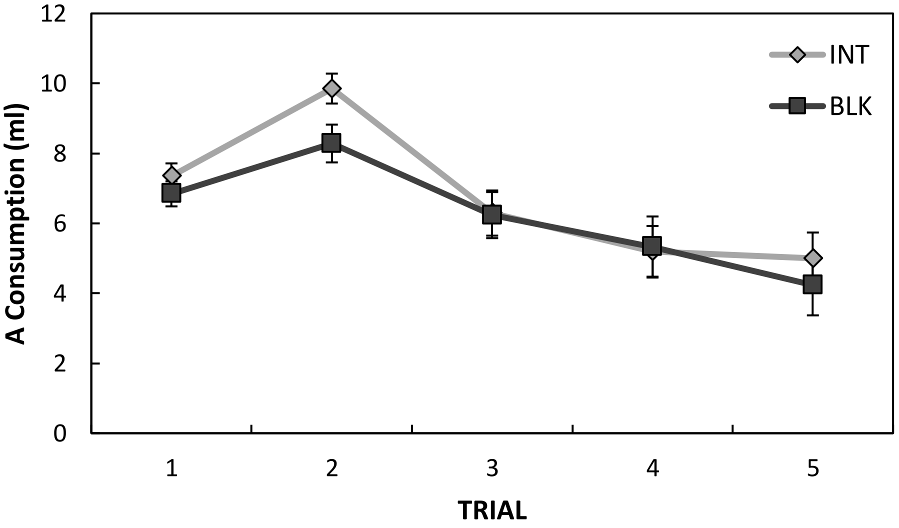

Figure 12. Experiment 2b: Average consumption (±SEM) of A in conditioning phase trials. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 13 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 and η2p =.43; Group *F(*1, 30) = 5.49, *p* < .05, MSE = 31.05 and η2p =.15 and Batch *F* (1, 30) = 9.26, *p* < .05, MSE = 31.05 and η2p =.24. The interaction between Trial and Group was also significant *F(*3, 90) = 3, *p* < .05, MSE = 2.02 and η2p =.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 and *d* =.85, test 3 *t*(32) = 2.59, *p* < .05 and *d* = 0.89, and Test 4 *t*(32) = 2.02, *p* = .05 and *d* = .69. No other interactions were significant (largest effect Group x Batch *F(*1, 30) = 2.07, MSE = 31.05, *p* > .05 and η2p =.06).

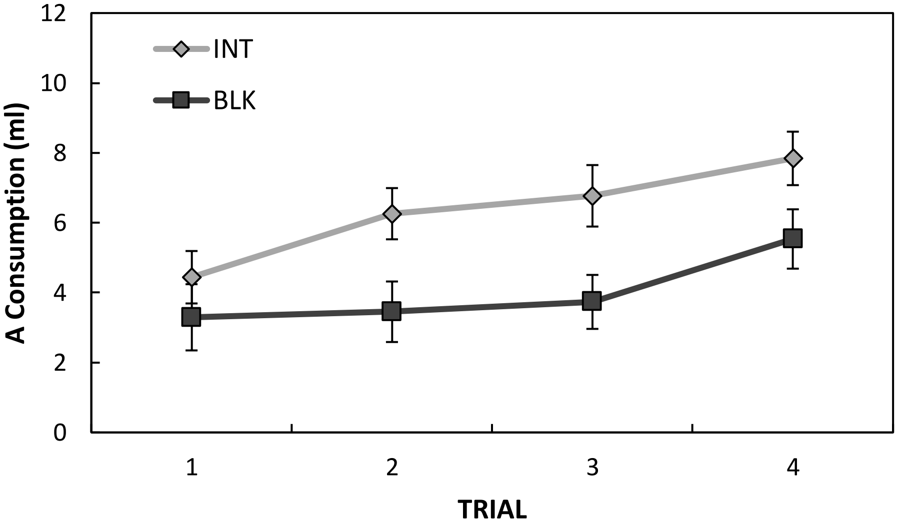

Figure 13. Experiment 2b: Average consumption (±SEM) of A in test phase during extinction trials. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure

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 and η2p = .4 and Batch *F(*1, 32) = 7.81, *p* < .05, MSE = 36.86 and η2p =.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 US 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). Because of 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., see Mondragón & Murphy, 2010 for an assessment of the common elements salience).

Experiment 3: Overshadowing Test

The design of this experiment is shown in Table 4. 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.

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 354g (range 307g-420g). 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: 357g and BLK: 350g). Following the same preexposure as in Experiment 2a, 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 2a.

Results

During the preexposure phase, the rats consumed virtually all the liquid available in the tubes. The AY consumption decreased throughout the two conditioning trials for INT group from 8.33ml to 4.44ml and for BLK group from 9.26ml to 4.56ml. 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, η2p = .5. Neither the Group factor nor the interaction Group x Trial was significant (*F*s < 1)

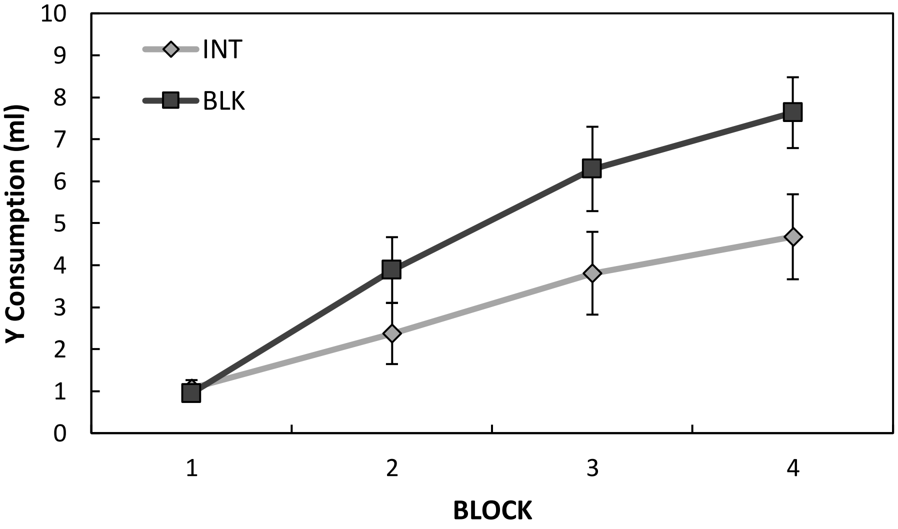

Figure 14. Experiment 3: Average consumption (±SEM) of Y in test phase compiled in blocks of 2 trials. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 14 presents the group mean scores for consumption of Y over four 2-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, η2p = .6; and an interaction Block x Group *F(*2.2, 64.8) =3.54, *p* < .05, MSE = 5.79, η2p = .1, but not effect of group *F(*1, 30) = 3.5, *p* > .05, MSE = 26.8 and η2p =.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.

Discussion

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 2b, 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

The I/B effects found from studies with human and non-human subjects using a short interval between presentations of two similar stimuli have been explained in terms of a processing bias of the unique elements due to a process of short-term habituation of the common ones during the Intermixed exposure (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, added that this processing bias favors the unitization of the unique elements. Thus, after Intermixed preexposure, the unique elements of the stimuli will be better represented in memory and can therefore be better discriminated when later presented at test with similar stimuli. Furthermore, following the model of McLaren et al. (1989), Recio et al. (2018) predict a lower salience and increased latent inhibition of these elements, making it more difficult for these elements to enter into new associations. 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 non-human animals.

Experiment 1 is a replication of Recio et al.'s (2018) Experiment 1 to reinforce the I/B effect found with an external inhibition test and odor/taste stimuli. After rapid 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; Wagner, 2003; Recio et al., 2018). 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, these two last findings suggests that A is rendered less effective by the rapid Intermixed exposure.

It should be noted that the results of Experiments 1 and 2 can be explained in terms of sensory preconditioning as we discussed in the previous chapter. 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 AY. 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 increased interference of A opposed to Y in the AY test and the reduced learning about A during conditioning, 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 intemixed group supports our salience reduction account rather than a sensory preconditioning effect.

It is worth mentioning that, while we agree with Ballesta et al. (2021) on the mechanism that reduce the salience of the unique elements after rapid Intermixed exposure, the results of our Experiment 1 are contrary to those reported by their Experiment 3. To put this in context, they exposed similar tones in rapid Intermixed or Blocked fashion (AX and BX), after which a new tone was conditioned with the arrival of food (Y), finally a preexposed unique element was presented together with the previous conditioned one (AY). Although is basically the same design as our Experiment 1, and that of Recio et al. (2018), these authors found that the Intermixed unique element interfered less with food approaching during the test, meaning that there was more generalization between Y and the AY compound in the Intermixed group. These authors interpreted the Intermixed unique element as being so low salience that it did not interfere with conditioned Y food-seeking behavior, rather than our interpretation that A would be more discriminable and in fact should not generalize this conditioned behavior.

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, their 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.

Lastly, the results presented here are incompatible with previous models such as Hall´s salience modulation model (2003). The rapid succession preexposure used here cannot provide an opportunity for the associative activation of the representation of the unique elements, as this mechanism critically needs a long time lapse to inactivate the elements. In fact, Hall’s model would have problems explaining the distractor effects reported by Dwyer et al. (2011) and Recio et al (2018). According to salience modulation theories (Hall, 2003), the opposite would be expected, the distractor should displace the unique element representation to an inactivate state, and the common element, that wouldn’t be habituated in short-term, 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) reflect the opposite, suggesting that the distractor disrupts short-term habituation of stimulus elements and thus eliminates any processing bias, removing the discriminative advantage in rapid Intermixed exposure.

In conclusion, these findings collectively support the notion that the comparison process in animals is based on the short-term habituation of the common elements and the processing bias towards the unique ones, as proposed by Honey and Bateson (1996). This mechanism enhances the unitization of unique elements, contributing to a great representation of the differential elements between similar stimuli and therefore facilitating the discrimination (Recio et al., 2018). Our results also indicate that, despite being more effective in reducing generalization between stimuli, these unitized elements exhibit lower associability and salience.

On the other hand, the changes in the properties of common elements in this comparison process and how they aid discrimination remain less clear. Returning to Gibson's (1969) theory of differentiation, the improvement in discrimination should be driven by the detection of the unique elements as the common elements are overlooked, reflecting the short-term habituation process, but do these common elements undergo any change during preexposure that aids subsequent discrimination of the stimuli? Exploring the impact on common elements in the rapid Intermixed exposure will be the focus of the next chapter.

CHAPTER VI – COMMON ELEMENTS

Introduction

Perceptual learning can be evidenced as the increased ability to discriminate among similar stimuli after mere exposure to them. This effect can be explained by an increase in the subject's ability to detect differences between the stimuli, by a reduction in attention paid to irrelevant features, or both. That is, successful discrimination between two similar stimuli requires that behavior be controlled by the distinctive features of the stimuli, rather than those features that they will hold in common. As we have seen, depending on the interval between stimuli presentations, Intermixed exposure of the similar stimuli promotes the increase in salience (Hall, 2003) or unitization (Recio et al., 2018) of the unique elements, which later helps the discriminative behavior of the subject.

Conversely, another possible source of this perceptual learning effect is that Intermixed exposure to AX and BX may be particularly effective in reducing the extent to which the common (X) features can acquire or exhibit control over behavior. This issue has been mostly investigated with non-human animal procedures involving long ISI and flavor-aversion learning paradigms. For the most part, however, direct testing of the properties acquired by the common features of the stimuli has revealed only weak evidence for such an effect, and these, have uniformly found that the properties of X, tested after Intermixed presentations of the compounds AX and BX, do not differ from those produced by a Blocked preexposure (Bennett & Mackintosh, 1999; Hall, 2020; Mondragón & Hall, 2002; Rodríguez & Alonso, 2004; 2008).

On the other hand, an effect has been obtained with appetitive conditioning procedures involving short ISI and auditory stimuli. Mondragón and Murphy (2010) rapidly presented their rats with Intermixed or Blocked exposure to compound auditory cues: high and low tones, each presented in combination with a common element, a white noise. The common noise was then trained as a cue for food and subjects' approach to the food tray was measured. Although there were no differences during the acquisition of the appetitive response, the results of an extinction test showed a lower level of approach to the food tray in the Intermixed group than in the Blocked group. These results may indicate either that after Intermixed exposure to auditory compounds the common white noise was less well associated with food during conditioning or that this exposure kept X's associability high and therefore enabled the extinction to proceed more readily (Mondragón & Hall, 2002). However, in a similar study, Ballesta et al. (2021) increased the amount of preexposure to auditory compounds and specifically found slower learning about the common sound during the conditioning phase. This result, added to that of Mondragón and Murphy (2010), rather seems to indicate that the common element is indeed less associable after rapid Intermixed exposure.

Whereas the perceptual learning effects obtained from widely spaced presentations of stimuli appear to be independent of the changes in the effectiveness of common features of the preexposed stimuli, it is possible that such changes do occur and are relevant to the effects obtained when presentations of the stimuli in initial training are closely spaced. As we have examined, the rapid Intermixed exposure to similar stimuli leads to a short-term habituation of the elements they have in common, favoring the processing of the unique ones (Honey & Bateson, 1996). Thus, it is possible that this short-term habituation of common elements develops into long term habituation reducing their effectiveness as Mondragón and Murphy (2010) showed during conditioning (also with longer exposure Ballesta et al., 2021). If so, it should be possible to obtain similar effects with the rapid exposure procedure used by Recio et al. (2018), with which we have previously found evidence for this mechanism.

The aim of the experiments to be reported was to extend the experimental procedure developed by Recio et al. (2018; 2019) to examine the effects of exposure to a pair of similar stimuli on the properties of a feature they hold in common. In the three experiments to be reported rats were given the preexposure to AX and BX flavors according to the procedures used by Recio et al. (2018; 2019), but with tests of the common feature, X. Experiment 1 used a version of the external inhibition test of Recio et al. (2018), with X being tested for its ability to modulate the response controlled by a separately trained cue. Experiment 2, used an overshadowing test, examining the ability of X to modify learning about another cue when the two are conditioned in compound. Experiments 3a and 3b looked simply at the effectiveness of X when trained as an excitatory conditioned stimulus.

Experiment 1: Superimposition Test

Two groups of rats received preexposure to two compound flavor stimuli following the schedule and timing used by Recio et al. (2018, Experiment 1). For one group (labeled INT in Table 5), both of the critical stimuli were presented on a given trial separated by an interval of only 5 min. For the other group (BLK in Table 5) a Blocked schedule was used, with the same flavor (i.e., AX or BX) being presented on both occasions, all presentations of AX occurring in one block of trials and all of BX in another. For these subjects the minimum interval between a presentation of AX and one of BX was 24 hr. Preexposure was followed by flavor aversion conditioning, in which a novel flavor (Y in Table 5) was associated with injections of LiCl. The final test consisted of presentation of the XY compound.

EXPERIMENT	Group	Preexposure	Conditioning	Test
1	INT	AX/W/BX	Y+	XY?
	BLK	AX/W/AX		
2	INT	AX/W/BX	XY+	Y?
	BLK	AX/W/AX		
3	INT	AX/W/BX	X+	X?
	BLK	AX/W/AX		

table 5. INT refers to intermixed preexposure, BLK refers to blocked preexposure. W means water. A and B are hazelnut and caramel aromas (counterbalanced). X is glutamate solution and Y is raspberry aroma. The "+" indicates an intraperitoneal injection of LiCl; "/" indicates rapid succession of stimuli within the same session. Note: during preexposure INT group also experienced trials in which BX preceded AX, and BLK group experienced trials in which both flavors were BX.

The addition of another flavor to one trained as a CS has been shown to attenuate the conditioned response, reducing the observed aversion (Recio et al., 2018). If closely spaced Intermixed preexposure can reduce the effectiveness of the X stimulus, as suggested by the results of Mondragón and Murphy (2010) and of Ballesta et al. (2021), then the attenuation of the aversion produced by adding X to the CS will be less for the INT group than for the BLK group.

Method

Subjects and Apparatus

Subjects were 16 naïve male Wistar rats with a mean ad libitum weight of 393g (range 430g-367g). The rats were housed individually in transparent plastic boxes measuring 35x22x18 cm, with sawdust for the bedding. They were kept on a 12-h light/dark cycle that began at 8:00 a.m. This sample size has proven adequate in the past to detect changes in common element properties following rapid preexposure to compound stimuli with similar procedures and designs (e.g., Ballesta et al., 2021; Mondragón & Murphy, 2010).The sample size in these studies was, as in our case, 8 subjects per group.

All the solutions used were prepared with tap water on the same day as the experimental session and were administered in the home boxes using 50-ml inverted centrifuge tubes with stainless steel ball-bearing-tipped spouts. Consumption was determined by weighing the tubes before and after the sessions. Stimuli AX and BX consisted of a glutamate solution (16.9 g/L) as X with hazelnut or caramel aromas counterbalanced as A and B, at 0.05% of the total volume of the solution. Flavor Y was a raspberry aroma, again as a0.05% solution. The aromas used were from the Manuel Riesgo brand (Madrid, Spain). For conditioning, 0.15M intraperitoneal injections of LiCl at 1% of the subject's body weight were administered.

Procedure

All the procedures used were approved by the Ethical Committee for Animal Experimentation (CEEA) of the University of Granada, number 06/06/2019/099, and were classified as low severity according to European guidelines. Access to water was restricted to two 30-minute sessions per day, at 11:00 and 16:00. The rats received 3 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. They were divided into two groups (INT and BLK) of eight approximately matched for weight (mean INT weight: 394 g; BLK: 392 g) and water consumption.

The preexposure phase lasted 4 days (Days 1-4). During the morning sessions 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 order of presentation of the stimuli was counterbalanced so that all subjects experienced AX first on half the trials and BX first on the other trials. The BLK group received the same presentation scheme, but with only one of the compounds being presented on a given day trial. Half received AX on the first two days, and BX on the next two days; half had the reverse arrangement. During the afternoon session both groups had free access to water for 30 min. On Day 4, after the afternoon session, the animals were weighed again to calculate the volume of LiCl that was to be injected during the conditioning phase.

On the following four days (Days 5-8) the rats received two conditioning trials (Days 5 and 7) and two recovery days (Days 6 and 8). On each conditioning day they had access to 30 ml of Y for 30 min, immediately followed by an intraperitoneal injection of LiCl. On the recovery days, the rats had free access to water for 30 min in the morning sessions. For one rat in the INT group this procedure failed to establish an aversion, and this subject was henceforth withdrawn from the experiment. Two test days followed (Days 9-10), on which the rats received free access to compound XY for 30 min in the morning session.

Statistical Analysis

A repeated measures analysis of variance (ANOVA) was performed to analyze the data, with Group as a between subjects variable and Trial as a repeated measure. We adopted a critical *p* value of .05 and used Greenhouse-Geisser and Welch corrections when necessary. Partial eta squared (η2p) and Cohen's d were used to measure the effect size. The JASP statistical program was used to carry out the analyses.

Transparency and Openness

This study was not preregistered. The raw data on which study conclusions are based are available in the APA´s repository on the Open Science Framework (OSF) https://osf.io/f4r2t/files/osfstorage/63906c4f8ad0c80717ffa599

Results

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 4.08ml and 4.75ml, respectively, of the AX solution, and 4.32ml and 4.58ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) as variables showed neither significant differences nor interactions in these respects (largest *F(*1, 13) = 1.69, p = .22, η2p = .11, MSE = 3.8 for group factor).

In the conditioning phase the consumption of Y decreased from the first to the second trial in both groups, consistent with the development of a conditioned aversion. The mean Y consumption for the INT group was 9.1 ml on the first trial and 4.6 ml on the second. For the BLK group, the equivalent Y consumption scores were 11.6 ml and 4.7 ml. A repeated measures ANOVA with Trial and Group as variables showed that the decrease in consumption across trials was significant, *F(*1, 13) = 43.71, *p* < .05, η2p = 0.77 and MSE = 5.54; neither the Group factor nor the interaction of Group x Trial was significant (*F*s <1).

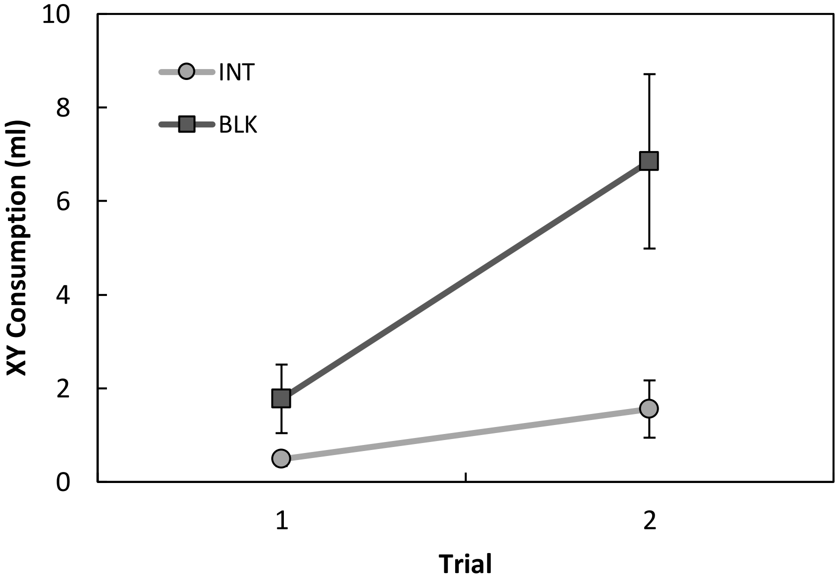

Figure 35. Experiment 1: Average direct consumption (±SEM) of XY in test phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure.

Figure 15 shows the consumption of the XY compound on the two test trials. Consumption was slightly less suppressed in the BLK group than in the INT group on trial 1, a difference that was clearly marked as consumption levels rose on the second test trial. A repeated measures ANOVA with Trial and Group as the variables confirmed these impressions showing a significant effect of Trial *F(*1, 13) = 15.41, *p*<.05, η2p = 0.54, MSE = 4.57 a significant effect of Group, *F(*1,13) = 5.79, *p*<.05, η2p = 0.31,MSE = 13.97, and a significant interaction between these variables, *F(*1,13) = 6.54, *p*< .05, η2p= 0.33, MSE = 4.57. The interaction was explored using independent samples *t*-tests. As Levene's test was statistically significant, indicating that the group variances were unequal, we corrected for this violation using the Welch adjusted *t*-statistic method. This showed a significant difference between the groups on trial 2 (adjusted *t*(8.48)=2.7, *p*<.05,*d*= 1.36).

Discussion

Consumption of flavor Y was substantially suppressed by the conditioning procedure. The addition of the preexposed flavor X was found to be less effective in attenuating this suppression in subjects that had experienced Intermixed presentations of AX and BX during the preexposure than in subjects that had experienced the Blocked arrangement. This difference was more evident on the second trial of the test with the XY compound than the first. This may indicate that the presence of X after Blocked exposure speeded the development of extinction; alternatively, it may indicate merely that the effect of X was better observed as consumption levels rose with repeated testing. The latter interpretation indicates that X loses effectiveness after Intermixed preexposure to AX and BX that prevent it from interfering with the expression of a conditioned response. Alternatively, it may be that X acquires such properties as a result of Blocked preexposure (or both of these possibilities). Further discussion will be postponed until other tests of X have been described.

Experiment 2: Overshadowing Test

Experiment 1 tested the properties acquired by stimulus X by assessing the ability of this stimulus to interfere with the expression of a separately acquired CR. In this experiment we used the same initial training procedure, (that is, Intermixed or Blocked, closely spaced presentations of AX and BX), but tested the ability of the X stimulus to interfere with acquisition of a CR. Thus, after the initial preexposure phase the subjects received aversion conditioning with an XY compound (i.e., with X in compound with a novel flavor Y). The presence of X can be expected to overshadow to some extent acquisition by Y. Will the two schedules of preexposure differ in this respect?

Method

Subjects and Apparatus

The subjects were 16 male Wistar rats with a mean ad libitum weight of 415g (range 300g – 460g). They had had previous experience with tastes and aromas, but these were different from those used in this experiment. The animals were maintained as described for Experiment 1. The Apparatus used and the flavors and concentrations of the stimulus solutions were the same as described for Experiment 1

Procedure

The design of the experiment is summarized in Table 5. The subjects were divided into two groups (INT and BLK) each of eight rats of equivalent weight (INT mean: 416g; BLK mean: 414g). As in Experiment 1, there were four preexposure days, with the flavor used differing within trials for the INT group, but across days for the BLK group. After preexposure, there were two conditioning trials (Days 5 and 7)on each of which access to 30 ml of an XY solution was followed by an injection of LiCl. Each conditioning day was followed by a rest day (Days 6 and 8). Finally, there were four test trials (Days 9-12) on which with free access to the Y solution was given for 30 min. During the procedure a rat from the INT group became ill and was withdrawn from the experiment. Other details not mentioned here were the same as described for Experiment 1.

Results

During the preexposure phase the rats consumed virtually all the liquid available. The subjects in groups INT and BLK consumed an average of 5.09ml and 4.95ml, respectively, of the AX solution, and 4.43ml and 4.78ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) as variables showed neither significant differences nor interaction in these respects (largest *F(*1, 13) = 1.84, p = .2, η2p = .12, MSE = 2.75 for stimulus factor).

The conditioning phase saw a decrease in XY consumption from the first to the second trial. The INT group consumed a mean of 15.7ml on the first and of 3.5 ml on the second; the scores for the BLK group were 15.7ml and 5.4 ml. A repeated measures ANOVA with Trial and Group as the variables showed a significant effect of Trial, *F(*1, 13) = 42.24, *p*< .05, η2p = 0.76, MSE = 19.84. Neither the effect of Group nor the interaction was significant (*F*s < 1).

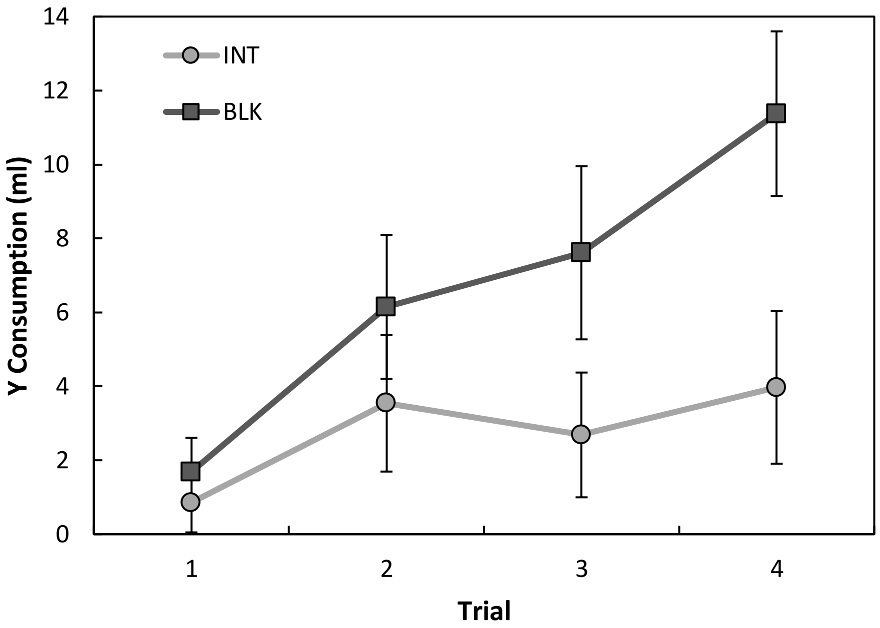

Figure 16. Experiment 2: Average direct consumption (±SEM) of Y in test phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. Error bars show the standard error of the mean.

Consumption of flavor Y over the four test trials is shown in Figure 16. Initially consumption was suppressed in both groups, but with the increase in consumption over the extinction trials of repeated testing, a difference emerged, with the BLK group consuming more than the INT group. A repeated measures ANOVA with Trial and Group as the variables showed no main effect of Group (*F*< 1) but there was a significant effect of Trial ,*F(*3, 39) = 13.61, *p*< .05, η2p = 0.51, MSE = 7.61, and a significant Trial x Group interaction *F(*3,39) = 4.00, *p*< .05, η2p = 0.24, MSE = 7.61. This interaction was explored using independent samples t-test, which showed significant differences for both groups on test 4 (*t*(13)=2.41, *p*<.05 and d= 1.25).

Discussion

The result presented in Figure 16 can be interpreted in terms of overshadowing between separate stimulus elements, with the test of Y alone giving a measure of the extent to which the X element was able to restrict acquisition by Y during conditioning with the compound. The stronger aversion shown by the INT group is consistent with the proposal that after Intermixed preexposure stimulus X was less effective in limiting acquisition by Y. The result is also compatible with an interpretation of the overshadowing effect is in terms of the extent to which there is generalization between the XY compound (or configure) used in conditioning and the Y stimulus presented alone on the test. If the X stimulus is particularly noticeable its omission can be expected to reduce such generalization. That the conditioning response remains strong in the INT group despite the omission of X on the test implies that for them X was not an important constituent of the conditioned configure, i.e. that the INT preexposure procedure reduced the effectiveness of X in this regard.

Experiments 3a and 3b: Direct Conditioning Assessment

The experiments by Mondragón and Murphy (2010) and by Ballesta et al. (2021) tested the properties of the X stimulus after Intermixed or Blocked preexposure by using it as the CS in a simple excitatory conditioning paradigm. The present Experiment 3a (see Table 5) used the same procedure. That is, after Intermixed or Blocked preexposure, as in the previous experiments, all subjects received conditioning trials on which X was followed by an injection of LiCl. The strength of the acquired aversion was then assessed by presenting X on a series of extinction trials. In addition, Experiment 3b was conducted with the same design, except that in this case the volume of LiCl injected during the conditioning phase was halved. This gave us the opportunity to administer more conditioning trials and to observe the associability of X in more detail. Consequently, this procedural change resulted in a deeper aversion and more extinction trials were given as well.

Experiment 3a

Method

Subjects and Apparatus

The subjects were 32 male Wistar rats with previous experimental experience but with stimuli different from those used in this experiment. Their mean ad libitum weight was 492g (range 432g – 613g). They were divided into four groups (two INT and two BLK) of eight, matched for weight: For Experiment 3a the mean weights were INT: 485 g; BLK: 489g, while for Experiment 3b they were INT weight: 492g and BLK: 502g. For Experiment 3b, raspberry odor was used as a unique element instead of caramel odor, as the latter eventually expired.

Procedure

As in the previous experiments, there were four preexposure days with AX and BX as the stimuli, the flavor used differing within trials for the INT group, but across days for the BLK group. For Experiment 3a there were two conditioning trials (on Day 5 and Day 7) while for Experiment 3b this phase lasted four trials (on Day 5, Day 7, Day 9 and Day 11). On all of these, 30 ml of the X solution was made available followed by a 0.15M intraperitoneal injection of LiCl, however for Experiment 3a the doze was administered at 1% of the subject's body weight while for Experiment 3b this was at 0.5%. Days 6 and 8 were rest days, and also days 10 and 12 for Experiment 3b. On the test trials that followed all subjects were given free access to the X solution for 30 min. For Experiment 3a test phase lasted four trials (Days 9 – 12), while for Experiment 3b this phase lasted ten trials (Days 13-22). Procedural details not specified here was the same as described for Experiment 1.

Results

During the preexposure phase the rats consumed virtually all the liquid available. The subjects in groups INT and BLK consumed an average of 4.84ml and 4.86ml, respectively, of the AX solution, and 4.93ml and 5.14ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) as variables showed neither significant differences nor interactions in these respects (largest $F(1, 14) = 1.35$, $p = .26$, η2p = .088, MSE = 0.79 for the stimulus factor).

In the conditioning phase there was a decrease in consumption of X from the first to the second trial in both groups. Group means for the two trials were 16.1 ml and 13.4 ml for the INT group, and 15.6ml and 12.6 ml for the BLK group. A repeated measures ANOVA with Trial and Group as the variables showed a significant effect of Trial, $F(1, 14) = 6.4$, $p < .05$, η2p = 0.3, MSE = 10.22 (other *F*s < 1). Figure 17 shows consumption of X over the 4 test days. Consumption was suppressed on the first trial but was restored with repeated testing. There was no difference between the groups on these tests. A repeated measures ANOVA with Trial and Group as the variables showed only a significant effect of Trial, $F(3, 42) = 28.6$, $p <. 05$, η2p = 0.7, MSE = 5.22. Neither the effect of Group ($F < 1$) nor the interaction, $F(3, 42) = 1.5$, $p > .05$, η2p<0.1, MSE = 5.22, was significant.

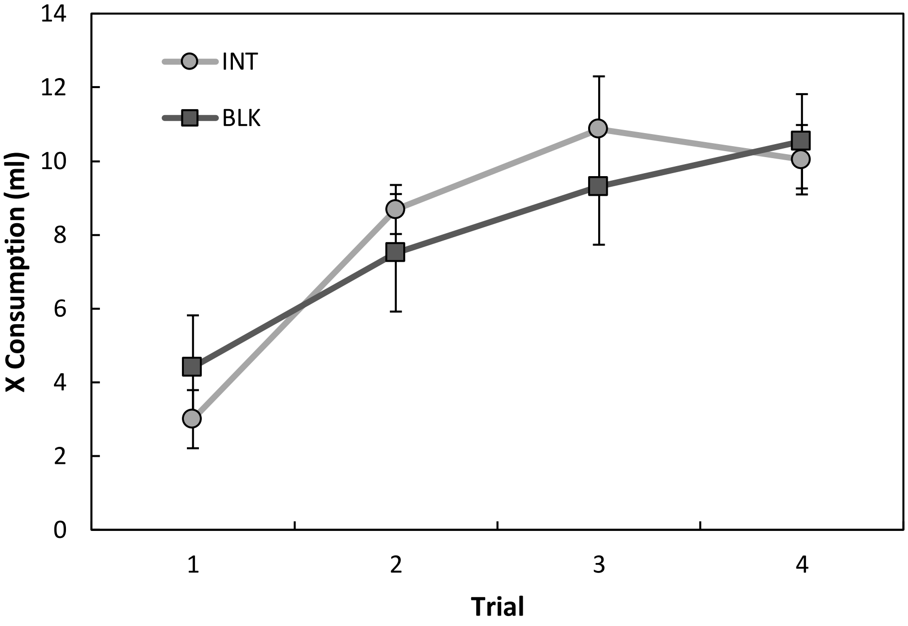

Figure 17. Experiment 3a. Group means for consumption of X in the test phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. Error bars show the standard error of the mean.

Experiment 3b

Method

Subjects and Apparatus

The subjects in groups INT and BLK consumed an average of 4.09ml and 4.2ml, respectively, of the AX solution, and 4.33ml and 5.2ml, respectively, of the BX solution. A repeated measures ANOVA with Stimulus (AX and BX) and Group (INT and BLK) as variables showed neither significant differences nor interactions in these respects (largest *F(*1, 14) = 0.43, *p* = .52, η2p = .03, MSE = 0.99 for the Stimulus x Group interaction).

Results

In the conditioning phase it was observed a slow decrease in X consumption from the first to the fourth trial, INT consumed on average: 11.7 ml, 11.1 ml, 5.5 ml and 1 ml; and BLK: 10.3 ml, 10.2 ml, 6.6 ml and 2.2 ml (Figure 18). A repeated measures ANOVA with Trial and Group as factors showed that this decrease in consumption was significative for trial, F (1.7, 23.9) =49.7, p<.05, η2p = 0.8 and MSE = 11. Neither Group factor F <1, nor interaction F (1.7, 23.9) =1.2, p>.05 and η2p<0.1 were significant (Fs < 1). Figure 19 shows the consumption of X during the 10 test days, rats increased their consumption at a very slow rate but with similar levels for both groups. A repeated measures ANOVA with Trial and Group as factors showed that the increase in consumption was significative for trial, F (9, 126) = 26.5, p<.05, η2p = 0.7 and MSE = 3. Neither Group factor (F (1, 14) =2.3, p>.05, η2p=0.1 and MSE = 40.1) nor interaction (F <1) were significant.

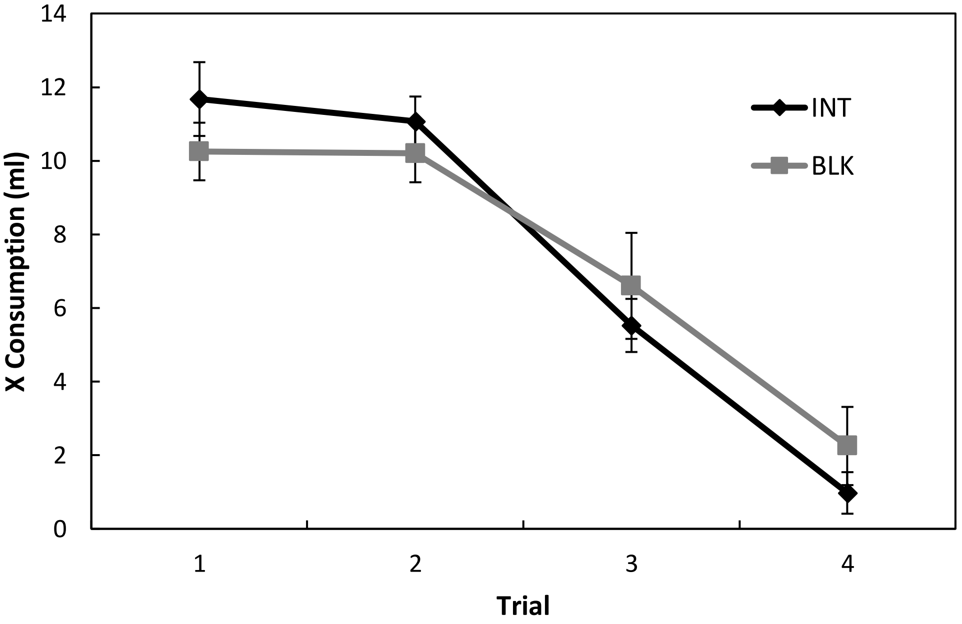

Figure 18. Experiment 3b. Group means for consumption of X in conditioning phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. Error bars show the standard error of the mean.

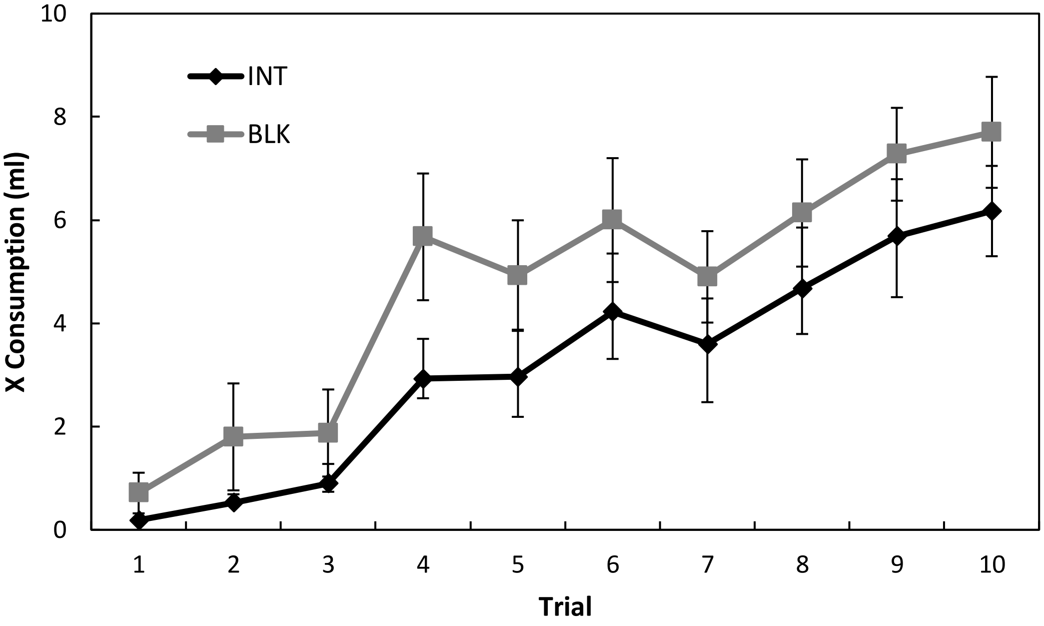

Figure 19. Experiment 3b. Group means for consumption of X in test phase. INT refers to the group that received Intermixed exposure and BLK refers to the group that received Blocked exposure. Error bars show the standard error of the mean.

Discussion

Given the results of Experiments 1 and 2 (and of Mondragón & Murphy, 2010,and Ballesta et al., 2021), the absence of an effect of the preexposure condition in these experiments was unexpected. For Experiment 3a one possibility is that, after preexposure, the common element suffered sufficient latent inhibition as to preclude acquisition of a conditioned aversion with only two conditioning trials (this is plausible, since on the second conditioning trial the consumption of X for both groups was still quite high). Accordingly, we modified the parameters for the conditioning and test phases in Experiment 3b in order to make our procedure more sensitive to this variable. In this experiment we administered half the volume of LiCl (0.5% of the subject's body weight) during 4 conditioning trials, which effectively supressed X consumption, but again this procedure showed no significant differences for X consumption between groups in either the acquisition or extinction phase.

We will not speculate at length on interpretation of these null results, but one possibility may be considered. The preexposure procedure used in these experiments is clearly effective in that it produced a difference between the Intermixed and Blocked groups in the tests employed in Experiments 1 and 2. Is it possible that the test procedures used in these experiments are more sensitive than simple excitatory conditioning with X as the CS? A feature of the tests used in Experiments 1 and 2 is that they involved presenting the critical X stimulus in compound with another flavor. The preexposure phase of those experiments also involved presenting X in a compound. It is possible that preexposure effects will generalize more readily from training to test in these conditions than when X is presented alone on test, as in the present experiments. We acknowledge that additional assumptions are required in order to explain why Mondragón and Murphy (2010), and Ballesta et al. (2021) obtained effects on conditioning with X in their experiments using stimuli from another sensory modality.

General Discussion

The preexposure procedure used in the experiments reported here has been shown to be capable of producing a perceptual learning effect. Experience of closely spaced, Intermixed, presentations of the compound stimuli, AX and BX, will promote discrimination between them (Recio et al., 2018, 2019; Sánchez et al., 2022). Moreover, the present experiments demonstrate that this training regime can produce a change in the properties of the common, X, element of the stimuli. Specifically, X is less able to overshadow conditioning to another flavor, and less able to interfere with the CR established to a separately trained CS. Previous experiments using widely spaced presentations of flavored compounds have failed to find any reliable effect of this form of preexposure on X properties (see Hall, 2020). The assumption that the presentation of closely spaced stimuli is key to producing a change on X properties is consistent with the findings reported by Mondragón and Murphy (2010) and Ballesta et al. (2021) who also demonstrated an effect on X (although using a different method of testing) in subjects given closely spaced Intermixed presentations of compound auditory stimuli.

Once again, a general conclusion that could be drawn from these results is that the mechanisms responsible for the perceptual learning effect observed after closely spaced stimulus presentations differ from those responsible for the effect observed after widely spaced presentations. The effects of preexposure with widely spaced presentations have been better explained in terms of changes in the effectiveness of the distinctive features of the stimuli rather than changes on the properties of the common features (e.g., Hall, 2003; McLaren & Mackintosh, 2000). Yet, in our study, such changes may also play a role in the effect produced by closely spaced training. Specifically, if the common elements of two stimuli are reduced in effectiveness, then discrimination between them, which requires control by the distinctive rather than the common features, will be enhanced (Gibson, 1969). It is now necessary to attempt to specify more what learning processes might change the effectiveness of X.

Mondragón and Murphy (2010) suggested that one aspect of X effectiveness that might be reduced by the Intermixed preexposure is its associability (i.e., the readiness with which it will enter into association). According to Mackintosh's attentional theory (1975), when a stimulus is a bad predictor for any consequence its alpha parameter (associability value) decreases, and conversely it increases when that consequence is well predicted. After Intermixed preexposure, X could be perceived as a poor predictor of the unique elements because these have been changing on each trial. However, during Blocked preexposure X is able (at least) to correctly predict the unique element associated on each block of trials. Such a difference in associability values could explain results of Experiment 2 in which the test involved conditioning of the XY compound. If X loses its associability after Intermixed preexposure it would be less effective in establish associations with the US during the conditioning phase, and, competition for associative strength would be “won” by the element Y, which will result more aversive on the following tests. After Blocked preexposure, X would be perceived as a good predictor for the unique elements, this would increase its associability, and promote competition with Y during the conditioning phase, restricting acquisition of aversion by Y. It is a problem for this account, however, that we observed no difference between the groups in Experiments 3a and 3b, where a difference in associability might have been expected to produce a difference in acquisition of the aversion.

Furthermore, another aspect of the effectiveness of X that may be differentially affected by the form of exposure is its salience. This is a slightly different proposal from that just discussed according to theories (like that of Pearce & Hall, 1980) that make a distinction between the associability of a stimulus and its salience; the former governing the rate of learning whereas the latter also determines the vigor of the response. Ballesta et al. (2021; see also Artigas & Prados, 2014, 2017) proposed that during Intermixed preexposure, X would form inconsistent and weak associations with the unique elements, which ultimately results in separate representations for each element (A, B and X), whereas Blocked exposure would establish stronger associations in each block of trials generating configural-like representations (AX and BX). The latter configural-like representations is assumed to be less vulnerable to the effects of exposure than are elemental-like representations, as the strong associations between X and the unique elements reduce the amount of salience lost by each separate element. This account allows an explanation of the results of Experiments 1 and 2. In the test of Experiment 1, a low-salient X, as produced by Intermixed preexposure, would be less able to draw attention away from the conditioned Y element, resulting in greater expression of the conditioned aversion to Y on test. The same analysis can apply to explain the results of Experiment 2; a low-salient X produced by the Intermixed procedure would be less able to compete for associative strength with a novel Y during conditioning. However, this account would also predict slower learning to X after Intermixed preexposure in Experiments 3a and 3b, which was not obtained.

An alternative account of how Intermixed preexposure can reduce X salience is found in the theory of habituation offered by Hall and Rodríguez (2019; 2020). This theory postulates that associative learning will change the salience of a stimulus as a function of the consequence that follows it. When a stimulus is followed by no consequence this results in inhibitory learning, characterized as "stimulus-no event" learning. This habituation training progressively negates the initial expectation that some event will follow the stimulus, and, as the expectation declines, the salience goes down. However, this learning process only would be able to operate effectively if X is fully perceived as a separate element, which, as Ballesta et al. (2021) suggest, will be more likely after Intermixed preexposure. In any of these cases, the habituation training promoted by the Intermixed schedule would reduce the salience of the common element X and this could explain the results presented here and those of Ballesta et al. (2021).

It remains to explain the results of our Experiments 3a and 3b in which using X as the CS in a conditioning procedure failed to reveal any difference between the preexposure conditions. One possibility comes from the account offered by Hall and Rodríguez (2019, 2020) which proposes that repeated exposure to a stimulus will change not only its effective salience, but also its associability. Specifically, associability is assumed to go down when a stimulus is reliably paired with an associate but will be maintained when its consequences are variable (Pearce & Hall, 1981). This allows, at least with certain parameters, for the possibility that the preexposure procedures used in the present experiments will actually leave X with a higher associability after Intermixed than after Blocked training. In the latter case X comes to the test after a block of trials in which its associate has been constant; in the former the associate of X has changed from trial to trial. A difference between the groups in the level of associability of X will not be relevant in the present Experiment 1 in which there is no further conditioning with X as the CS. However, differences in associability level could be of importance in Experiments 2 and 3. In Experiment 2 enhanced associability in the INT condition might actually increase the ability of X to interfere with conditioning to Y, reducing the size of the effect generated by a difference in effective salience. And in Experiment 3, in which acquisition by X is the sole measure on test, enhancement of the associability of X could play a major role. With this test procedure, the difference between the INT and BLK groups might be expected to be quite small (as it was in the experiments by Mondragón & Murphy, 2010, and Ballesta et al., 2021), or even absent (as in our Experiments 3a and 3b). In fact, during the test phase of Experiment 3b it can be observed a tendency for the Intermixed group to retain the aversion more strongly during the extinction trials than the Blocked group

It should be acknowledged that, for the most part, the learning mechanisms considered so far would apply as readily to procedures in which stimulus presentations are widely spaced as to those reported here (and also those in Artigas & Prados, 2017; Ballesta et al. 2021; and Mondragón & Murphy, 2010). Although no evidence has been found that the preexposure schedule determines the properties of the X element when stimulus presentations are widely spaced (see for a review Hall, 2020), this does not necessarily imply that the mechanisms described above are ineffective. Rather, a specification of the reasons why changes in the properties of X are only clearly evident with close stimulus presentations would be necessary. This would be a crucial step for future research, as it would demonstrate the differences within the same experiment between the effect of widely spaced and closely spaced presentation of stimuli in perceptual learning.

One final analysis that deals directly with the processes that will be acting when stimulus presentations are closely spaced comes from experiments with human subjects by Mundy et al. (2007), and by Dwyer et al. (2011). In these experiments, they obtained a perceptual learning effect (better discrimination after an Intermixed preexposure than after Blocked) with presentations of the stimuli separated by just 500 ms. They attributed this effect to better encoding of the unique features of the stimuli during Intermixed preexposure, as a consequence of short-term habituation of the common element. Thus, for example, when BX follows AX after a short interval, X, which has been previously processed, will free up resources for better processing of B. This short-term habituation of X has some support from the evidence that introducing a distractor in the interstimulus interval attenuate the perceptual learning effect, however, this account does not generate predictions about how X will behave when used in a subsequent training or testing procedure. In order to account for our results, it is necessary to assume that the short-term changes in the properties of X postulated by Dwyer et al. (2011) can become sustained and thus influence performance on a test given later.

The interpretations just offered are no more than possibilities, and in the absence of further evidence, it would be fruitless to continue speculation along these lines. We return to the basic finding, which is that the effectiveness of the X element appears to be reduced by closely spaced AX/BX training. Although an effect of this sort seems absent when stimulus presentations are widely spaced, it is likely to be of importance in producing perceptual learning effects when stimuli are presented in a way that allows direct and immediate comparison. In any case, the following chapter will attempt to explore the mechanisms of perceptual learning when stimuli are presented in a spaced manner (Hall, 2003; McLaren and Mackintosh, 2000), and contrast them with the rapid comparison mechanism proposed by Honey and Bateson (1996) and Recio et al. (2018).

CHAPTER VII – MECHANISMS UNDERLYING PERCEPTUAL LEARNING

Introduction

Gibson (1969) proposed that, in perceptual learning, the opportunity to compare may increase the discrimination between similar stimuli. By comparison we mean the close presentation of stimuli in such a way that differences and similarities can be contrasted. It has been found in experiments with humans and non-human animals (e.g. Dwyer et al., 2011; Recio et al., 2018) that presenting similar stimuli rapidly and alternately increases their subsequent discrimination to a greater extent than separate Blocked presentations. This has been explained by the short-term habituation that common elements undergo, because they are always present, which increases the processing resources towards the unique elements and thus enhances discrimination between similar stimuli (Honey & Bateson, 1996).

However, perceptual learning experiments that have used spaced presentations of similar stimuli with long intervals between them have also found an improvement in discrimination, even though for these procedures a direct comparison seems unlikely. For example, Symonds and Hall (1995) preexposed an Intermixed group of rats to AX at 11:00h and to BX at 17:00h, resulting in a 6h ISI. They then aversively conditioned the AX stimulus and subsequently tested BX, finding that these rats discriminated better both stimuli than rats that had experienced AX and BX in separated blocks. It does not seem very plausible that subjects kept the AX representation active until the moment when BX was presented, so a comparison process between stimuli does not seem possible. Based on Honey and Bateson's (1996) mechanism, it also seems unlikely that the common elements remained habituated when BX arrived, so the possibility of a processing bias sounds excluded as well.

The perceptual learning effect observed when stimulus presentations are widely spaced has been explained by different associative models in terms of modulation of salience. These models are based on two assumptions. The first assumption is that, during preexposure, the stimuli and their elements lose effectiveness, both because they unitize with the context and gain latent inhibition (McLaren et al., 1989) or because they become habituated (Hall, 2003). Second, that preexposure to similar stimuli favors the formation of intracompound associations between unique and common elements (McLaren et al. 1989). Through these associations the presentation of a stimulus, e.g. AX, will associatively activate by the common element, X, the absent unique one, B, and vice versa on BX trials (McLaren & Mackintosh, 2000). Salience models propose that, through associative activations, Intermixed spaced arrangements can preserve the effectiveness of unique elements and thus improve discrimination. Instead, this is less likely on Blocked exposure, where only the first unique element exposed would be activated during the second block of trials, and yet, this association would tend to disappear over time.

According to McLaren and Mackintosh's (2000) model, during preexposure the sampled elements of the stimuli will form associations with themselves and with the context, that is a process of unitization, which would increase the latent inhibition of their elements and reduce their associability. However, the associative activation of the unique elements will extinguish these associations formed by their unique subelements with themselves and with the context, a deunitization effect, reversing the latent inhibition and restoring the associability. On the other hand, Hall’s model (2003) proposes that the associative activation of these elements produces a discrepancy in the processor system, as it was expected that both the common and the unique element previously experienced would be physical presented together again. Therefore, the associative activation of the unique element is unexpected and promotes the subject's responsiveness to that element in future encounters, thus increasing its salience and associability. Convergent, both theories predict that after Intermixed spaced exposure the increased effectiveness of the unique element over the common favors its discrimination rather than generalization, but not so in the Blocked group where effectiveness is scarce among the elements.

These proposals are supported by multiple experiments which find evidence for increased salience and associability of these elements after spaced Intermixed exposure. Blair and Hall (2003a) exposed rats to Intermixed spaced trials of AX and BX, along with a block of CX, after which they aversively conditioned the X element and tested the BX and CX compounds. Rats showed greater consumption of the BX compound than the CX, suggesting that element B was more salient after Intermixed exposure and interfered to greater extent with X aversion than C did. Conversely, in a similar design with X as saline solution, rats injected with furodoca, which increases salt demand, consumed more CX than BX, also indicating a greater salience of B which interferes with X perception. In another study, Blair et al. (2004) preexposed salt as unique element, Intermixed (B) or Blocked (C), then paired the salt with a new Y element and gave subjects a furodoca injection. The results showed a higher intake of Y after they paired it with B being salt, indicating a higher associability due to Intermixed exposure, than when the salt was C. In a final experiment they found, after direct conditioning of element B and C, that the Intermixed preexposed unique element was more readily associated with aversion and that this association was more resistant to extinction on subsequent non-reinforced trials than the Blocked preexposed unique element.

These are just a few examples of the numerous experiments that demonstrate the increased effectiveness of unique elements following Intermixed in contrast to Blocked preexposure when the procedure is spaced (see also Mitchell & Hall, 2014, for a review). In particular, spaced Intermixed preexposure produces unique elements with higher salience and associability, which is the opposite of what rapid Intermixed preexposure would produce. As we have seen in Chapter 2, rapid Intermixed exposure causes short-term habituation of common elements, biasing processing resources towards unique ones (Honey & Bateson, 1996), which increases their discrimination but also reduces their associability and salience (Recio et al., 2018). Some studies have attempted to contrast the salience and associability of unique elements after both types of exposures. For example, Lombas et al. (2008) preexposed two Intermixed groups with either 5 min or 24h ISI, after which element A was aversively conditioned and its extinction was measured in test. Although greater associability with aversion was expected in the spaced exposure than in the closer one, they found no differences in either conditioning or extinction phases.

In this chapter we will look for evidence of both mechanisms using our rapid preexposure procedure. We consider that the two mechanisms of perceptual learning are not mutually exclusive, so we expect that depending on the demands of the procedure one or the other will be triggered. This procedure has already shown in previous chapters a better discrimination of rapidly Intermixed stimuli, as well as a reduction in the associability and salience of its unique elements. Here we add an Intermixed group with spaced ISI that we expect will produce an opposite effect: an increase in the salience and associability of its unique elements, while also improving stimulus discrimination.

Experiment 1: Superimposition Test

In Experiment 1 we will test the associative activation of unique elements as a mechanism to improve discrimination within our rapid procedure. The design of Experiment 1 is summarised in Table 6, all the rats will be preexposed in morning sessions to AX and BX in rapid alternation with 5 min of a distractor in between, and, in the evening sessions half of the rats will have access to water and the remaining to X. After the preexposure phase, all rats will be aversively conditioned to a new Y element and subsequently tested with the AY compound. The distractor will disable the short-term habituation of the common elements, eliminating the rapid mechanism of perceptual learning (Recio et al., 2018).

Thus, we expect that presentation of the common element spaced in the afternoon to associatively activate the unique elements and thus enhance subsequent discrimination between the aversive Y and AY in the test much more than the Water group.

Some experiments that have presented AX and X in Intermixed spaced way have found better discrimination between them than when they were exposed in blocks (Rodríguez & Alonso, 2004; 2008). Specifically, with this AX-X spaced exposure, Rodríguez et al. (2008) found better discrimination in a superimposition test between a new aversive element Y and the AY compound, in contrast to Blocked exposure. This is explained by the fact that salience modulation mechanisms only need the formation of intra-compound associations and the separate presentation of X to associatively activate the absent unique elements, and thus restore their effectiveness.

EXPERIMENT	Group	Preexposure		Conditioning	Test
		Morning	Afternoon		
1	INT_X	AX/D/BX	X	Y+	AY?
	INT_W	AX/D/BX	W		

Table 6. INT refers to Intermixed preexposure. W means water and D means distractor which was a sucrose solution. A and B are hazelnut and caramel aromas (counterbalanced). X was salt solution and Y was acid solution. The "+" indicates an intraperitoneal injection of LiCl; "/" indicates rapid succession of stimuli within the same session. Note: during preexposure INT group also experienced trials in which BX preceded AX.

Method

Subjects and Apparatus

Subjects were 16 naïve male Wistar rats with a mean ad libitum weight of 452 g (range 544 g-404 g). The rats were housed individually in transparent plastic boxes measuring 35x22x18 cm, with sawdust for the bedding. They were kept 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 and were administered in the home boxes using 50-ml inverted centrifuge tubes with stainless steel ball-bearing-tipped spouts. Consumption was determined by weighing the tubes before and after the sessions. Stimuli AX and BX consisted of a saline solution (9 g/L) as X with hazelnut or caramel aromas counterbalanced as A and B, at 0.05% of the total volume of the solution. Flavor Y was a 0.5 g/L solution of citric acid and the distractor was a 40g/L sucrose solution. The aromas used were from the Manuel Riesgo brand (Madrid, Spain). For conditioning, 0.15M intraperitoneal injections of LiCl at 1% of the subject's body weight were administered.

Procedure

All the procedures used were approved by the Ethical Committee for Animal Experimentation (CEEA) of the University of Granada, number 06/06/2019/099, and were classified as low severity according to European guidelines. Access to water was restricted to two 30-minute sessions per day, at 11:00 and 16:00. The rats received 3 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. They were divided into two groups (INT_X and INT_W) of eight approximately matched for weight (mean INT_X weight: 443 g; INT_W: 451 g) and water consumption.

The preexposure phase lasted 4 days (Days 1-4). During the morning sessions all rats received access to compounds AX and BX. The subjects first received 6 ml of one solution for 10 min, followed by 4 ml of distractor for 5 min, and finally 6 ml of the other solution for 10 min. The order of presentation of the stimuli was counterbalanced so that all subjects experienced AX first on half the trials and BX first on the other trials. During the afternoon session, the INT_W group had free access to water for 30 minutes, while the INT_X group first had 10 minutes of 10ml of X and then 20 minutes of free access to water. On Day 4, after the afternoon session, the animals were weighed again to calculate the volume of

LiCl that was to be injected during the conditioning phase. Afterwards the afternoon session provided just 30 min of water for all the rats.

On the following four 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 15 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 two test days (Days 9 and 10), the rats received free access to compound AY for 30 min in the morning session.

Statistical Analysis

A repeated measures analysis of variance (ANOVA) was performed to analyze the data, with Group as a between subjects variable and Trial as a repeated measure. We adopted a critical p value of .05, and used Greenhouse-Geisser and Welch corrections when necessary. Partial eta squared (η2p) and Cohen's d were used to measure the effect size. Outlier analysis were based on Tukey’s rule, where outliers are values more than 1.5 times the interquartile range from the quartiles: either below Q1 − 1.5 IQR, or above Q3 + 1.5IQR. Two rats, one from each group, tested positive in the outlier analysis and consequently their data were removed from further analysis. The JASP statistical program was used to carry out all analyses.

Transparency and Openness

This study was not preregistered. All data from this study are available by emailing the corresponding authors.

Results

In the morning sessions during preexposure phase, the rats consumed virtually all the liquid available in the tubes, both the flavored compounds and distractor. For the afternoon session rats from group INT_X consumed a mean of 4.8ml from X solution. In the conditioning phase, Y consumption decreased across the two trials in accordance with the establishment of aversion. The consumption decreased in the INT_X group from 8.16ml to 6.26ml, and for the INT_W group from 8.34ml to 6.44ml. A repeated-measures ANOVA with Trial and Group as factors neither showed differences between trials, *F* (1, 12) = 3.93, MSE = 6.44, *p*= .07 and η2p = 0.25, between groups nor interaction between these factors (*F*s<1).

Figure 20 shows the consumption of AY during the two test days in Experiment 1. It can be observed that although both groups started consuming the same amount of AY, the INT_X group finally increased its consumption on the second test more than the INT_W. A repeated-measures ANOVA with Trial and Group as factors showed significant effect of Trial *F* (1, 12) = 16.06, MSE = 3.23, *p*<.05 and η2p = 0.57, not significant effect of Group, *F* (1, 12) = 1.76, MSE = 4.76, *p*>.05 and η2p = 0.13 but interaction between these factors F (1, 12) = 9.37, MSE = 3.23, p<.05 and η2p = 0.44. The Trial x Group interaction was analyzed using an independent samples t-test which showed significant differences between groups on Test 2, *t*(12)=2.57, *p*<.05 and *d*=1.37.

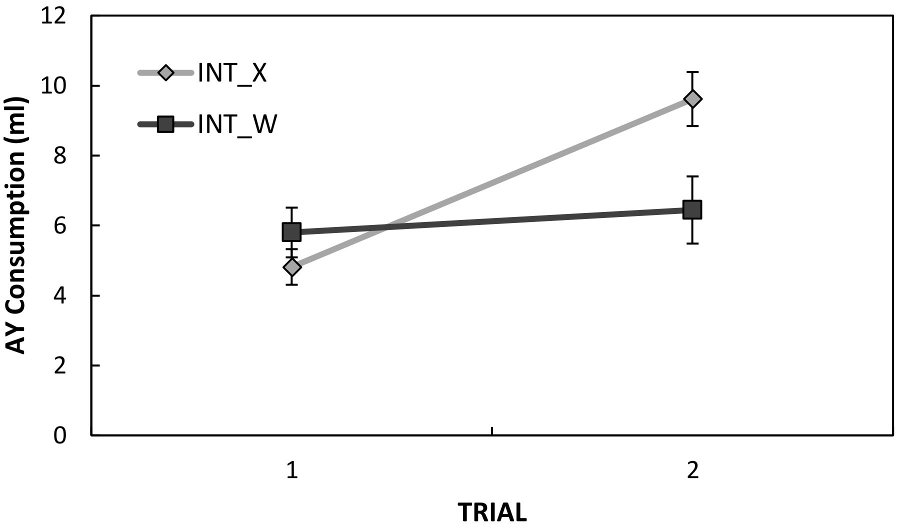

Figure 20. Experiment 1: Average direct consumption (±SEM) of AY in test phase. INT refers to the group that received Intermixed exposure in the morning sessions, W that received only water in the afternoon sessions and X that also received the common element in the afternoon sessions.

Discussion

These results have shown better discrimination between the aversive conditioned Y element and the AY compound for the INT_X group which had also experienced the common element in the afternoons during preexposure. Both groups were preexposed in Intermixed fashion to rapid presentations of AX and BX with a distractor between them. The distractor was introduced to eliminate any rapid mechanism that could modify the properties of the stimuli during the morning sessions, as would do the short-term habituation of common elements and the consequent processing bias (Honey & Bateson, 1996). The critical factor was the introduction of the common element, X, for the INT_X group during the afternoon sessions of preexposure phase, while the INT_W was receiving just Water. With this change, the common element could activate associatively the absent unique ones in the afternoon sessions in the INT_X group, and therefore restore their effectiveness lost during preexposure. Later, in the superimposition test, the INT_X group would perceive that element A more salient, interfering with the aversion associated to Y and, therefore, increasing the AY consumption.

This experiment has showed that our procedure is able to produce a perceptual learning effect even when the short-term mechanisms are disabled. The associative activation and increased salience of the unique elements was developed instead by the presentation of the common element in the afternoon sessions. This experiment validates the theories of salience modulation and allows us to use this procedure to observe within the same experiment the proposed mechanisms for rapid and spaced perceptual learning. In the next Experiment 2 we will introduce a rapid Intermixed group, a spaced Intermixed group and a Blocked group (all without a distractor), after which the unique element will be directly associated with an aversion and both its acquisition and extinction will be measured.

Experiment 2: Conditioning of A after Short Intermixed, Spaced Intermixed or Blocked preexposure

The design of this Experiment 2 is summarized in Table 7. In this experiment we will pre-expose subjects for 10 minutes of two stimuli with 5 minutes of a small amount of water in between. Short-Intermixed group will receive in the same session both stimuli, AX and BX; Long-Intermixed group will receive the same stimuli twice within the same session but alternate between sessions, e.g. AX and AX on even days and BX and BX on odd days; finally Blocked group will receive one stimulus twice on the first 5 sessions and the other in the days remaining. By using a 24h ISI for the INT_Long group we ensure to match the number of presentations and schedule time for each stimulus. After 10 preexposure sessions, the unique element A will be conditioned aversively with a low dose of LiCl so that after further trials differences in acquisition can be observed, and finally extinction will be measured in unreinforced test trials. We expect to observe differences in the associability of unique elements depending on the perceptual learning mechanism that is involved.

In the Short-Intermixed group we expect the rapid alternation of AX and BX to habituate the common element in the short term, so that attentional resources better process the unique elements (Honey & Bateson, 1996). This bias will lead the unique sub-elements to become highly unitized, which will develop a great representation of the unique element (Recio et al., 2018). This will increase the unique elements discriminability but also reduce their associability, as they are unitized with the context as well and have increased latent inhibition (McLaren et al., 1989).

On the other hand, we expect that in the Long-Intermixed group the spaced presentation of AX and BX will promote the formation of associations between their unique and common elements, and that through these the common element will associatively activate the unique elements in the trials in which they are absent. Through the associative activation the unique elements will restore their associability, either by deunitization of the elements with themselves and with the context (McLaren & Mackintosh, 2000), or by a discrepancy in the processing system that increases the subject's surprise at the stimulus (Hall, 2003).

The final prediction is that, in contrast to the Blocked unique element, the Long-Intermixed unique element will acquire aversion faster during conditioning and will also remain aversive longer during extinction trials, but the Short-Intermixed will be more difficult to condition and will extinguish the aversion readily.

EXPERIMENT	Group	Alternation	Preexposure	Conditioning	Test
2	INT_SHORT	in Session	AX/W/BX	A+	A?
	INT_LONG	each Day	AX/W/AX		
	BLK	each 5 Days	AX/W/AX		
3	INT_LONG	each Day	AX/W/AX	A+	A?
	BLK	each 5 Days	AX/W/AX		

Table 7. Experiment 2 and 3: INT refers to Intermixed preexposure, BLK refers to Blocked preexposure. W means water. A and B are hazelnut and raspberry counterbalanced aromas. X is saline solution. This "+" inidicates an i.p.injection of LiCl at 0.5% b.w. and this "/"indicates rapid sucession of stimuli within the same session. Long refers to an ISI between different stimuli of 24h, while Short refers to an ISI of 5min. "Alternation" indicates how often the identity of the stimulus changed.

Method

Subjects and Apparatus

Subjects were 32 naïve male Wistar rats with a mean ad libitum weight of 266 g (range 306 g-242 g). They were divided into groups INT_SHORT, INT_LONG and BLK of 11, 11 and 10 rats respectively matched for weight (mean groups INT_SHORT weight: 267 g, INT_LONG weight: 270 g; BLK: 259 g) and water consumption. Caramel aroma expired and was replaced by raspberry aroma as element A or B at 0.05% of the total volume of the solution. Throughout the procedure all rats received just 30 min of water in the afternoon session.

Procedure

The preexposure phase consisted on 10 morning sessions (Days 1-10). INT_Short group received one stimulus on the first session presentation and the other similar after the 5 min of water. The other two groups received each session the same stimulus twice but group INT_Long changed it each day and group BLK changed it at the middle of preexposure (after day 5). The order of presentation of the stimuli was counterbalanced. On the following 10 days (Days 11-20), the rats received five conditioning trials (Days 11, 13, 15, 17 and 19) and five recovery days, respectively (Days 12, 14, 16, 18 and 20). In each conditioning day, the rats had access to 30ml of A for 30 min, immediately followed by an intraperitoneal injection of 0.15M LiCl at 0.5% volume of subject's body weight. During the next ten test days (Days 21 to 30), the rats received free access to A solution for 30 min in the morning session. Other details not mentioned here were identical to Experiment 1.

Results

During the morning sessions in the preexposure phase, the rats consumed virtually all the liquid available in the tubes, both flavored compounds and water. The consumption of A in the conditioning phase decreased slowly from the first to the fifth trial. As we can see in Figure 21, the acquisition of aversion by the INT_Short group was less profound than for the other two groups, but also the INT_Long group seemed to have associated aversion more strongly than the BLK group. A repeated-measures ANOVA with Trial and Group as factors showed differences between trials, *F* (2.9, 83.9) = 94.9, MSE = 5.77, *p*<.05 and η2p = 0.77, and between groups, *F(*2, 29)=3.75, MSE= 13.69, *p*<.05 and η2p = 0.2, but not interaction between these factors.

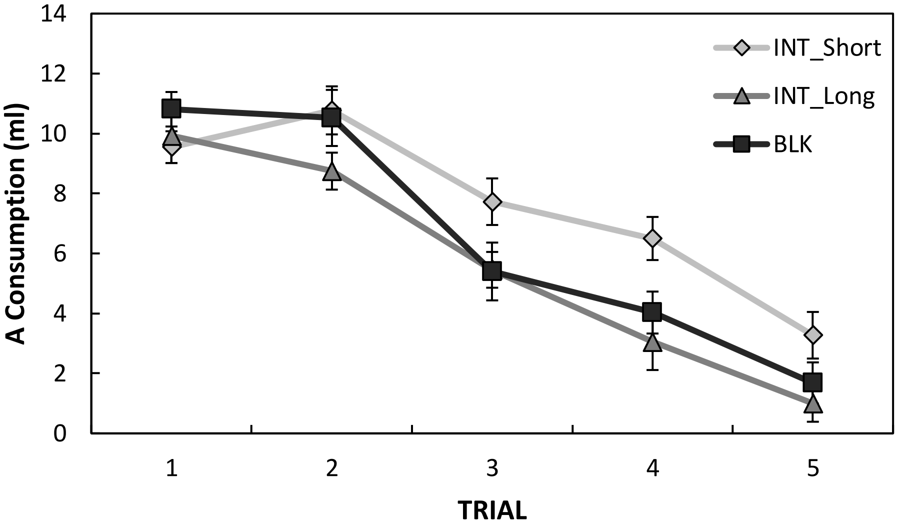

Figure 21. Experiment 2: Average consumption (±SEM) of A in conditioning phase trials. INT_Short refers to the group that received Intermixed exposure within sessions, INT_Long refers to the group that received Intermixed exposure between days and BLK refers to the group that received Blocked exposure.

A separate repeated measures ANOVA with groups INT_Short and INT_Long showed effect of Vonditioning Trial, *F* (4, 80) = 61.16, MSE = 3.87, *p*<.05 and η2p = 0.75; effect of Group, *F* (1, 20) = 6.98, MSE = 14.63, *p*<.05 and η2p = 0.26; and interaction between Trial x Group, *F* (4, 80) = 2.8, MSE = 3.87, *p*<.05 and η2p = 0.12. This interaction was explored using an independent T-Samples analysis which showed significant differences between groups on conditioning trial 3, *t*(20)=2.32, *p*<.05 and *d*=0.99, conditioning trial 4, *t*(20)=2.91, *p*<.05 and *d*=1.24, and conditioning trial 5, *t*(20)=2.3, *p*<.05 and *d*=0.98. Another separate repeated measures ANOVA with groups INT_Short and BLK showed effect of Trial, *F* (4, 76) = 67.13, MSE = 3.67, *p*<.05 and η2p = 0.78; interaction between Trial x Group, *F* (4, 76) = 3.53, MSE = 3.67, *p*<.05 and η2p = 0.16, but not effect of Group. This interaction was explored using an independent T-Samples analysis which showed significant differences between groups on conditioning trial 4, *t*(19)=2.45, *p*<.05 and d=1.07. A final repeated measures ANOVA with INT_Long and BLK groups only showed significant differences on Conditioning Trials, *F(*2.5, 47.6)=63.3, MSE=47.57, *p*<.05 and η2p = 0.77.

Figure 21 shows the consumption of A during the ten test days. As we can observe the INT_Short group extinguished the conditioned response much faster than the other groups, but in addition the INT_Long group maintained the aversion more deeply than the rest during almost the whole phase, while the BLK group remained in the middle of these two groups. A repeated-measures ANOVA with Trial and Groups as factors showed significant effect of Trial *F* (3.6, 104.7) = 39.99, MSE = 9.53, *p*<.05 and η2p = 0.458; and Group *F* (2, 29) = 16.22, MSE = 48.86, *p*<.05 and η2p = 0.53; but not interaction between these factors.

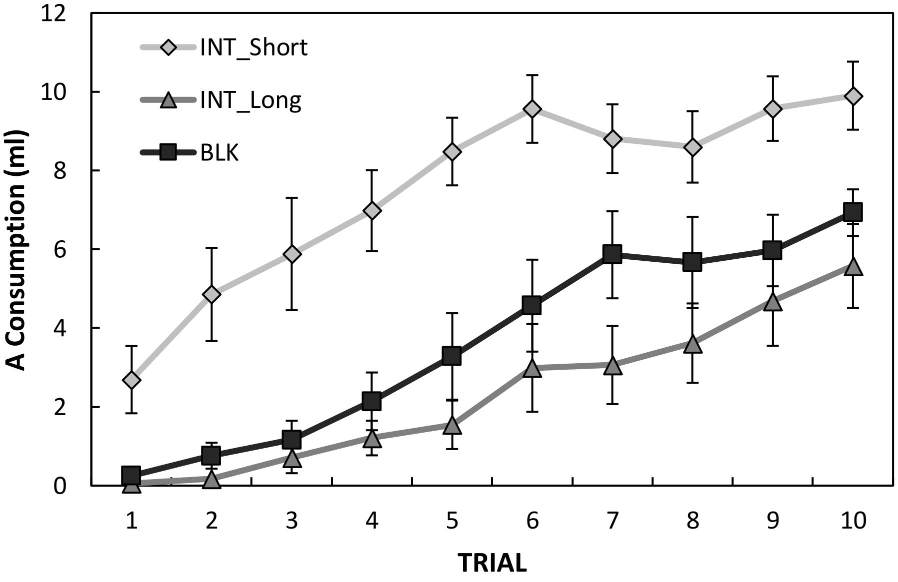

Figure 22. Experiment 2: Average consumption (±SEM) of A in conditioning phase trials. INT_Short refers to the group that received Intermixed exposure within sessions, INT_Long refers to the group that received Intermixed exposure between days and BLK refers to the group that received Blocked exposure.

A separate repeated measures ANOVA with groups INT_Short and INT_Long showed effect of Test Trial, *F* (3.6, 72.2) = 23.15, MSE = 10.22, *p*<.05 and η2p = 0.54; effect of Group, *F* (1, 20) = 28.53, MSE = 51.54, *p*<.05 and η2p = 0.59; but not interaction between Trial x Group. Another separate repeated measures ANOVA with groups INT_Short and BLK showed effect of Trial, *F* (3.4, 65) = 30.76, MSE = 10.05, *p*<.05 and η2p = 0.62; effect of Group, *F* (1, 19) = 14.1, MSE = 55.76, *p*<.05 and η2p = 0.43, but not interaction Trial x Group. A final repeated measures ANOVA with INT_Long and BLK groups only showed significant differences on Test Trials, *F(*3.1, 59.6)=27.87, MSE=10.14, *p*<.05 and η2p = 0.59.

Discussion

The results showed that the unique element A was less associable with the aversion during conditioning for the INT_Short group than for INT_Long and BLK groups, but also the former extinguished this association easier than the other two during test trials. However, the INT_Long and BLK groups didn't differ between each other about conditioned aversion level in neither conditioning nor test.

The first part of the results replicate our previous findings and is consistent with our proposal, that rapid exposure in the INT_Short group would habituate their common elements and bias the processing resources towards A, increasing its unitization and reducing its associability. However, these differences were also expected in the opposite direction, i.e. that the unique element from the INT_Long group would acquire the aversion easier than in the Blocked group, and that this would be slower to extinguish. This was anticipated on the basis that INT_Long group would activate associatively the element A in BX trials through intracompound associations, and therefore restore the salience and associability lost in preexposure. Because BLK group cannot activate associatively the unique elements (or generate a processing bias towards them) their salience and associability would be gradually lost during preexposure. The difference in salience resulting from both preexposures should have reflected more aversion during conditioning and extinction in the INT_Long group.

One possibility is that the INT_Long group experienced an excessively long ISI and that this was detrimental for the performance of salience modulation mechanisms. It is true that perceptual learning experiments typically present each stimulus in morning and afternoon sessions with an aproximated ISI of 6h, however there is literature supporting the use of a 24h ISI as an interval for Intermixed exposures capable of producing perceptual learning (e.g., Symonds & Hall, 1995, Experiment 1). Furthermore, we also found no explanation why a longer ISI would reduce the association between X and A, or otherwise impair the ability of X to associatively activate A. Another possibility is that the preexposure phase was too long to reflect a salience difference between the BLK and INT_Long groups. That is, if the salience lost by the unique elements is greater than the salience restored by associative activation, over many trials it would tend to zero as the BLK group, and since salience cannot be further reduced both unique elements would result in a similar level of associability. However, there are also examples in the perceptual learning literature showing enhanced discrimination after 10 or more Intermixed trials in contrast to the respective Blocked arrangement, which also rules out the above hypothesis (e.g., 12 preexposure days in Recio et al., 2019).

However, given that most of the findings in perceptual learning with spaced presentations have shown an increase in the effectiveness of their unique elements, and adding the results we obtained from our Experiment 1, we decided to repeat this experiment by directly comparing the salience resulting from the unique elements of the INT_Long and BLK groups.

Experiment 3: Conditioning of A after Spaced Intermixed or Blocked preexposure

The design of Experiment 3 is summarised in Table 7. The procedure is exactly the same as in the previous Experiment 2 of this Chapter, but with only the INT_Long group and the BLK group. During the 10 preexposure trials both groups will receive the same stimulus twice in each session, but the INT_Long group will change stimulus after each session and the BLK group after session 5. Then, the consumption of element A will be measured during the 5 conditioning trials, in which half the LiCl dose will be used, and during the non-reinforced extinction trials. As before, we expect that preexposure in the INT_Long group will develop a more salient element A, reflecting a deeper acquisition of aversion during conditioning and thus a slower extinction during trials, than the element A of BLK group.

Method

Subjects and Apparatus

Subjects were 16 naïve male Wistar rats with a mean ad libitum weight of 527 g (range 590 g-487 g). They were divided into two groups (INT_LONG and BLK) of eight approximately matched for weight (mean INT_LONG weight: 524 g; BLK: 529 g) and water consumption. These two groups were treated exactly as in Experiment 2 and the test phase lasted 6 trials in this experiment. Data from one rat in the INT_Long group was excluded from the analysis because it was positive in the outlier analysis, it was impossible to establish a conditioned aversion for this rat which after 5 conditioning trials still consumed 8.7ml of A in test 1. Other details not mentioned here were identical to Experiment 2.

Results

During the morning sessions in the preexposure phase, the rats consumed virtually all the liquid available in the tubes, both flavored compounds and water. As shown in figure 23, the consumption of A in the conditioning phase increased slightly from the first to the second trial, but then decreased slowly until the fifth trial; in any case this curve was apparently equal for both groups. This initial increase in consumption could be due to the high latent inhibition carried over by A after 10 days of preexposure. A repeated-measures ANOVA with Trial and Group as factors showed differences between trials, *F* (4, 52)

= 46.45, MSE = 3.62, *p*<.05 and η2p = 0.78, but neither between groups nor interaction between these factors (largest *F(*4, 52)=2.03, MSE= 3.63, *p*>.05 and η2p = 0.13).

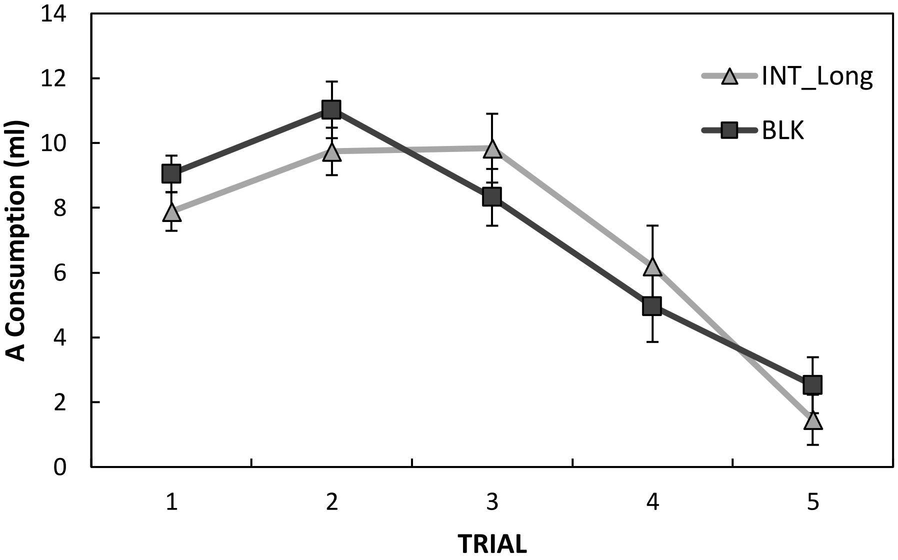

Figure 23. Experiment 3: Average consumption (±SEM) of A in conditioning phase trials. INT_Long refers to the group that received Intermixed exposure between days and BLK refers to the group that received Blocked exposure.

Figure 24 shows the consumption of A during the six test days, where the INT_Long group showed lower consumption than the BLK group on all the tests although both increased slowly across extinction trials. A repeated-measures ANOVA with Trial and Groups as factors confirmed these impressions, revealing a significant effect of Trial *F* (2.1, 27.8) = 8.68, MSE = 15.21, *p*<.05 and η2p = 0.4; and Group *F* (1, 13) = 4.59, MSE = 33.23, *p*=.05 and η2p = 0.26; but not interaction between these factors.

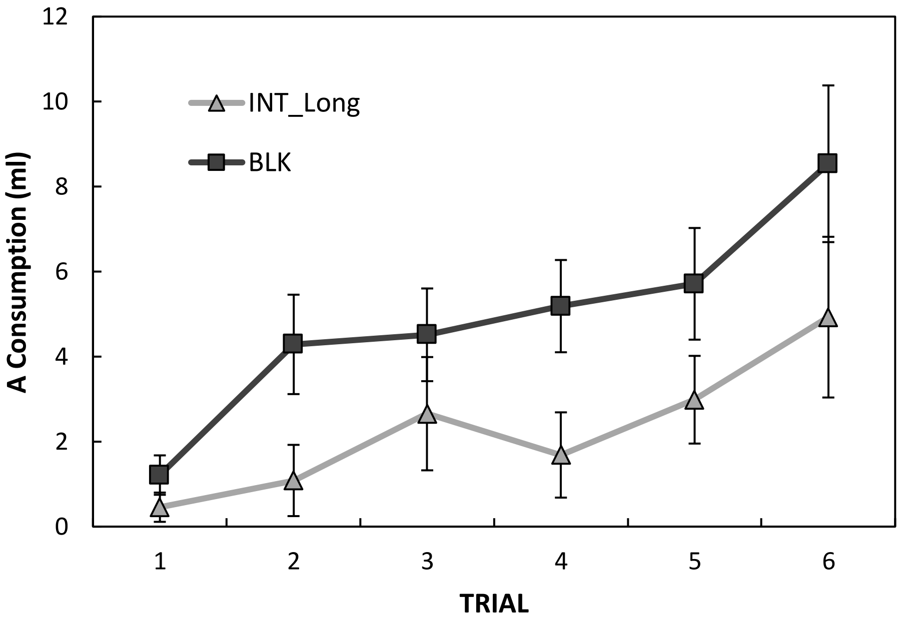

Figure 24. Experiment 3: Average consumption (±SEM) of A in test phase trials. INT_Long refers to the group that received Intermixed exposure between days and BLK refers to the group that received Blocked exposure.

Discussion

The results obtained from Experiment 3 show a similar acquisition rate for both groups during conditioning, but a flatter extinction curve for the INT_Long group at test, suggesting a better associated aversion to A in the INT_Long group than in the BLK. These results are congruent with salience modulation theories. During Intermixed spaced preexposure X will activate the element A through intracompound associations in BX trials, this according to McLaren and Mackintosh (2000) produces a deunitization of the unique element that reduces latent inhibition and increases associability, whereas for Hall (2003) the absence of this element is unexpected and the processor increases responsivity to it. In either case, both predict a stronger association of A with aversion after Intermixed spaced exposure than Blocked, which is what we found.

These results replicate previous findings such as those of Blair et al. (2004; see also Mondragón & Hall, 2002), who found after spaced Intermixed preexposure a lower extinction of conditioned aversion to A (Experiment 3a) and after modifying certain parameters also a deeper conditioning of this aversion (Experiment 3b). Anecdotally, a repeated measures ANOVA was carried out with the aggregated data of the INT_Long and BLK groups from Experiments 2 and 3, which still shows significant differences between these groups on the first 6 tests, $F(1, 34)=5.69$, MSE=28.48, $p<.05$ and $\eta 2p = 0.14$.

Finally, considering the differences also found with the INT_Short group in Experiment 2, the data from both experiments reflect that the different ways in which similar stimuli are exposed modify the properties of their elements in order, in the case of Intermixed exposures, to improve their discrimination. This suggests that perceptual learning is a flexible phenomenon that, depending on the demands of the task, may involve one mechanism or another.

General Discussion

In this chapter we have tested the proposed mechanisms from salience models to explain perceptual learning when stimuli are spaced apart and, thus, a direct comparison is not possible. Experiment 1 preexposed in the morning two similar stimuli in rapid alternation, with a distractor between them, and in the afternoon the common element for half of the rats and water for the remaining. Then a new element Y was aversely conditioned and the generalization of the aversion to AY compound measured at test. The results showed a higher intake of the AY compound by rats that received X presentations apart, suggesting that the unique element A was so salient that it interfered with the Y conditioned aversion. Because the distractor prevented any rapid comparison mechanism to act (Dwyer et al., 2011; Recio et al., 2018), this results has been explained in terms of salience modulation. Stimuli presented in morning sessions would develop associations between their unique and common elements, so that when the common element was presented in the afternoon it would associatively activate the unique one and restore its salience. McLaren and Mackintosh (2000) would explain that this associative activation would weaken the unitization of the unique elements with themselves and with the context, so they become less latent inhibited and gain effectiveness. On the other hand, Hall (2003) would say that the associative activation of the unique element is surprising to the subject, because it used to be presented physically with the common element, and therefore subjects are henceforth susceptible to it, i.e. it became more salient.

In the following experiments we evaluate these spaced mechanisms along with the rapid comparison mechanism, by measuring the associability of unique elements after a preexposure with different inter-stimulus intervals. In Experiment 2, rats in the INT_Short group received AX and BX separated by 5 min of water, rats in the INT_Long group received a different stimulus each day, and rats in the BLK group received one stimulus in the first half of preexposure and the other on the remaining days. Subsequently, the A element would be associated with a conditioned aversion and the extinction of this association would be measured during non-reinforced A trials. The INT_Short group was introduced to compare both rapid and spaced perceptual learning mechanisms versus a BLK group which would have no perceptual learning mechanism and would serve as a control.

On the one hand, the INT_Short group was expected to habituate common elements in the short term by increasing the processing of unique elements (Honey & Bateson, 1996), this bias will enhance the unitization of such elements by increasing their discrimination but reducing their associability (Recio et al., 2018). On the other, the INT_Long group was expected to increase the associability of unique elements as proposed by salience modulation models (Hall, 2003; McLaren & Mackintosh, 2000). The results of Experiment 2 showed in the INT_short group a lower associability of element A during conditioning and also a faster extinction of this association during the test than for the other two groups, while the latter did not differ in any respect.

This result was congruent with our previous findings and with the proposed mechanisms for rapid comparison in perceptual learning, however the absence of differences between the INT_Long and BLK groups was unexpected on the basis of previous findings. Experiments such as that of Blair et al. (2004) have previously shown that spaced Intermixed preexposure increases the associability of unique elements during conditioning and extinction more than Blocked preexposure. Accordingly, we expected the INT_Long group to show a faster conditioning with the aversion and a more resistant association during extinction than in group BLK. Since these predictions were based on previous findings, we conducted Experiment 3 with the same procedure but only in INT_Long and BLK groups. This time, in agreement with Blair et al. (2004), the INT_Long group reflected a stronger association between element A and aversion than the BLK group during the extinction phase. In fact, pooling the results of both tests still shows differences in this respect between the INT_Long and BLK groups (and respectively with the INT_Short group from Experiment 2).

In view of the different mechanisms underlying perceptual learning, our theoretical proposal is that depending on the demands of the task, any of them can be activated, affecting differently the salience and associability of unique and common elements, but in any case leading to a better discrimination of similar stimuli, that is perceptual learning (see Figure 25). As we have seen in previous chapters, the rapid presentation of similar stimuli produces a habituation of the common elements that are always present, leading in Intermixed schedules to a processing bias towards the unique ones on alternated trials (Honey & Bateson, 1996). This improved processing increases the unitization of the unique sub-elements with themselves, which creates a high quality and easily discriminable representation, but also with the context, which increases the latent inhibition and reduces their associability and salience (Recio et al., 2018).

On the other hand, Intermixed spaced presentations use other mechanisms based on restoring the salience lost during preexposure of the unique elements to increase discrimination. These salience models assume that exposure produces intracompound associations between unique and common elements, so that on Intermixed trials the spaced presentation of a stimulus, e.g. AX, will activate through the associations with the common element, X, the unique one absent, B, and vice versa on alternating trials. For McLaren and Mackintosh (2000) associative activation of unique elements implies that associations within sub-elements and with the context will be weakened, that is a deunitization process, which reverses the latent inhibition and restores the associability. Instead, Hall (2003) would explain that the absence of the unique element was unexpected, as it used to appear together with the associated common element, which will produce a discrepancy in the processing system of the subject and increase the responsiveness to it that is its salience.

Finally, the main conclusion that emerges from these experiments is that perceptual learning is a flexible phenomenon that, depending on the demand of the task or the environment, will activate one mechanism or another ('rapid' or 'spaced') to improve subsequent discrimination between similar stimuli. Furthermore, it has been proposed that these task-dependent mechanisms which enhance discrimination are indeed universal, meaning that they transcend not only differences between individuals, but also between species (Recio et al., 2018). Therefore, in the next chapter, we will evaluate in humans the effects of rapid, blocked and intermixed exposure to similar visual stimuli. We expect to find better discrimination of intermixed stimuli, but critically, also worse associability of these stimuli due to the unitization mechanism. These results would replicate and complement our results already found in animals.

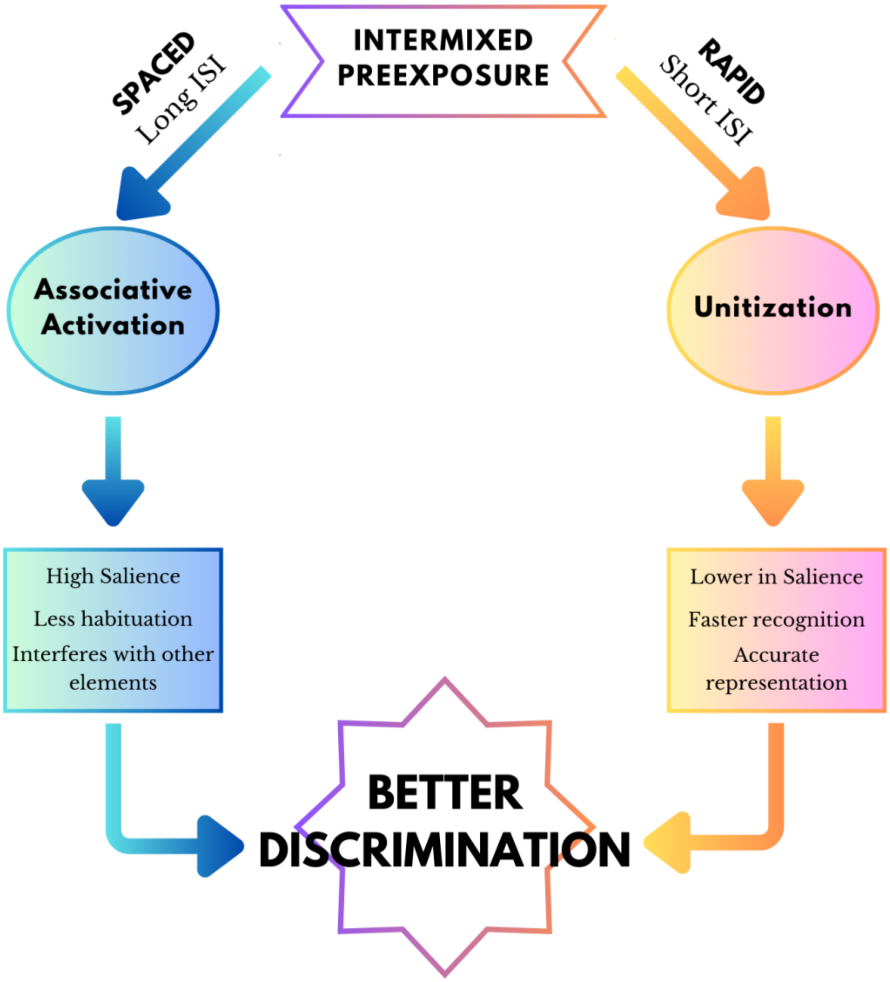

Figure 25. Shows how Intermixed presentation of similar stimuli takes different paths, depending on the interval between presentations, each involving different mechanisms and changes in the properties of the stimuli but finally both leading to a better discrimination

CHAPTER VIII – HUMAN COMPARISON

Introduction

It has been shown that subjects, human and non-human, improve their subsequent discrimination between similar stimuli when previously these have been rapidly exposed in an Intermixed rather than a Blocked scheme (e.g., Ballesta et al., 2021; Dwyer et al., 2011; Lavis et al., 2011; Mitchell et al., 2008a; Mundy et al., 2007; Recio et al., 2018; 2019; Sánchez et al., 2022). Honey and Bateson (1996) proposed that rapid alternating presentation of similar stimuli habituates the common elements in the short term, freeing resources to better process the unique ones. Additionally, Recio et al. (2018) suggested that this processing bias should increase the unitization of unique elements, and thus favor the representation and discrimination of stimuli while reducing their associability and salience. We have positively tested these latter predictions in previous chapters using animals as subjects and flavored beverages as stimuli, now our aim is to assess these mechanisms in the human domain.

Briefly, the I/B effect has been demonstrated numerous times in humans with rapidly presented visual stimuli (e.g., checkerboards in Lavis & Mitchell, 2006; Recio et al., 2016; and faces in Mundy et al., 2007) and it is comfortably explained by the short-term habituation mechanism of Honey and Bateson (1996). Indeed, Dwyer et al. (2011) showed that introducing a distractor between stimuli suppressed the advantage of Intermixed exposure, as it supposedly disrupted the short-term habituation of common elements thus eliminating the processing bias. However, little research has been done to understand what this enhanced processing of the unique elements actually means. If, according to Recio, it results in a better unitization of the unique elements, the prediction that follows is that these elements will be better discriminated and recognised but will increase their latent inhibition, meaning that they lose associability.

In these sense, Lavis et al. (2011) preexposed colored checkerboards AX/BX Intermixed and CX_DX Blocked, after which the colored square patterns that make the unique elements (A, B, C and D) were presented uncolored in test for participants to choose the color with which they were exposed. The color-match test results reflected better accuracy for the unique elements that were preexposed in Intermixed fashion. These results suggest a unitization of the unique element in the Intermixed exposure, since in the test the sampling of the sub element "shape" would favor the associative activation of the sub-element "color". Similarly, De Zilva and Mitchell (2012) used different matrices of 12 figures (3x4) in which one figure represented the unique element (e.g., A) and the remaining 11 the common background (X). Two pairs of matrices were presented Intermixed (AW/ BW and CX/DX) and two Blocked (EY_FY and GZ_HZ). The Same/Different test showed better discrimination for the Intermixed matrices, but also better subsequent identification of the unique Intermixed figures in a recognition test. Better recognition is also likely to reflect greater unitization, as sampling one sub element would associatively activate the whole representation of that element.

Our main goal in this chapter is to test the unitization mechanism in perceptual learning human tasks by assessing the recognition and associability of visual stimuli after rapid Intermixed and Blocked exposure. So, some procedural considerations relating to the human condition must be taken into account beforehand.

First, we want to provide a procedure capable of avoiding localisation and instruction biases. For example, Lavis et al. (2011) found that additional exposure to 2 unique elements (A and B) enhanced subsequent discrimination for stimuli containing them (AX and BX). However, Recio et al. (2016) were unable to replicate this effect when changing the location of the unique elements in the additional exposure, possibly reflecting that participants were biased to attend only to the place where differences appeared. Furthermore, Recio et al. (2016) were unable to find the basic I/B effect with checkerboards

(Lavis & Mitchell, 2006) when they changed the instructions that encouraged subjects to look for differences to irrelevant ones or even when they removed the instructions. Unlike discriminative learning that uses instructions to reinforce finding differences, perceptual learning should enhance discrimination by simple exposure without reinforcement.

Secondly, we aim to develop an attractive way to present stimuli and assess learning, as typical human procedures use to be repetitive and without interesting stimuli, e.g., Lavis et al. (2008) presented 320 checkerboards to each participant. There have been some studies which have used videogames as procedures and have obtained optimal results (e.g., Pineño, Ortega & Matute, 2000). For example, Nelson and Sanjuan (2009; see also Nelson, Navarro & Sanjuan, 2014) assessed perceptual learning using a video game in which participants had to attack enemy spacecraft to score points. They preexposed participants to similar colored sensors (AX and BX) in Intermixed or Blocked fashion while they fired at enemies. In conditioning, the AX sensor was presented followed by an incoming enemy attack that rendered participants' weapons useless, then participants tended to suppress their shots when AX was presented. At the final test, BX sensor was presented followed by no attack, and participants tended to reset their firing more readily when the sensors had been preexposed Intermixed than Blocked, or even not preexposed. This experiment shows lower generalization between two similar stimuli, previously preexposed in rapid alternation, when one of them is conditioned and the other is not, the classic I/B effect.

Similar to Nelson and Sanjuan (2009), we have developed a method to assess the discrimination and associability of visual similar stimuli based on the famous saga of “Pokémon” games. We believe that using this kind of procedure, different from the classical ones, has some advantages such as keeping the attention of the participants from the first to the last answer ensuring the quality of the data. Following the short-term habituation mechanism (Honey & Bateson, 1996) we would expect, as in the case of animals, that the stimuli previously exposed in rapid Intermixed fashion would be better recognizable because they are better unitized but also that they would be more difficult to associate to other events because they have increased latent inhibition.

Experiment 1: Recognition Test

Experiment 1 (Table 8) presented a short computer task to human participants, similar to a video game with visual stimuli. An in-game instructor (Professor Oak) will ask them to take pictures of different creatures, Pokémon, that will appear on the screen. These Pokémon were fantastic but based on real animals, and each of them had some variants with small differences that were used as similar stimuli. First, the instructor took the subjects to a practice block where they were asked to press a key on the keyboard to take a picture of the Pokémon as soon as it appeared; this was the general instruction to ensure that the subject paid attention to the stimuli presented. After this phase, the instructor gave the same instructions and the preexposure began. Four variants of a Pokémon were rapidly presented, two of them Intermixed (AX/BX) and the other two in separated blocks (CX_DX). Instructions and preexposure were repeated again for other different Pokémon variants, a pair in Intermixed fashion (EZ/FZ) and another pair in Blocked (GZ_HZ) as well. Finally, separated recognition test were carried out for both Pokémon variants (practice Pokémon were excluded for the test). In the test the four preexposed variants of each Pokémon were presented among a variable number of distractor variants, subjects had to select specifically the variants that were preexposed. The rapid alternation of the Intermixed variants would habituate their common elements in the short term, freeing up resources to process the unique elements, making it easier for participants to recognise the Intermixed variants among the distractors rather than the Blocked ones. We expect that sampling of unique elements from Intermixed exposure would active the whole element representation due to a greater unitization.

EXPERIMENT 1

Practice	Preexposure1	Preexposure2	Recognition Test1	Recognition Test2
QZ, RZ, SZ & TZ	AX, BX, AX, BX...	EY, FY, EY, FY...	AX-BX-CX-DX	EY-FY-GY-HY
randonm order	CX, CX…, DX, DX…	GY, GY…, HY, HY…	IX-JX-KX-LX…	MY-NY-OY-PY

Table 8. Within-subjects design. Practice block presented similar stimuli in random order. Preexposure phases presented different pairs of similar stimuli in Intermixed arrangement and another pairs in Blocked. Recognition test presented the preexposed similar stimuli among other similar distractors. During practice and preexposure phases subjects had to press a key as soon as the stimuli is presented. In Recognition test subjects had to select the stimuli that had been previously presented during preexposure. During preexposure the order for Intermixed or Blocked arrangement was counterbalanced.

Method

Subjects

Subjects were 53 students from the University of Granada predominately between the ages of 18 – 22 (81% female) who, after being informed that they would take part in an experiment involving cognitive tasks, agreed to participate in exchange for psychology course credits or voluntarily. All participants had normal or corrected-to-normal vision. The procedure used a within-subjects design, so all subjects went through all stages of the procedure. This procedure was approved by the Comité de Ética de la Universidad de Granada 694/CEIH/2018 (Ethics Committee of the University of Granada).

Apparatus and Stimuli

The stimuli were 4 variants of each of three Pokémon animal-based: a deer, a butterfly and a panda. The deer variants were differentiated by antler decorations. The butterfly variants had different colored patterns on the wings. The panda variants differed in the fur spots location, size and shape. The basic Pokémon made up the common element (e.g., X) and its differences (e.g., A, B, C, and D) the unique elements. The four variants of each Pokémon appeared at different fixed stages, the deer variants were used in practice because they were very easy to discriminate, the butterfly variants were used for Preexposure1 and the panda variants for Preexposure2, the latter two also appeared for their recognition test (1 and 2) among a number of the corresponding distractor variants.

Participants interacted with the program using a Spanish QWERTY keyboard and a wired mouse. The keys used throughout the experiment were F to take the pictures, Space to advance through the instructions, Q to exit at the end of the experiment and the left mouse button to select their responses in the recognition tests. Before the start of each phase, the image of the instructor was always presented on a black background with white letters giving the instructions, and to indicate that pressing Space either advanced to the next instruction or started the task (or at the end that Q exited the experiment). The stimuli were presented on a 17-inch PC screen, they were always centred during practice but during preexposure they were also placed oriented to each corner of the screen. In the practice and preexposure phases, a black fixation cross was presented in the centre of the screen before each stimulus. The background used whenever stimuli were presented was a clear, well-lit image of an imaginary forest. During the practice phase they were provided with information in black letters in the centre of the screen about the speed at which they pressed the F key when the stimulus appeared.

Design and Procedure

The participants were required to sign a consent form before carrying out the task. They were seated in front of the computer in an adjustable chair, at approximately 1 m from the screen, in a small isolated room. They were asked to read the instructions carefully and to resolve any doubts with the experimenter before the start of the experiment.

The experiment consisted of three phases: practice, preexposure, and test. In the practice phase, four deer variants were used, each presented twice. The instructions for practice and preexposure phases, translated from the Spanish, were as follows:

[...] *Take a picture as fast as you can every time a Pokémon appears by pressing the F key* [...]

Instructions for recognition tests, translated from the Spanish, were as follows:

[...] *Click with the mouse on the 4 Pokémon that you have photographed* [...]

Each trial began with a fixation point on the centre of the screen for 300 ms, followed by the stimulus. The stimulus remained on the screen until the subject responded in practice phase. The participants received a feedback screen, with duration of 1.000 ms, showing the response time made. The RT was included to give plausibility to the task given to these subjects. Before the next trial, there was a variable interval of between 500 and 1.500 ms, during which the screen remained with the forest background.

Preexposure phase used the same trial sequence except that the stimuli remained in the screen during 480 ms, independently of the subject response, and feedback was not provided. The participants received a reminder of the instructions on screen before each preexposure phase began. There were 80 trials in total divided in two preexposure phases; the first was always with the butterfly variants and the second with the panda variants. For each preexposure phase there were 40 trials, 10 for each variant. Therefore, in a preexposure phase 20 trials consisted of the Intermixed exposure of AX and BX (AX/BX/AX/BX . . .), and 20 of the Blocked preexposure of CX and DX (CX/CX . . . DX/DX . . .). The order of the type of exposure was randomized between participants. Also, the stimuli were presented twice randomly in 5 different positions on the forest: top-left, top-right, centre, bottom-left and bottom-right. To maintain the game gravity illusion, the pandas were also presented in these 5 positions, but on the forest floor.

At the end of the panda preexposure phase, participants were given new instructions about the test. They were told that all the photographs they had taken were mixed up with other participants photographs by mistake and that they needed to identify them by left-clicking on the 4 variants of each Pokémon to which they had been preexposed. Two recognition tests were performed, first always the butterfly test followed by the panda test. In each test the 4 preexposed variants were presented simultaneously with other non-preexposed variants of the same Pokémon, all of which remained on the screen until the end of the test. Due to the predetermined base of variants, the butterfly test was able to add 16 distractors and the panda test only 4. In total there were 4 test response types: Intermixed-Butterfly, Blocked-Butterfly, Intermixed-Panda and Blocked-Panda, as we had two stimuli for each condition the total score for each response type could be 0, 1 or 2. They were strongly cautioned not to click repeatedly on the same stimulus or on another stimulus-free space, as the program proceeded to the next procedure stage after the first 4 clicks. To discourage this, a counter was added to the number of stimuli selected and these were marked with a red tick until the next click.

Statistical Analysis

The analyses were conducted on the percentage of correct responses for each type of test trial. General linear model null hypothesis testing analyses were conducted, adopting a rejection level of $p < 0.05$, and used Greenhouse-Geisser corrections when needed. Partial eta squared (η2p) and Cohen's d were used to report effect sizes. Within-group components of the design were analyzed using repeated-measures ANOVA, with Test Stimulus (Butterfly – Panda) and Preexposure type (Intermixed – Blocked) as within-subjects factor. Interactions between these factors were explored using independent samples t-Tests. Data from 6 participants were removed from the analyses because they selected parts of the screen in the test where no stimulus was present, or they selected the same stimulus several times. The JASP software was used to carry out all statistical analyses.

Results

Figure 26 shows the percentage of correct responses for each trial type. The average percentage of correct responses for Intermixed stimuli was 67.02% and for Blocked 56.38%. Separated by Test the mean correct responses of the Butterfly test was 68.09% for Intermixed stimuli and 50% for the Blocked stimuli, and the mean percentage for the Panda test was 67.02% and 61.7% respectively. As expected, subjects were better able to identify Intermixed preexposed stimuli than Blocked preexposed stimuli. Repeated measures ANOVA with Test and Preexposure as within-subjects factor (2 x 2) confirmed this impressions and showed significant effect of Preexposure type, *F(*1, 46) = 6.58, *p* < .05, η2p = .12, MSE = 1262.72; but no effect of Test, *F(*1, 46) = 1.24, *p* > .05, η2p = .03, MSE = 1262.72; and no interaction between these factors, *F(*1, 46) = 6.58, *p* > .05, η2p = .03, MSE = 1262.72. One sample T-Test using 50 (%) as fixed value for the alternative hypothesis showed differences in the Intermixed stimuli, *t*(46) = 4.99 and *p* < .05, but not in the Blocked stimuli, *t*(46) = 1.95 and *p* > .05. The latter analysis confirms that response scores for stimuli preexposed in a Blocked fashion were random, but not for stimuli preexposed in an Intermixed manner.

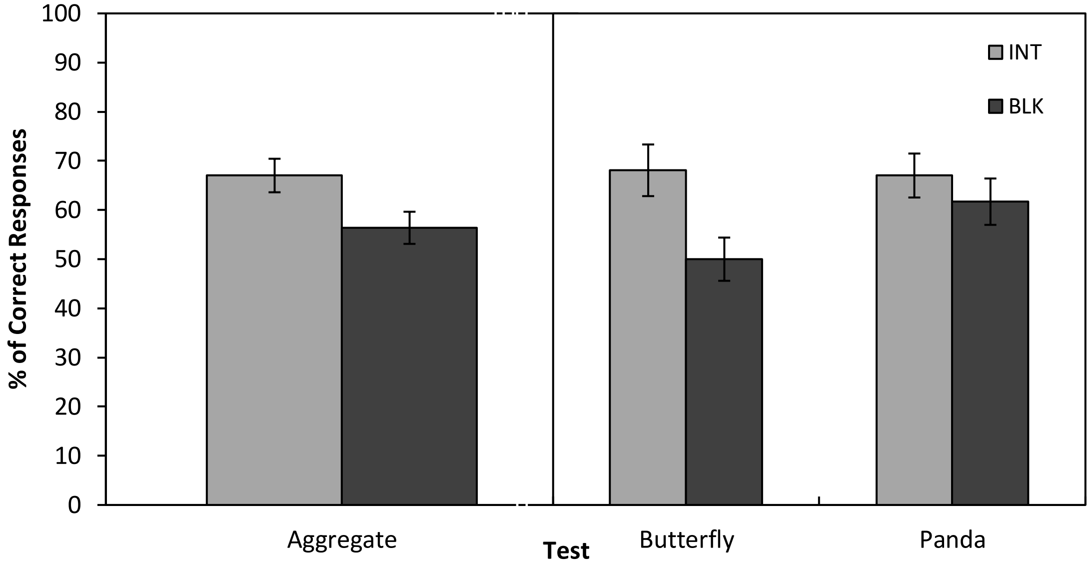

Figure 26. Experiment 1: Percentage of test correct responses in aggregate (left panel) and by stimuli (right panel): the Butterflies (left columns) and Pandas (right columns), each composed of Intermixed (INT label) and Blocked (BLK label) type of preexposure, with error bars indicating SEMs.

Discussion

We have found with human participants that rapid Intermixed presentation of similar stimuli improves their recognition later in the test more than their presentation in separate blocks. According to previous studies, rapid alternating presentation would cause the common elements of butterflies or pandas to become habituated in the short term (Honey & Bateson, 1996), freeing up processing resources to unitize the differential elements of the variants (Recio et al., 2018). Consequently, these stimuli would be more recognisable than less-unitized Blocked stimuli and distractors. The sampling of one unitized sub-element from Intermixed stimuli would prime the activation of the others and of the unique element itself, favoring their recognition and selection. In fact, the analyses showed that the Blocked stimuli were selected at the level of chance, making their recognition as likely as that of the non-preexposed distractors.

Secondary, we accomplished this effect while avoiding the two biases that can normally affect human performance, instructional and locational bias. Perceptual learning experiments typically encourage subjects to find differences between stimuli during preexposure, these differences can be detected easier in the Intermixed exposure and lead to better subsequent discrimination against Blocked stimuli. Our experiment 1 found the I/B effect with instructions focused on the masking task, i.e., taking a picture of each Pokémon variant by pressing F. We used this instruction to keep participants' attention on the screen and ensure that they were being exposed to the stimuli. However, they were never told to look for differences, the closest prompt was that different variants would appear and that they "gotta photograph'em all". Accordingly, other procedures had also found the I/B effect with instructions focused on the masked task (Angulo et al., 2019), although it must be acknowledged that normally this effect is larger when using instructions focused on searching differences.

Finally, to prevent subjects from developing a location bias towards differential elements or a particular part of the screen, the stimuli were presented in random order at 5 different locations on the screen. It has been shown by eye-tracking methods that participants more easily focus attention during preexposure on unique Intermixed elements than on Blocked elements (Wang & Mitchell, 2011), presumably due to the trial-by-trial change these are easily detectable. However, when the location of these elements is changed, focused attention fails and the I/B effect is eliminated (Recio et al., 2016). Using eye-tracking recordings, Wang et al., (2012) preexposed two Intermixed checkerboards, and switched their unique elements for new ones in the test. They found that these checkerboards were better discriminated than two new ones that had incorporated the previously preexposed unique elements in other locations. Eye gaze registration showed that participants focused on the locations where the unique elements used to be, so the new ones were easily detected, but they failed to discriminate the preexposed unique elements in other locations. It is true that the relative position of the unique elements within our stimuli didn’t change, but indeed, our procedure induced participants only to look for the stimuli as a whole to take a picture, and the random order of position forced the subject to change the location of attention.

To sum up, our game-like procedure found the classic I/B effect with position-changing stimuli and instructions focused on a masking task, which supports perceptual learning and the short-term habituation mechanism in humans (Honey & Bateson, 1996). The next step is to find evidence that this improved recognition was due to greater unitization of the Intermixed stimuli. For this purpose, Experiment 2 will assess the associability of our stimuli after the preexposure phase. If unique elements become more unitized after Intermixed exposure, these stimuli should be more difficult to associate with new events than Blocked stimuli, and even more so than non-preexposed stimuli.

Experiment 2: Conditioning Test

Although there were no differences between test stimuli in Experiment 1, a larger effect was observed for butterflies. It may be that the pandas' spots were easily discriminated and this increased Blocked recognitions, or perhaps simply the fact that only 4 distractors were added for this stimulus increased the probability of a correct response. In any case, for the following experiment we will use only the butterflies.

Experiment 2 (Table 9) used virtually the same practice block with deer and the same preexposure with butterflies as Experiment 1. The last of the deer in the practice block laid an egg, which surprised the instructor who, at that point and before the preexposure began, changed the instructions. The participants would enter a forest and observe different butterflies, some of which would be females that, after a period of familiarisation (preexposure), would start laying eggs. Then the task of the participants was to take pictures of the eggs as fast as they could. Preexposure to the butterflies occurred exactly as in Experiment 1 (without any eggs) and was followed directly, without any interrruption, by the reaction time test phase. This phase presented at the centre of the screen in random order two Intermixed, two Blocked and two Non-Preexposed butterflies, one of each type followed by an egg (female) and the other half not (male). Participants were required to press F to photograph the eggs as quickly as possible, this measure of reaction time allowed us to infer the level of associability and predictability of each butterfly towards the egg. Finally, in the expectancy test, the 6 butterflies used were presented in random order and subjects were asked to judge from 0% to 100% the probability of that butterfly being female.

We expect that the more associable butterflies (Blocked and Non-Preexposed) will be better linked to the outcome eggs and, therefore, on subsequent trials, the presentation of these butterflies will associatively prime the egg representation and boost participants' responses showing shorter RTs. Conversely, the Intermixed butterflies with more difficulties to establish associations with the egg, will show higher RT than for the other two conditions. In parallel, we anticipate participants to assess more accurately the egg expectancy following Blocked and Non-Preexposed stimuli than Intermixed.

EXPERIMENT 2

Practice	Preexposure	Reaction Time Test	Expectancy Test	
RY, SY, TY & UY	AX, BX, AX, BX...	AX+, BX-,	AX BX	+?
		CX+, DX-,	CX DX	
random order	CX, CX…, DX, DX…	EX+, FX-.	EX FX	

Table 9. Experiment 2: Within-subjects design. Practice block presented similar stimuli in random order. Preexposure phases presented different pairs of similar stimuli in Intermixed arrangement and in Blocked. Conditioning exposure presented these pairs and another new, which one member of each pair was followed by an egg and the other member by nothing. Test showed each of the members of the pairs and a scale to rate how possible is that stimulus was followed by an egg.

Method

Subjects

Subjects were 86 students from the University of Granada predominately between the ages of 18 – 22 (88% female). The RT correction method used, which will be explained in the statistical section, eliminated all responses from 1 participant whose data was consequently removed from the experiment. Finally, although students were warned not to participate in this experiment if they had already participated in Experiment 1 above, we found two participants who had, so both data were excluded from the final analysis as well.

Apparatus and Stimuli

For the practice block we again used the same 4 deer. For the rest of the procedure, we used 3 pairs of butterflies, one Intermixed, one Blocked and one Non-Preexposed. These butterflies were the 4 variants used in the previous experiment plus 2 new variants that were used previously as distractors, all counterbalanced so that even those used as distractors could now be Intermixed or Blocked preexposed. We also introduced a white egg with red spots for the practice block and a yellow egg with pink spots for the reaction time test.

Design and Procedure

The experiment consisted of four phases: practice, preexposure, reaction time test and expectancy test. The practice phase was the same as in Experiment 1 above, but after the last presentation of a deer an egg appeared. Then the instructor came along and suggested that some of the Pokémon, deer or butterflies, might be female and therefore capable of laying eggs. Then, in the next phase, the new task was to look carefully at the butterflies and take a photo as soon as they laid an egg by pressing the F key again. The preexposure phase was immediately followed by the reaction time test phase without any interruption perceptible to the subject. This was implemented because some studies with humans have found that giving instructions or a long interval between these phases removes latent inhibition of the preexposed stimuli. We expected that telling subjects to remain attentive to any time the butterflies laid an egg would be sufficient to maintain attention from the preexposure phase, which lasted only 2 minutes, to the reaction time test beginning.

The preexposure phase was identical to the butterfly preexposure of Experiment 1, although this time two new butterflies could also be part of the four preexposed stimuli. The reaction time test phase presented all stimuli randomly in the centre of the screen; a black fixation cross was presented for 300 ms followed by a butterfly lasting 600 ms and, depending on the condition, this was followed by an egg or nothing for 1000 ms. There was a variable interval of 500-1500 ms between the end and start of each trial. Each of the butterflies presented belonged to one of 6 conditions, Intermixed preexposed followed by an egg (INT+), Blocked preexposed followed by an egg (BLK+), Non-Preexposed followed by an egg (NP+), and their counterparts followed by nothing (INT-, BLK- and NP-). Each butterfly was presented 4 times in random order. The response to the egg was recorded as RT, we expect that better egg-butterfly associations will promote faster responses.

After the reaction time test phase, the instructor appeared again and asked participants to rate with the left mouse button the probability that each butterfly presented in the procedure was female, i.e. followed by an egg, on a scale from 0% to 100%. The 6 expectancy test trials were randomly ordered; the butterflies were presented large in the centre of the screen with the task instructions above, the scale at the bottom, all in white letters, and to the left the selected percentage in blue. In addition, on the right side of the screen subjects were told that, after selecting a score, they could either validate it by pressing F, which took them to the next trial, or change their score by pressing J. Validation instructions were written in green and change instructions in red. Once all six butterflies had been evaluated, the instructor reappeared and said goodbye to the subject. Other details not mentioned were the same as in Experiment 1.

Statistical Analysis

Analyses of the reaction time test phase were performed with the subjects' mean RTs for the stimulus conditions followed by the egg. A repeated measures ANOVA was performed with the mean RTs of each participant for the INT+, BLK+ and NP+ trials. Some extreme RTs values reflected that subjects were not paying attention to the stimuli, e.g. 7ms or 984ms, so we decided to clean the data by removing the responses below or above two standard deviations to perform a more reliable analysis (Miller, 1991; see also Berger & Kiefer, 2021 for a comparison between different corrections of RT data). Because each subject only had 4 responses for each condition, we decided to apply this correction for each of the 6 stimulus condition rather than for each subject. Test analyses were performed on the percentage response for each stimulus condition, INT+, BLK+, NP+, INT-, BLK- and NP-. A repeated measures ANOVA was performed with preexposure (INT, BLK and NP) and conditioning (+ and -) as within-subjects factors. Two subjects' four RT responses for BLK+ and NP+ respectively were excluded by standard deviation correction, so the mean of all subjects for each of both conditions was used to replace the values.

Results

Figure 27 shows the subjects mean RT in reaction time test phase when the egg appeared preceded by each type of stimulus. It can be observed from the figure that the egg was faster anticipated by subjects when it was preceded by a Non-Peexposed butterfly than an Intermixed butterfly, but also when the egg was preceded by a Blocked butterfly. The mean RT for INT+ trials was 421.7ms, for BLK+ was 399.54ms and for NP+ was 405.91ms. A repeated measures ANOVA carried out with each subject average RT for each type of trial showed differences in this regard, *F(*2, 164) = 5.32, *p* < .05, η2p = .06, MSE = 2029.68. A paired samples T-Test was used to analyze these differences between the three type of trials, showing significant differences between INT+ and BLK+, *t*(82) = 3.26, *p* < .05 and *d* = 0.36, and between INT+ and NP+, *t*(82) = 2.17, *p* < .05 and *d* = 0.24, but not differences between BLK+ and NP+ trials, *t*(82) = 0.92, *p* > .05 and *d* = 0.1. Anecdotally, the same analyses were performed on the raw data and the same pattern of results was found.

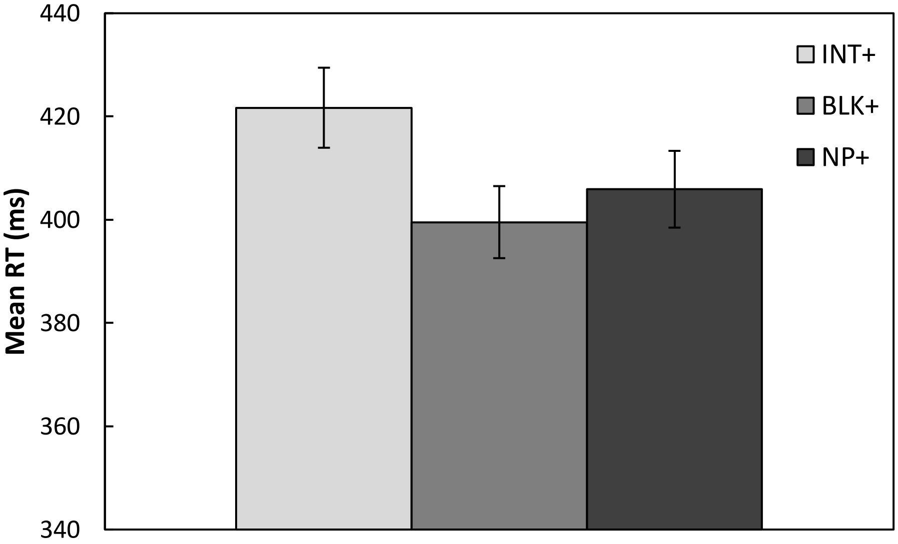

Figure 47. Experiment 2: Mean response time (TR) to the egg stimulus as a function of the preceding butterfly that could have been exposed Intermixed (INT+), Blocked (BLK+) or not exposed (NP+), with the error bars indicating SEMs.

The expectancy test phase indicates subject's judgements as 0% that a butterfly was never followed by an egg and as 100% that a butterfly was always followed by an egg. Figure 28 shows the average rating for each of the 6 conditioned butterflies, which scores were as follows: INT- 47.73%, INT+ 52.48%, BLK- 45.12%, BLK+ 46.7%, NP- 42.37% and NP+ 42.87%. Inspection of figure 28 seems to reflect that all mean ratings appear to be at the chance level. In fact, a repeated measures ANOVA with preexposure type (INT, BLK and NP) and conditioning (+ and -) only showed significant effect of preexposure type, *F(*2, 164) = 4.71, *p* < .05, η2p = .05, MSE = 495.22, but no effect of conditioning, *F(*1, 82) = 1.02, *p* > .05, η2p = .01, MSE = 630.47, or interaction, *F(*2, 164) = 0.4, *p* > .05, η2p < .01, MSE = 506. Paired Samples T-Test showed significant differences between the ratings of the Intermixed and Non-Preexposed butterflies, *t*(82) = 2.94, *p* < .05, *d* = 0.32, but no differences between Intermixed and Blocked, *t*(82) = 1.77, *p* > .05, *d* = 0.19, or between Blocked and Non-Preexposed butterflies, *t*(82) = 1.36, *p* > .05, *d* = 0.15. Moreover, a One Sample T-Test analysis using as critical value the chance level (50%) showed that this differed in the case of Non-Preexposed butterflies, *t* (82) = 3.36, *p* < .05, *d* = 2.13, and in the case of Blocked butterflies, *t* (82) = 2.1, *p* < .05, *d* = 2.59.

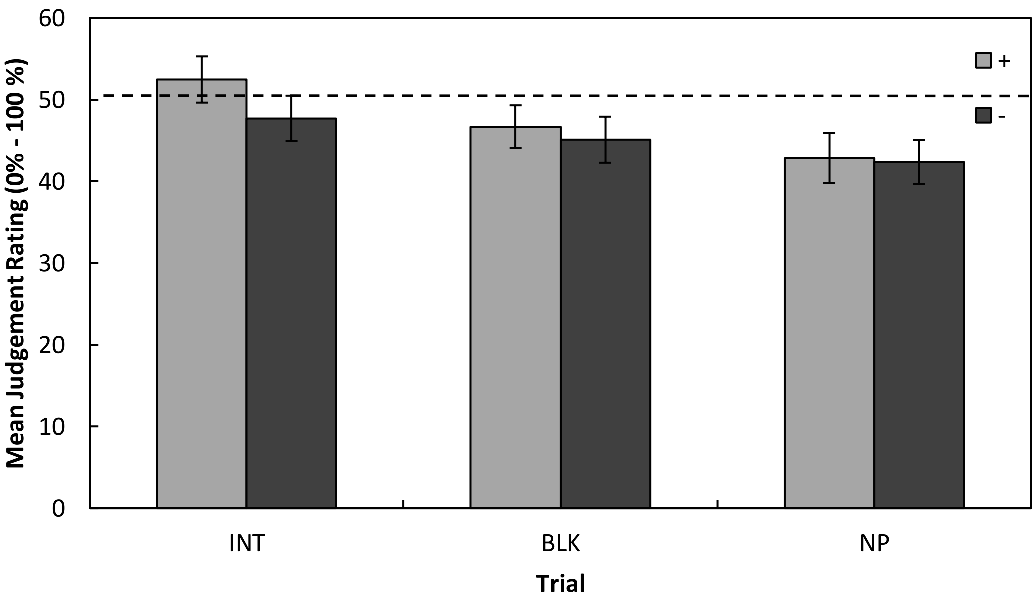

Figure 28. Experiment 2: Percentage of the mean ratings for each butterfly condition: Intermixed (INT), Blocked (BLK), or Non-Preexposed (NP). Vertical axe shows percentage of ratings, where 0% means that a butterfly was never followed by the egg while 100% means that a butterfly was always followed by the egg. Different colored columns indicate for that type of butterfly if it was followed (+) or not (-) by the egg, with error bars indicating SEMs. Also the chance level (50%) is indicated with a dashed line.

Discussion

The results from reaction time test phase showed that subjects were slower to anticipate the egg when it was preceded by the Intermixed butterfly than when it was preceded by the Blocked or Non-Preexposed butterfly. These results are congruent with our hypothesis, that Intermixed rapid exposure to similar butterflies unitizes them to such extent that impairs their association with the egg, and subsequently hinders any priming effect to anticipate the egg arrival.

It was also expected in this phase that, since unexposed butterflies had no latent inhibition, their association with the egg would be the greatest and, therefore, subjects would anticipate the response more readily. Surprisingly, Blocked butterflies, which carry some latent inhibition, showed the same level of associability than Non-Preexposed butterflies. It may be that the participants had little experience with the Non-Preexposed butterflies and so even if they were well associated with the egg, the subject could not remember them and didn't benefit from the prime effect. Another possibility comes from Ballesta et al.'s (2021) experiments with rats, which suggest that Blocked exposure increases the associability of stimuli. They proposed that Blocked preexposure develops a configurational representation of similar stimuli, which reflects increased internal association between unique elements and common elements. Then, after preexposure, an encounter with, for example, DX would create a discrepancy in the subject's higher-order processor, as element X used to be configured also with C, which is not present. This discrepancy would return salience to the Blocked stimuli and, therefore, associability.

On the other hand, the expectancy test results showed no differences in the conditioning variable (+ or -) or for any of the preexposure conditions (INT, BLK and NP). It is possible that only 4 conditioning trials for each condition were not sufficient to establish a strong association between egg and butterfly that could be recovered later in an explicit test. Instead, we found differences between the ratings of the Intermixed butterflies and the Non-Preexposed butterflies. This may reflect that the

Intermixed butterflies were actually better recognised and therefore participants felt more confident in their ratings. This is congruent with Experiment 1 results. In fact, we found that the Intermixed butterflies were the only condition rated at the chance level, while the other conditions were more likely to be rated as not being followed by the egg, probably because subjects did not remember having seen them, so it is unlikely that they remembered that some were followed by an egg. In any case, the Reaction Time data we have obtained support the unitization of stimuli during rapid Intermixed exposure, which is in fact an objective measure without the need to be conscious, unlike participants' expectancy rating which is subjective.

General Discussion

We have developed a procedure capable of producing perceptual learning in humans, unlike other classical procedures, without difference-seeking instructions and without localised attentional bias. The experiments presented have shown that visual stimuli exposed in an Intermixed form improve their subsequent recognition and reduce their associability in contrast to when they are presented in separate blocks, in parallel to previous results found in animals.

In humans the I/B effect has been explained in terms of the mechanism proposed by Honey and Bateson (1996), i.e., the rapid alternation of similar stimuli habituates the common elements in short term and biases the processing resources towards the unique ones. Furthermore, Recio et al. (2018) added that this enhanced processing would also favor the unitization of unique elements, increasing their recognition, but also decreasing their associability. Our Experiment 1 was designed to assess the recognition of similar visual stimuli after rapid preexposure. We rapidly exposed participants to similar Pokémon (butterflies and pandas) in an Intermixed or Blocked form, after which these were presented in recognition tests among multiple similar distractors. The results showed better recognition of

Pokémon exposed in Intermixed form, rather than Blocked Pokémon that were randomly chosen, meaning that they were as recognisable as unexposed distractors. According to Recio et al. (2018), after preexposure the sampling of any unique sub-element in the test would associatively activate in memory the unitized remainder favoring its recognition among the non-unitized stimuli.

Meanwhile, better unitization of an element also increases its latent inhibition, as it is more familiar and also unitizes with the context, reducing its associability. This latter assumption was tested in the Experiment 2. After the same preexposure as in Experiment 1, some butterflies started to be followed by an outcome, an egg, and participants had to respond as fast as they could to it. This phase showed slower responses for the egg when it was preceded by an Intermixed butterfly than by a Blocked or Non-Preexposed butterfly. Because Intermixed stimuli would be highly unitized their associability would be reduced, therefore participants would establish weaker egg-butterflies contingencies and show slower implicit responses than for non-unitized stimuli.

In a final test, participants were asked to rate the probability that each stimulus was followed by an egg. Unfortunately, this test showed no difference in expectancy power, as all butterflies were rated at the chance level as egg-followed. This test was not sensitive enough to parallel the RT results, perhaps because subjects were too little exposed to the stimuli to later explicitly recall a contingency between the butterflies and the eggs. However, increasing trials could mean losing differences in conditioning, since in the end learning would reach an asymptote and all butterflies would be correctly judged as CS+ and CS-. It is also important to differentiate between the two measures of associability in Experiment 2. In the Expectancy Test, the subject is asked to make an inference based on the associated outcome; the subject is required to give an explicit and conscious response. Unlike the response time in the Reaction Time Test, which is an objective measure without the need to be conscious.

Although the results are clear and congruent with our hypothesis, there are some stimuli limitations to consider. First, because the stimuli used were prefabricated by Game Freak Company (which provide the Pokémon to Nintendo), the degree of similarity between each pair of stimuli could vary without any experimental standardisation. In addition, the limited stimulus base provided a smaller number of pandas in Experiment 1, which may have reduced the effect size. In fact, at the end of the experiments, a few participants spontaneously declared that, having played Pokémon before, they recognised the Pokémon presented, although they acknowledged that they did not know whether they were specifically these variants or others. On the other hand, participants stated that they liked this kind of procedure and stimuli, which made the experiment more engaging for them. In this way we believe that the quality of participants' responses is preserved from the first to the last, as participants remain focused on the task throughout the experiment. For future research it might be optimal to use a standardised base of stimuli that can be used in video game-like procedures or to create one of their own, as for example Kilpatrick, Ćwiek and Kawahara (2023), who created their own Pokémon stimuli set.

In summary, these results would support the better discrimination in perceptual learning in terms of unitization, which also reduces the associability of the stimuli. This interpretation is supported by both animal and human results, suggesting that this is a common mechanism across species. Indeed, Honey and Bateson's (1996) mechanism was initially proposed for animals, but because sensory preconditioning obscured results with rapid procedures, perceptual learning studies began to use spaced procedures involving other mechanisms (Hall, 2003; McLaren & Mackintosh, 2000). Perhaps the most accurate conclusion is that perceptual learning is flexible and has several shared mechanisms, such as inhibitory links or salience modulation, but that depending on the task it will use one or the other. Likewise, just as the human experiments are easily explained by the mechanism of Honey and Bateson (1996), it would be interesting to replicate the spaced mechanisms also in the human domain.

Unfortunately, the conditions for this type of experimentation are complicated and it does not seem to be possible to carry it out.

PART III: GENERAL DISCUSSION AND CONCLUSIONS

CHAPTER IX – GENERAL DISCUSSION AND CONCLUSIONS

9.1 - SUMMARY OF THE RESULTS

Perceptual learning refers to the phenomenon by which mere exposure to similar stimuli (e.g., AX & BX) results in better subsequent discrimination between them. According to Gibson (1969), the opportunity to compare these stimuli launches a process of differentiation, whereby the effectiveness of their unique elements (A & B) will be enhanced relative to that of their common elements (X), improving their discrimination. Consistently, it has been shown on many occasions that exposure to similar stimuli in an Intermixed fashion increases their discrimination to a greater extent than exposure to them in separate blocks, which has been termed as the Intermixed/Blocked (I/B) effect. In this thesis, we have conducted a wide range of experiments with the aim of assessing the role of stimulus comparison in perceptual learning and the mechanisms underlying it.

To start with, it has been amply demonstrated that rapid Intermixed presentations of similar stimuli, an arrangement that favors comparison, clearly benefit discrimination in humans, but, conversely, appear to hinder it in non-human animals. This effect has been explained in terms of sensory preconditioning (SPC) in animals, whereby close experience with two (or more) stimuli will promote the subject to associate them with each other, increasing generalization rather than discrimination.

In *Chapter IV* we preexposed similar tastes to rats, in rapid Intermixed or Blocked arrangements, with a small amount of water in between to prevent them from establishing excitatory associations that could lead to SPC. Following preexposure, we observed that the Intermixed group discriminated better than the Blocked group between two stimuli, one that was aversively conditioned and the other that was not (Experiment 1 and 2), but that this I/B effect disappeared if water was removed from preexposure (Experiment 2). These results were obtained when direct consumption of stimuli was measured, but not when lick cluster size was measured. This is the first time this measure has been used in perceptual learning, and although it did not find differences in stimulus generalization, it was effective in assessing the acquisition of aversion during conditioning, in other words, it measured the change in the hedonic value of the stimulus. Finally, in Experiment 3, we directly measured the supposed associations responsible for the SPC effect. Following a rapid Intermixed or Blocked preexposure without ISI water, we aversively conditioned a unique element and assessed generalization to the other. The test results showed a decrease in consumption for the Intermixed element, reflecting that this preexposure effectively promoted the formation of associations between the stimuli and may ultimately induce a generalization between them.

Following, given that this rapid procedure has shown able to produce the I/B effect without apparently being affected by SPC, we decided to evaluate the mechanisms involved in the comparison process. In humans, it has been proposed that rapid alternation of stimuli produces a short-term habituation of their common elements, as they are always present, which causes a processing bias towards the unique ones (Honey & Bateson, 1996). This bias would favor the unitization of the unique elements, namely, the formation of associations between its unique sampled sub-elements and with the context (Recio et al., 2018). This process favors the discrimination of unique elements, as it increases the number of sub-characteristics added to their representation and increases in correspondence with reality, but at the same time it reduces the effectiveness as it also unitizes with the context and becomes more familiar (McLaren et al., 1989).

In order to evaluate this proposed comparison mechanism, we assessed the effectiveness of unique elements in *Chapter V*. After rapid Intermixed or Blocked preexposure to flavored compounds, rats in Experiment 1 were aversely conditioned to a new element Y and then this element was tested in compound with a preexposed unique element (AY). Consumption increased in the case of Intermixed rats, reflecting that they discriminated better between the aversive element, Y, and the similar test stimulus, AY. This was explained in terms of better unitization, as sampling a unique sub-element in the test would prime the activation of the complete representation of A, impairing any generalization of the aversion carried by the sampled sub-elements of Y. Secondly, Experiment 2 (a & b) assessed the associability of the unique elements after preexposure. We directly conditioned an aversion to A and measured the level of aversion associated on unreinforced A test trials. Results showed that the aversion endured more trials for the Blocked unique elements, reflecting that the Intermixed ones were less associable during conditioning. Lastly, we measured the ability of unique elements to interfere with the conditioning of a new element Y (Experiment 3). After preexposure, the AY compound was aversely conditioned and then the level of aversion linked to Y tested. The results revealed that Y resulted more aversive when it was conditioned with the Intermixed unique element, demonstrating that the latter was less effective and interfering, than the Blocked unique one.

These results support the short-term habituation mechanism of common elements, and the processing bias that favors the unitization of unique elements. The experiments in *Chapter V* demonstrated that rapid Intermixed exposure to similar stimuli, while increasing their discrimination, also reduces the effectiveness of their unique elements, as they become more familiar and associated with the context.

In the following *Chapter VI* we used the same procedures as in *Chapter V*, but this time to evaluate the effectiveness of the common elements. Unfortunately, here there is no clear theoretical interpretation of how the mechanism of comparison would affect these elements. First, Experiment 1 showed that after conditioning a new element Y, the consumption of a compound with the common one, XY, decreased in the Intermixed group. This could reflect that the rapid Intermixed exposure reduced the discriminability of the common element with respect to Blocked exposure, but also that its effectiveness was diminished. In the following Experiment 2, X was paired with Y during the aversion conditioning phase, and later the consumption of Y alone was measured. Again test results showed a reduced consumption after Intermixed exposure. This result was clearer, as it indicated that after Intermixed preexposure, X was less salient and able to interfere during aversive conditioning with Y. Finally, in Experiment 3 (a & b), after preexposure we directly conditioned the aversion to X and evaluated this association during extinction trials, however, this time no differences in this regard were obtained. The overall results in this *Chapter VI* seem to indicate that rapid Intermixed exposure to AX and BX reduces the effectiveness and discriminability of X, however, the same level of associability in Experiment 3 was unexpected.

Having assessed the comparison mechanism and the changes in stimulus properties that enhance discrimination, it is now time to contrast it with other perceptual learning mechanisms that occur during spaced presentations, which supposedly do not allow comparison. Models of salience modulation explain that during preexposure, while increasing habituation and latent inhibition of stimuli, intracompound associations are formed between unique elements and common elements. Thus, on Intermixed trials, the common element presented in any stimulus, e.g. X on trial BX, will associatively activate the absent unique element, A, on that trial. McLaren and Mackintosh (2000) explained that this associative activation would weaken the associations formed between the unique sub-elements with themselves and with the context, that is a deunitization effect, thus restoring the effectiveness lost of the element. In contrast, Hall (2003) indicates that the associative activation of this unique element, which used to be physically presented with the common one, increases the responsiveness to it for the next encounters, increasing its salience. Both mechanisms must first wait for the stimulus presentation to end and the representation of the unique element to decay in deactivation to allow for associative activation, which is why these mechanisms require spaced presentations and cannot account for rapid comparison effects.

In *Chapter VII*, firstly, we presented in rapid Intermixed manner similar stimuli to rats, but with a distractor in between them to prevent the rapid comparison mechanism (Experiment 1). Meanwhile in afternoon preexposure sessions half of the rats received water, whereas the rest received the common element to favor the associative activation the unique elements and restore their salience. After that, rats were aversely conditioned to Y and tested with the compound AY; results showed increased discrimination for the rats which experienced the common element in the preexposure afternoons. This experiment demonstrates that our rapid procedure is able to increase the discriminability of the unique elements if we spaced enough the stimuli presentations. Next, we attempt to involve both, rapid and spaced, mechanisms within the same procedure. Experiment 2 introduced a rapid Intermixed group with 5 min of ISI, a spaced Intermixed group with 24 h of ISI and a Blocked group, then after preexposure the unique element was aversively conditioned and finally its associability was tested in extinction trials. Results showed during conditioning and test less aversion for the rapid Intermixed group than for the others, but not differences between these latter two. Then, we replicated this procedure in Experiment 3 but using only the Intermixed spaced group and Blocked. This time results showed increased aversion for the Intermixed spaced group in extinction trials. With these preparations we demonstrate that perceptual learning is flexible; that depending on the demands of the task it can apply a rapid mechanism, which reduces the effectiveness of the unique elements, or a spaced mechanism, which increases it, but that eventually both enhance the discrimination of stimuli.

Finally, we returned to exploring human perceptual learning in *Chapter VIII*. As discussed above, the I/B effect in the human domain has been comfortably explained by the short-term mechanism proposed by Honey and Bateson (1996). However, the evidence for a consequent unitization is more limited. Thus, we preexposed to humans Intermixed and Blocked similar butterflies and pandas in rapid succession, after which they had to recognise them among a group of non-preexposed distractors (Experiment 1). The results showed that participants recognized the Intermixed butterflies and pandas better than the Blocked stimuli, which were randomly selected. Because the Intermixed stimuli were unitized, sampling any sub-elements in the panel among distractors would lead to full activation of the unique elements of those stimuli facilitating recognition.

In the next Experiment 2, we gave participants initially the same Intermixed and Blocked preexposure to butterflies, and then suddenly, one of the Intermixed, Blocked and non-preexposed butterflies started to be followed by an egg. In this conditioning phase, participants had to respond as fast as they could to the egg, helped by the butterfly that appeared before as a cue. The next phase was an explicit test, in which we asked participants to rate on a scale of 0 to 100 how confidently they believed each butterfly was followed by the egg. The conditioning phase showed that participants responded more quickly to the Blocked and non-preexposed butterflies than to the Intermixed butterfly, that is, the former get associated and predicted the outcome better. Because the Intermixed stimuli would be more unitized, the association with the egg would be weaker in this condition to ultimately help predict an outcome. Unfortunately, in the explicit test, no differences were observed. Given that on this last phase all butterflies were responded at the chance level, we hypothesized that the conditioning trials were not sufficient to elicit an explicit recall of the butterfly-egg association. We ended this chapter with the conclusion that perceptual learning has several mechanisms that are flexible but also appear to be shared across species.

9.2 - IMPLICATIONS AND FUTURE DIRECTIONS

9.2.1 - THEORETIAL IMPLICATIONS

The experiments presented above have served to test both spaced and rapid procedures of perceptual learning, the latter in different species, and to advance in the knowledge of the underlying associative mechanisms.

Early on, based on animal experiments Honey and Bateson (1996) proposed that rapid Intermixed presentation of similar stimuli would promote short-term habituation of their common elements, which would allow processing resources to be focused on encoding the unique elements. However, the influence of sensory preconditioning in this species made it difficult to observe that mechanism, as the rapid presentation of stimuli caused them to be pre-associated leading to subsequent generalization rather than discrimination. Because of this, the classical animal experiments proceeded to use spaced presentations that avoided the formation of associations between stimuli but also any possible comparison between them, and whose effects were well explained by salience modulation mechanisms (e.g., Hall, 2003). In contrast, the I/B effect was readily found in humans, which seemed to support the mechanism first proposed by Honey and Bateson (1996), and some authors even declared that human but not animals could benefit from a comparison mechanism (Mitchell & Hall, 2014).

To test this assumption, Recio et al. (2018) developed a procedure, similar to that used in humans (e.g., Dwyer et al., 2004), that rapidly exposed animals to similar tastes with 5 min of water in between and obtained the I/B effect. This was significant, as SPC was understood to be a matter of contiguity, but no one was able to demonstrate this after an interval of more than 9 seconds between stimuli (Lavin, 1976). Our studies assumed that flavored stimuli such as those commonly used in perceptual learning remain residually in the subjects' sensory receptors until the next stimulus arrives, leading to the direct experience of both stimuli at the same time and, reasonably, to their association. Therefore, using the procedure of Recio et al. (2018) our experiments showed that when water is introduced between the presentations of sapid stimuli to prevent the formation of associations, a rapid Intermixed preexposure can enhance their subsequent discrimination, but that this effect is eliminated if we remove the water. Consequently, this procedure has been able to allow us to study in animals the rapid comparison mechanism proposed by Honey and Bateson (1996). Nevertheless, it should be noted that animal experiments in perceptual learning commonly use this stimulus modality, and it might be preferable for future experiments to switch to others that are less susceptible to SPC. For example, auditory stiuli as the used by Mondragon and Murphy (2010) or visual stimuli as in the case of Honey and Bateson (1996). Indeed, it might be worthwhile for future research to address the conditions under which SPC can act and thus control it for other perceptual learning preparations.

Following, Recio et al. (2018) added an assumption to this mechanism; that processing bias would largely unitize Intermixed unique elements. This idea was initially proposed by McLaren et al. (1989), whereby sub-elements sampled during an exposure would tend to form associations with each other creating a large quality representation of this element, but would in turn form associations with the context increasing latent inhibition and reducing its effectiveness. With these assumptions in mind, we used the procedure of Recio et al. (2018), to test the supposed rapid comparison mechanism. In Experiment 1 we showed that rapid Intermixed exposure effectively reduced generalization between two similar stimuli (replica of Recio et al. 2018, Experiment 1), and in the following two experiments that Intermixed unique elements were in fact less salient and associable. Therefore, our evidence seems to support that comparison relies ultimately on the unitization of the unique elements, which increases its discriminability due to a great formed representation, but also reduces its effectiveness.

As a counterpart, we analyzed the changes that this mechanism would produce in the common elements and how these would help discrimination. Our experiments showed that after rapid Intermixed exposure, these elements were less effective in disrupting generalization between similar stimuli and at conditioning of other elements, but we found no differences in associability with other events. Apparently, our findings, in line with the Gibson (1969) differentiation proposal, support that comparison promotes the overlooking of these stimuli to help detect the unique ones. However, associative theories are not fully certain about how this effect is achieved. Some theories have added that because X is a bad predictor of the unique element during Intermixed exposure this led to a reduction in its perceived salience (Mondragon & Hall, 2010) or even that X is learned to be irrelevant (Hall & Rodríguez, 2019), but contrary another theories would claim that an uncertain predictor as X for unique elements would be perceived more salient (Pearce & Hall, 1980). Another theory suggests that it is the Blocked exposure that protects the salience of the common element, as during this arrangement habituation is exerted on the stimuli as a configuration, which reduces their effect on each element. In contrast, in Intermixed preexposure, the elements are perceived more individually, and therefore habituation is suffered to a large extent by each element (Ballesta et al., 2021).

In resume, these common element theories could apply to both rapid and spaced exposure procedures, but these latter experiments never showed any change in the properties of common elements (see for a review Hall, 2020). Contrary, Ballesta et al. (2021) and Mondragon and Hall (2010) were able to found a reduction in the effectiveness of such elements with rapid procedures. Following a more straightforward assumption might be that the short-term habituation that common elements undergo during rapid Intermixed exposure can be maintained and developed into long-term habituation (Honey & Bateson, 1996). In any case, there seems to be a need for more research on the effects these mechanisms may have on these commonalities and how that would help discrimination.

9.2.2 - FLEXIBLE MECHANISMS

After having evaluated the rapid comparison mechanism, we decided to contrast it with other spacing mechanisms that also produce perceptual learning. The latter are based on the associative activation of unique elements, which requires prior spacing and eventually deactivation of their representation. The end result is that these elements have a high effectiveness with respect to the common elements, which helps their subsequent detection and discrimination of the stimuli.

In chapters 4 and 5 we have shown that rapid mechanisms favor the discrimination of stimuli while reducing the effectiveness of unique elements. In chapter 7 we have observed that the spaced mechanism also increases the discriminability of stimuli, but conversely increases the effectiveness of their unique elements. These results are very positive for psychology, as they demonstrate that perceptual learning is a ubiquitous phenomenon that can be triggered in a wide variety of situations to favor the subject's adaptation to the task. Whether in rapid presentations of similar stimuli such as those of air traffic controls or spaced presentations such as doctors' x-rays, perceptual learning promotes better discrimination of similar stimuli. It seems therefore that the mechanisms deployed by perceptual learning depend on the demands of the environment, which is why the adjective that characterises this phenomenon is "flexible".

9.2.3 - UNIVERSALLITY

Finally, we explored the universality of the comparison mechanism across species. Although initially the mechanism proposed by Honey and Bateson (1996) was demonstrated in human experiments, the unitization process added by Recio et al. (2018) had not been fully contrasted.

First, we focused on assess the implications of the comparison mechanism on humans. We exposed to participants Intermixed and Blocked stimuli in rapid succession to then asked them to select these stimuli from a panel of distractors. As usual in these experiments, we found that Intermixed stimuli were better discriminated, the classic I/B effect. Subsequently, after the same rapid exposure, these stimuli were to be conditioned with an outcome. What we found, as in the case of animals, was that Intermixed stimuli were more difficult to associate than Blocked stimuli or those not preexposed. Thus, our experiments supported that the mechanism of short-term habituation of the common elements (Honey & Bateson, 1996) and a consequent better unitization of the unique elements (Recio et al., 2018) appear to be present on both human and non-human animals, in other words it seems shared across species.

Secondly, the issue of perceptual learning transference fall a bit short in the human domain. Just as animal experiments have difficulty adapting rapid tasks of humans, human experiments also struggle to take adapted spaced tasks of animals. It would be very interesting to see if humans can also benefit from spaced mechanisms; however, evaluating this seems difficult because controlling exposure to similar stimuli over the long term in humans is challenging. It could be done, for example, with uncommon sensory modalities, such as using tones or flavors that the participant would unlikely encounter outside the experiment.

A final problem we tried to manage was the validity of experiments with humans. As we have seen in the thesis, these experiments often suffer from instruction or location biases. We attempted to distance the subject from the experimental situation by giving them fictitious instructions focused on an entertaining task, such as achieving a goal in a video game, and not specifically aimed at seeking differences between stimuli (which would be instead discriminative learning). Additionally, the position of the stimuli in our task constantly changed, and the differential elements were a pattern of sub-elements which could not be discriminated solely by position. It might be fruitful to investigate this rapid comparison mechanism in humans with eye-tracking procedures, since once the location bias is removed, the subject would examine the entire stimulus and focus on the critical features to be discriminated. However, we know from our animal experiments that the rapid comparison mechanism reduces the salience of unique elements and also appears to reduce the salience of common ones.

In conclusion, when overcome biases suffered by both humans and animals, the comparison mechanism seems to be shared across species. However, there are still some questions that need to be further investigated, such as the properties of the elements that humans use after comparison to discriminate, or the possibility that humans also use spaced perceptual learning mechanisms.

9.2.4 - TRANSFERENCE

Although perceptual learning may seem an abstract phenomenon only observable in the laboratory under strict conditions, the truth is that it is deeply embedded in our daily lives and helps us to adapt by guiding our behavior.

We can observe perceptual learning in everyday situations which require a quick and complex discrimination: recognition of faces, identification of toxic tastes in the food, perception of different tones and timbres in music etc... However an important aspect of our lives that can be influenced by this phenomenon in long term is nutrition. By the process of sensory specific satiation (SSS) we tend to devalue the recently ingested food or drink, so we desire to consume another different, thus ensuring nutritional variety (Reichelt, Morris & Westbrook, 2014). As an instance, Neanderthals would sensory satiate of apples from the closest tree and rather would prefer go hunting for meat; this can be exemplified by the phrase "there's always room for dessert". Therefore perceptual learning can improve detecting different foods and thus promote the most varied diet possible. This can have both healthy and unhealthy consequences: discriminating from a wide variety of vegetables will promote an increase in the amount of healthy food intake, but conversely a wide variety of junk food will increase the intake of unhealthy food. Thus, knowing the mechanisms underlying perceptual learning can help to modulate our intake and ultimately our health (González, Recio, Sánchez, Gil & de Brugada, 2018), specifically that of the youngest which are nowadays massively exposed to candy and fast food variety.

On the other hand, this learning can be observed in certain areas that require the development of expert discriminative skills. For example, chicken sexers are able to distinguish male from female genitalia of day-old chickens at a glance (Bierderman & Shiffrar, 1987). In these cases, it has been found that repeated exposure to the target stimuli is critical for this. Beer tasters who have been repeatedly exposed to a wide range of different beers are able to discriminate between them and also identify their properties in a greater way than other novice drinkers who hasn't been exposed to so many varieties (Peron & Allen, 1988). In summary, we can assume that perceptual learning is involved in many other expert skills: identification of traffic signs and other traffic events, detection of events on radar and sonar screens, detection of anomalies in X-rays or CT images. The fact that we understand perceptual learning mechanisms can afford the opportunity to develop special training programs to increase the accuracy in these jobs. For example, Levenson, Krupinski, Navarro and Wasserman (2015) developed discriminative learning procedures by which pigeons acquired the ability to discern between cancerous and healthy breast tissue. These studies are very promising, especially for the medical field where discriminate between similar samples can ultimately save a life.

Finally, it is noteworthy that computers and software nowadays possess the capacity to learn as well. New artificial intelligences are grounded in algorithmic rules that, through experience, i.e., the inputs they receive, adapt and mold themselves to offer better responses, the outcomes they give. In this context, perceptual learning could be integrated into artificial intelligence through a comparison mechanism, allowing, for instance, the collection of unique elements of stimuli through exposure while filtering out common ones, thereby enabling the identification of inputs for better outcomes (Bredeche, Shi & Zucker, 2006). For example, algorithms could be devised to create a program that aggregates information about faces from surveillance cameras and distinguishes a criminal who has undergone facial surgery or a missing person who has aged since their last photo was taken. Similarly, another algorithm based on internet images could be developed to identify unhealthy food in a factory or detect unripe fish at a fish auction. While this thesis does not delve into the development of robotic behavior, it is conceivable that if we can discern the behavior of living beings, we may replicate it artificially, hopefully for the benefit of humanity.

9.3 - FINAL COMMENTS AND CONCLUSIONS

Perceptual learning has been defined as the improvement in discrimination following exposure to similar stimuli; although Gibson (1969) suggested that the opportunity to compare would enhance this process, she never proposed any mechanism for it. The aim of this thesis was to investigate the mechanisms involved in comparison in perceptual learning and the generality of this process.

Historically, difficulties have been encountered in the study of the comparative process, because when given the opportunity to compare between stimuli, humans improved their discrimination but not animals. This led to a split in the mechanisms of perceptual learning used by humans and animals, suggesting that the latter were unable to compare. In this thesis we have studied the procedural differences that led to such disparate results. Specifically, sensory preconditioning counteracted the discriminative enhancement of comparison, but once it is controlled, we have seen how animals can also benefit from the opportunity to compare. From hereafter, we have investigated the mechanism underlying this process. Based on the standard models of associative learning, we described the comparative process as a mechanism that reduces attention to common elements of the stimuli and improves the representation formed of the unique ones in memory. Positively, we tested this mechanism and its implications in both humans and animals obtaining results that support our hypothesis. In addition, we have observed that there are other perceptual learning mechanisms that are not incompatible with comparison, but importantly that are triggered by other the demands of the task as the time laps between the exposure to the stimuli.

We therefore conclude that perceptual learning is flexible, as can use different mechanisms, but contrary to what was believed the comparison process is shared across species. Finally, we hope that these results will be useful for certain domains, as expertise learning or nutrition, and that it will be further investigated in the future as there are some questions we left here open, as the role of common elements in comparison or the spaced mechanisms in humans.

CHAPTER X - RESUMEN, IMPLICACIONES Y CONCLUSIONES

El aprendizaje perceptivo es la mejora en discriminación entre estímulos similares tras su mera exposición. Tradicionalmente, se ha observado que la oportunidad de comparar entre estos estímulos, como presentarlos rápidamente de forma intercalada, aumenta esta discriminación en humanos pero no en animales. En esta tesis hemos investigado los mecanismos subyacentes a la comparación y su generalidad entre especies.

En el *Capítulo IV* presentamos de forma rápida compuestos de sabores a los animales, pero entre cada ensayo se les daba un poco de agua para que no se mezclasen. Con este procedimiento encontramos que: 1) los animales también son capaces de beneficiarse de la comparación para aumentar su discriminación, y 2) la presentación rápida de estímulos similares propicia, si no se controla, la formación de asociaciones entre los estímulos que contrariamente aumenta su generalización.

Utilizando este procedimiento analizamos el mecanismo propuesto y subyacente al proceso de comparación. De acuerdo con Honey y Bateson (1996), la rápida alternancia de estímulos similares hace que sus elementos comunes se habitúen a corto plazo, pues siempre están presentes, liberando recursos atencionales que procesan en mayor medida los elementos únicos de estos estímulos. En adición, Recio et al. (2018) sugirieron que este sesgo propiciaría la mayor unitización de los elementos únicos, es decir, la formación de asociaciones intracompuesto entre las subcaracterstícas únicas, generando una mejor representación de estos elementos. Consecuentemente, los estímulos serian mejor diferenciados por tener estos elementos bien representados, pero a la vez estos estarían muy unitizados con el contexto también, por lo que reducirían su saliencia y asociabilidad.

En el *Capítulo V* evaluamos esta propuesta en animales. Replicamos el efecto de que una exposición rápida e intercalada favorece una discriminación posterior entre estímulos similares, y demostramos que esta exposición reduce la asociabilidad y saliencia de sus elementos únicos. Estos resultados apoyan el mecanismo propuesto por Honey y Bateson (1996) y el proceso de unitización añadido por Recio et al. (2018). En el *Capítulo VI* examinamos los cambios que produce la comparación en las propiedades de los elementos comunes. En este caso encontramos que tras la exposición intercalada rápida estos elementos son menos salientes y discriminables, pero no observamos cambios a nivel de asociabilidad. En cualquier caso las teorías del aprendizaje perceptivo no son muy claras respecto a los cambios producidos en estos elementos y su papel en la discriminación.

En el *Capítulo VII* utilizamos nuestro procedimiento para observar al mismo tiempo los mecanismos de aprendizaje perceptivo rápido (comparación) y espaciado. El mecanismo espaciado se basa en las asociaciones intracompuesto que se forman entre el elemento común y los únicos, y en la perdida de efectividad de los estímulos por exposición repetida. En la exposición intercalada espaciada los elementos comunes activan a través de las asociaciones intracompuesto los elementos únicos que no están presentes en ese ensayo, esta activación devolvería cierta efectividad a los elementos únicos y favorecería la discriminación posterior (Hall, 2003; McLaren y Mackintosh, 2000). En este capítulo encontramos que presentar el elemento común por la tarde, para producir la activación asociativa de los elementos únicos, favorece la posterior discriminación de los estímulos. Además, al evaluar la efectividad de los elementos únicos tras exposición intercalada encontramos que el elemento único rápidamente expuesto es más difícil de asociar a un evento que el elemento espaciado. Esto apoya la teoría de la modulación de saliencia en los procedimientos espaciados, y refuerza la de la habituación a corto plazo y unitización en los procedimientos rápidos.

Finalmente, en el *Capítulo VIII* evaluamos el mecanismo de comparación en humanos. Encontramos que estímulos expuestos rápidamente de forma intercalada eran posteriormente mejor reconocidos de entre un panel de distractores que estímulos expuestos en Bloques separados. Además, los estímulos Intercalados también eran más difíciles de asociar a un evento que los estímulos Bloqueados o que unos No Preexpuestos, apoyando la unitización de los elementos únicos en el mecanismo de comparación.

Conocer los mecanismos subyacentes a la comparación en el aprendizaje perceptivo es de gran importancia, ya que este fenómeno no solo se encuentra en situaciones cotidianas como discriminar entre dos imágenes o sabores, si no que está en la base de aspectos fundamentales como la nutrición o habilidades expertas. De esta forma, se pueden implementar programas de exposición para reducir la obesidad o incrementar ciertas habilidades como distinguir señales en un radar de tráfico aéreo. Cabe mencionar que, hoy en día, la implementación de las reglas por las que se rige un aprendizaje como el perceptivo en inteligencia artificial también puede ser beneficiosa para la sociedad, por ejemplo a la hora de encontrar personas desaparecidas o clasificar automáticamente productos como no aptos dentro de una fábrica.

Como comentario final, recalcar la importancia de esclarecer la generalidad del mecanismo de comparación en el aprendizaje perceptivo. Tradicionalmente se pensaba que humanos, pero no animales, podían utilizar la comparación, aquí hemos aportado evidencia de que la comparación es un mecanismo compartido entre las especies. Aun mas importante, hemos observado que el aprendizaje perceptivo es un fenómeno flexible, ya que dependiendo de las demandas del entorno puede poner en marcha un mecanismo u otro que favorezca la discriminación entre estímulos semejantes y por tanto la adaptación al medio del individuo. Si bien es cierto que quedan algunas preguntas sin resolver, como la generalidad de los mecanismos espaciados en humanos o el rol de los elementos comunes en la comparación, esperamos haber sentado las bases para futuras investigaciones y que este conocimiento aporte grandes beneficios a la sociedad.

BIBLIOGRAPHY

REFERENCES

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

Angulo, R., Alonso, G., Di Stasi, L. L., & Catena, A. (2019). Stimulus comparison: Effects of the pre-exposure schedule and instructions for perceptual learning and attention. *Learning and Motivation*, 65, 20-32. https://doi.org/10.1016/j.lmot.2018.11.001

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. https://doi.org/10.1037/a0026399

Artigas, A. A., & Prados, J. (2014). Perceptual learning transfer: Salience of the common element as a factor contributing to the intermixed/blocked effect. *Journal of Experimental Psychology: Animal Learning and Cognition*, 40(4), 419. https://doi.org/10.1037/xan0000039

Artigas, A. A., & Prados, J. (2017). Perceptual learning transfer in an appetitive Pavlovian task. *Learning & Behavior*, 45, 115-123. https://doi.org/10.3758/s13420-016-0245-y

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. https://doi.org/10.1037/0097-7403.32.2.173

Atkinson, R. C., & Estes, W. K. (1963). Stimulus sampling theory. In R. R. Bush, E. Galanter, and R. D. Luce (Eds.), *Handbook of mathematical psychology* (pp. 121–268). New York: Wiley

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. https://doi.org/10.1037/xan0000279

Bennett, C. H., & Mackintosh, N. J. (1999). Comparison and contrast as a mechanism of perceptual learning?. *The Quarterly Journal of Experimental Psychology: Section B*, 52(3), 253-272.

Bennett, C. H., Scahill, V. L., Griffiths, D. P., & Mackintosh, N. J. (1999). The role of inhibitory associations in perceptual learning. *Animal Learning & Behavior*, 27, 333-345. https://doi.org/10.3758/BF03199732

Bennett, C. H., Wills, S. J., Wells, J. O., & Mackintosh, N. J. (1994). Reduced generalization following preexposure: Latent inhibition of common elements or a difference in familiarity?. *Journal of Experimental Psychology: Animal Behavior Processes*, 20(3), 232. https://doi.org/10.1037/0097-7403.20.3.232

Berger, A., & Kiefer, M. (2021). Comparison of different response time outlier exclusion methods: A simulation study. *Frontiers in psychology*, 12, 675558. https://doi.org/10.3389/fpsyg.2021.675558

Berkeley, G. (1709). *An essay towards a new theory of vision*. Dublin: Aaron Rhames.

Biederman, I., & Shiffrar, M. M. (1987). Sexing day-old chicks: A case study and expert systems analysis of a difficult perceptual-learning task. *Journal of Experimental Psychology: Learning, memory, and cognition*, 13(4), 640. https://doi.org/10.1037/0278-7393.13.4.640

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

Blair, C. A. J., & Hall, G. (2003b). Changes in stimulus salience as a result of stimulus preexposure: Evidence from aversive and appetitive testing procedures. *Animal Learning & Behavior*, 31, 185-191. https://doi.org/10.3758/BF03195981

Blair, C. A. J., 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. https://doi.org/10.1037/0097-7403.30.4.317

Brandon, S. E., Vogel, E. H., & Wagner, A. R. (2003). Stimulus representation in SOP: I: Theoretical rationalization and some implications. *Behavioral Processes*, 62(1-3), 5-25. https://doi.org/10.1016/S0376-6357(03)00016-0

Bredeche, N., Shi, Z., & Zucker, J. D. (2006). Perceptual learning and abstraction in machine learning: an application to autonomous robotics. *IEEE Transactions on Systems, Man, and Cybernetics, Part C (Applications and Reviews)*, 36(2), 172-181. https://doi.org/10.1109/TSMCC.2006.871139

Brogden, W. J. (1939). Sensory pre-conditioning. *Journal of experimental psychology*, 25(4), 323. https://doi.org/10.1037/h0058944

Contel, D. M., Sansa, J., Artigas, A. A., & Prados, J. (2011). Salience modulation and associative inhibition interaction: Short but not long exposure to similar stimuli protects the salience of the unique elements. *Behavioral processes*, 86(1), 21-29. https://doi.org/10.1016/j.beproc.2010.08.001

Davis, J. D., & Smith, G. P. (1992). Analysis of the microstructure of the rhythmic tongue movements of rats ingesting maltose and sucrose solutions. *Behavioral neuroscience*, 106(1), 217. https://doi.org/10.1037/0735-7044.106.1.217

De Houwer, J., Thomas, S., & Baeyens, F. (2001). Association learning of likes and dislikes: A review of 25 years of research on human evaluative conditioning. *Psychological bulletin*, 127(6), 853. https://doi.org/10.1037/0033-2909.127.6.853

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. https://doi.org/10.1080/17470218.2011.644304

Domjan, M. (1975). Poison-induced neophobia in rats: Role of stimulus generalization of conditioned taste aversions. *Animal Learning & Behavior*, 3, 205-211. https://doi.org/10.3758/BF03213432

Dwyer, D. M. (2012). Licking and liking: The assessment of hedonic responses in rodents. *Quarterly journal of experimental psychology*, 65(3), 371-394. https://doi.org/10.1080/17470218.2011.652969

Dwyer, D. M., Bennett, C. H., & Mackintosh, N. J. (2001). Evidence for inhibitory associations between the unique elements of two compound flavors. *The Quarterly Journal of Experimental Psychology: Section B*, 54(2), 97-107. https://doi.org/10.1080/713932748

Dwyer, D. M., Burgess, K. V., & Honey, R. C. (2012). Avoidance but not aversion following sensory preconditioning with flavors: A challenge to stimulus substitution. *Journal of Experimental Psychology: Animal Behavior Processes*, 38(4), 359. https://doi.org/10.1037/a0029784

Dwyer, D. M., Hodder, K. I., & Honey, R. C. (2004). Perceptual learning in humans: Roles of preexposure schedule, feedback, and discrimination assay. *The Quarterly Journal of Experimental Psychology Section B*, 57(3b), 245-259. https://doi.org/10.1080/02724990344000114

Dwyer, D. M., & Honey, R. C. (2007). The effects of habituation training on compound conditioning are not reversed by an associative activation treatment. *Journal of Experimental Psychology: Animal Behavior Processes*, 33(2), 185. https://doi.org/10.1037/0097-7403.33.2.185

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. https://doi.org/10.1037/a0023078

Dwyer, D. M., Mundy, M. E., Vladeanu, M., & Honey, R. C. (2009). Perceptual learning and acquired face familiarity: Evidence from inversion, use of internal features, and generalization between viewpoints. *Visual Cognition*, 17(3), 334-355. https://doi.org/10.1080/13506280701757577

Ebbinghaus, H. (1885). *Memory: A Contribution to Experimental Psychology*. Translated by Henry A. Ruger & Clara E. Bussenius (1913). Originally published in New York by Teachers College, Columbia University. https://doi.org/10.5214%2Fans.0972.7531.200408

Espinet, A., Iraola, J. A., Bennett, C. H., & Mackintosh, N. J. (1995). Inhibitory associations between neutral stimuli in flavor-aversion conditioning. *Animal Learning & Behavior*, 23(4), 361-368. https://doi.org/10.3758/BF03198935

Estes, W. K. (1950). Toward a statistical theory of learning. *Psychological review*, 57(2), 94. https://doi.org/10.1037/h0058559

Fudim, O. K. (1978). Sensory preconditioning of flavors with a formalin-produced sodium need. *Journal of Experimental Psychology: Animal Behavior Processes*, 4(3), 276. https://doi.org/10.1037/0097-7403.4.3.276

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

Gibson, J. J., & Gibson, E. J. (1955). Perceptual learning: Differentiation or enrichment?. *Psychological review*, 62(1), 32. https://doi.org/10.1037/h0048826

Gibson, E. J., & Walk, R. D. (1956). The effect of prolonged exposure to visually presented patterns on learning to discriminate them. *Journal of comparative and physiological psychology*, 49(3), 239. https://doi.org/10.1037/h0048274

Gibson, E. J., Walk, R. D., Pick Jr, H. L., & Tighe, T. J. (1958). The effect of prolonged exposure to visual patterns on learning to discriminate similar and different patterns. *Journal of Comparative and Physiological Psychology*, 51(5), 584. https://doi.org/10.1037/h0042523

González, A., Recio, S. A., Sánchez, J., Gil, M., & de Brugada, I. (2018). Effect of exposure to similar flavors in sensory specific satiety: Implications for eating behavior. *Appetite*, 127, 289-295. https://doi.org/10.1016/j.appet.2018.05.015

Groves, P. M., & Thompson, R. F. (1970). Habituation: a dual-process theory. *Psychological review*, 77(5), 419. https://doi.org/10.1037/h0029810

Hall, G. (1979). Exposure learning in young and adult laboratory rats. *Animal Behavior*, 27, 586-591. https://doi.org/10.1016/0003-3472(79)90194-5

Hall, G. (2001). Perceptual learning: Association and differentiation. *Handbook of Contemporary Learning Theories*, 367-407. Lawrence Erlbaum Associates Publishers.

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

Hall, G. (2020). *The role of elements common to the preexposed stimuli in the perceptual learning effect.* http://www-users.york.ac.uk/~gh1/publications.html

Hall, G., Blair, C. A. J., & Artigas, A. A. (2006). Associative activation of stimulus representations restores lost salience: Implications for perceptual learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 32(2), 145. https://doi.org/10.1037/0097-7403.32.2.145

Hall, G., Prados, J., & Sansa, J. (2005). Modulation of the effective salience of a stimulus by direct and associative activation of its representation. *Journal of Experimental Psychology: Animal Behavior Processes*, 31(3), 267. https://doi.org/10.1037/0097-7403.31.3.267

Hall, G., & Rodríguez, G. (2010). Associative and nonassociative processes in latent inhibition: An elaboration of the Pearce-Hall model. *Latent inhibition: Cognition, neuroscience and applications to schizophrenia*, 114-136. https://doi.org/10.1017/CBO9780511730184.007

Hall, G., & Rodríguez, G. (2019). Attention to perceive, to learn and to respond. *Quarterly Journal of Experimental Psychology*, 72(2), 335-345. https://doi.org/10.1080/17470218.2017.1339719

Hall, G., & Rodríguez, G. (2020). When the stimulus is predicted and what the stimulus predicts: Alternative accounts of habituation. *Journal of Experimental Psychology: Animal Learning and Cognition*, 46(3), 327. https://doi.org/10.1037/xan0000237

Helmholtz, H. V. (1867). Concerning the perceptions in general. *Treatise on physiological optics* (J. Southall, Trans., 3rd ed., Vol. III). New York: Dover.

Holmes, N. M., Wong, F. S., Bouchekioua, Y., & Westbrook, R. F. (2022). Not “either-or” but “which-when”: A review of the evidence for integration in sensory preconditioning. *Neuroscience & Biobehavioral Reviews*, 132, 1197-1204. https://doi.org/10.1016/j.neubiorev.2021.10.032

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. https://doi.org/10.1080/713932631

Honey, R. C., Bateson, P., & Horn, G. (1994). The role of stimulus comparison in perceptual learning: An investigation with the domestic chick. *The Quarterly Journal of Experimental Psychology Section B*, 47(1b), 83-103.

Honey, R. C., & Dwyer, D. M. (2021). Higher-order conditioning: What is learnt and how it is expressed. *Frontiers in Behavioral Neuroscience*, 15, 726218. https://doi.org/10.3389/fnbeh.2021.726218

Honey, R.C., & Dwyer, D.M. (2022). Higher-order conditioning: A critical review and a computational model. *Psychological Review*, 129(6), 1338. https://doi.org/10.1037/rev0000368

Honey, R. C., Dwyer, D. M., & Iliescu, A. F. (2020). HeiDI: A model for Pavlovian learning and performance with reciprocal associations. *Psychological Review*, 127(5), 829. https://doi.org/10.1037/rev0000196

Honey, R. C., & Hall, G. (1989). Enhanced discriminability and reduced associability following flavor preexposure. *Learning and Motivation*, 20(3), 262-277. https://doi.org/10.1016/0023-9690(89)90008-8

Honey, R. C., Horn, G., & Bateson, P. (1993). Perceptual learning during filial imprinting: Evidence from transfer of training studies. *The Quarterly Journal of Experimental Psychology*, 46(3), 253-269. https://doi.org/10.1080/14640749308401088

Jacoby, L. L. (1978). On interpreting the effects of repetition: Solving a problem versus remembering a solution. *Journal of verbal learning and verbal behavior*, 17(6), 649-667. https://doi.org/10.1016/S0022-5371(78)90393-6

James, W. (1890). *The Principles Of Psychology Volume II*. Macmillan.

Jones, S. P., & Dwyer, D. M. (2013). Perceptual learning with complex visual stimuli is based on location, rather than content, of discriminating features. *Journal of Experimental Psychology: Animal Behavior Processes*, 39(2), 152. https://doi.org/10.1037/a0031509

Kilpatrick, A. J., Ćwiek, A., & Kawahara, S. (2023). Random forests, sound symbolism and Pokémon evolution. *PloS one*, 18(1), e0279350. https://doi.org/10.1371/journal.pone.0279350

Kovach, J. H., Fabricius, E., & Falt, L. (1966). Relationships between imprinting and perceptual learning. *Journal of Comparative and Physiological Psychology*, 61, 449–454. https://doi.org/10.1037/h0023265

Lavin, M. J. (1976). The establishment of flavor-flavor associations using a sensory preconditioning training procedure. *Learning and Motivation*, 7(2), 173-183. https://doi.org/10.1016/0023-9690(76)90026-6

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 Behavior Processes*, 37(2), 211. https://doi.org/10.1037/a0021888

Lavis, Y., & Mitchell, C. (2006). Effects of preexposure on stimulus discrimination: An investigation of the mechanisms responsible for human perceptual learning. *Quarterly Journal of Experimental Psychology*, 59(12), 2083-2101. https://doi.org/10.1080/17470210600705198

Levenson, R. M., Krupinski, E. A., Navarro, V. M., & Wasserman, E. A. (2015). Pigeons (Columba livia) as trainable observers of pathology and radiology breast cancer images. *PloS one*, 10(11), e0141357. https://doi.org/10.1371/journal.pone.0141357

Locke, J. (1690). *An essay concerning human understanding*. Printed by Eliz. Holt, for Thomas Basset, at the George in Fleetstreet, near St. Dunstan's Church., London:, MDCXC [1690].

Lombas, A. S., Alonso, G., & Rodríguez, G. (2008). The influence of comparison between similar stimuli on the effectiveness of their unique features. *Behavioral processes*, 78(1), 112-116. https://doi.org/10.1016/j.beproc.2007.12.001

Love, J., Selker, R., Marsman, M., Jamil, T., Dropmann, D., Verhagen, J., Ly, A., Gronau, Q. F., Šmíra, M., Epskamp, S., Matzke, D., Wild, A., Knight, P., Rouder, J. N., Morey, R. D., & Wagenmakers, E.-J. (2019). JASP: Graphical Statistical Software for Common Statistical Designs. Journal of Statistical Software, 88(2), 1–17. https://doi.org/10.18637/jss.v088.i02

Lubow, R. E., Schnur, P., & Rifkin, B. (1976). Latent inhibition and conditioned attention theory. *Journal of Experimental Psychology: Animal Behavior Processes*, 2(2), 163. https://doi.org/10.1037/0097-7403.2.2.163

Lyn, E. A., & Capaldi, E. D. (1994). Robust conditioned flavor preferences with a sensory preconditioning procedure. *Psychonomic Bulletin & Review*, 1(4), 491-493. https://doi.org/10.3758/BF03210952

Mackintosh, N. J. (1975). A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological review*, 82(4), 276. https://doi.org/10.1037/h0076778

Mackintosh, N. J. (2009). Varieties of perceptual learning. *Learning & Behavior*, 37, 119-125. https://doi.org/10.3758/LB.37.2.119

Mackintosh, N. J., Kaye, H., & Bennett, C. H. (1991). Perceptual learning in flavor aversion conditioning. *The Quarterly Journal of Experimental Psychology Section B*, 43(3b), 297-322. https://doi.org/10.1080/14640749108401272

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). New York, NY, US: Clarendon Press/Oxford University Press.

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

Miller, J. (1991). Reaction time analysis with outlier exclusion: Bias varies with sample size. *The Quarterly Journal of Experimental Psychology Section A*, 43(4), 907-912. https://doi.org/10.1080/14640749108400962

Miller, N. E., & Dollard, J. (1941). *Social learning and imitation*. Yale University Press.

Mitchell, C., & Hall, G. (2014). Can theories of animal discrimination explain perceptual learning in humans?. *Psychological Bulletin*, 140(1), 283. https://doi.org/10.1037/a0032765

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

Mitchell, C., Nash, S., & Hall, G. (2008b). The intermixed-blocked effect in human perceptual learning is not the consequence of trial spacing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34(1), 237. https://doi.org/10.1037/0278-7393.34.1.237

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. https://doi.org/10.1080/02724990143000225

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

Müller, D., Gerber, B., Hellstern, F., Hammer, M., & Menzel, R. (2000). Sensory preconditioning in honeybees. *Journal of Experimental Biology*, 203(8), 1351-1364. https://doi.org/10.1242/jeb.203.8.1351

Mundy, M. E., Dwyer, D. M., & Honey, R. C. (2006). Inhibitory associations contribute to perceptual learning in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 32(2), 178. https://doi.org/10.1037/0097-7403.32.2.178

Mundy, M. E., Honey, R. C., Downing, P. E., Wise, R. G., Graham, K. S., & Dwyer, D. M. (2009b). Material-independent and material-specific activation in functional MRI after perceptual learning. *NeuroReport*, 20(16), 1397-1401. https://doi.org/10.1097/WNR.0b013e32832f81f4

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. https://doi.org/10.1037/0097-7403.33.2.124

Mundy, M. E., Honey, R. C., & Dwyer, D. M. (2009a). Short Article: Superior Discrimination between Similar Stimuli after Simultaneous Exposure. *Quarterly Journal of Experimental Psychology*, 62(1), 18-25. https://doi.org/10.1080/17470210802240614

Nachman, M. (1963). Learned aversion to the taste of lithium chloride and generalization to other salts. *Journal of comparative and physiological psychology*, 56(2), 343. https://doi.org/10.1037/h0046484

Navarro, A., Arriola, N., & Alonso, G. (2016). Instruction-driven processing in human perceptual learning. *Quarterly Journal of Experimental Psychology*, 69(8), 1583-1605. https://doi.org/10.1080/17470218.2015.1088556

Nelson, J. B., Navarro, A., & Sanjuan, M. D. C. (2014). Presentation and validation of "The Learning Game," a tool to study associative learning in humans. *Behavior research methods*, 46, 1068-1078. https://doi.org/10.3758/s13428-014-0446-2

Nelson, J. B., & Sanjuan, M. D. C. (2009). Perceptual learning in a human conditioned suppression task. *International Journal of Comparative Psychology*, 22(4). https://doi.org/10.46867/ijcp.2009.22.04.04

Oswalt, R. M. (1972). Relationship between level of visual pattern difficulty during rearing and subsequent discrimination in rats. *Journal of Comparative and Physiological Psychology*, 81(1), 122. https://doi.org/10.1037/h0033330

Parker, L. A., Limebeer, C. L., & Rana, S. A. (2009). Conditioned disgust, but not conditioned taste avoidance, may reflect conditioned nausea in rats. In S. Reilly & T. R. Schachtman (Ed.), *Conditioned taste aversion: Behavioral and neural processes* (pp. 92–113). Oxford University Press.

Patitucci, E., Nelson, A. J. D., Dwyer, D. M., & Honey, R. C. (2016). The origins of individual differences in how learning is expressed in rats: A general-process perspective. *Journal of Experimental Psychology: Animal Learning and Cognition*, 42(4), 313. https://doi.org/10.1037/xan0000116

Pavlov, P. I. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex*. Translated and Edited by G. V. Anrep. Oxford University Press, London, 142.

Pearce, J. M., & Hall, G. (1980). A model for Pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological review*, 87(6), 532. https://doi.org/10.1037/0033-295X.87.6.532

Peron, R. M., & Allen, G. L. (1988). Attempts to train novices for beer flavor discrimination: a matter of taste. *The Journal of general psychology*, 115(4), 403-418. https://doi.org/10.1080/00221309.1988.9710577

Pineno, O., Ortega, N., & Matute, H. (2000). The relative activation of associations modulates interference between elementally trained cues. *Learning and Motivation*, 31(2), 128-152. https://doi.org/10.1006/lmot.1999.1047

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 Behavior Processes*, 33(2), 115. https://doi.org/10.1037/0097-7403.33.2.115

Prados, J., Hall, G., & Leonard, S. (2004). Dissociation between the Espinet and perceptual learning effects in flavor aversion conditioning. *Behavioral Processes*, 65(3), 221-229. https://doi.org/10.1016/j.beproc.2003.10.002

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. https://doi.org/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. *Behavioral processes*, 166, 103900. https://doi.org/10.1016/j.beproc.2019.103900

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, 31-37. https://doi.org/10.1016/j.lmot.2016.09.001

Recio, S. A., Iliescu, A. F., Mingorance, S. P., Bergés, G. D., Hall, G., & de Brugada, I. (2016). The role of instructions in perceptual learning using complex visual stimuli. *Journal of Experimental Psychology: Animal Learning and Cognition*, 42(4), 359. https://doi.org/10.1037/xan0000113

Reichelt, A. C., Morris, M. J., & Westbrook, R. F. (2014). Cafeteria diet impairs expression of sensory-specific satiety and stimulus-outcome learning. *Frontiers in psychology*, 5, 103842. https://doi.org/10.3389/fpsyg.2014.00852

Rescorla, R. A. (1981). Within-signal learning in autoshaping. *Animal Learning & Behavior*, 9(2), 245-252. https://doi.org/10.3758/BF03197827

Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *American psychologist*, 43(3), 151. https://doi.org/10.1037/0003-066X.43.3.151

Rescorla, R. A., & Cunningham, C. L. (1978). Within-compound flavor associations. *Journal of Experimental Psychology: Animal Behavior Processes*, 4(3), 267. https://doi.org/10.1037/0097-7403.4.3.267

Rescorla, R. A., & Durlach, P. J. (1981). Within-event learning in Pavlovian conditioning. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 83-111). Hillsdale, NJ: Ertbaum. https://doi.org/10.4324/9781315798820

Rescorla, R. A., & Wagner, A. R. 1972. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. Black & W. Prokasy (Eds.), *Classical conditioning II: Current theory and research*. New York: Appleton-Century-Crofts.

Rizley, R. C., & Rescorla, R. A. (1972). Associations in second-order conditioning and sensory preconditioning. *Journal of comparative and physiological psychology*, 81(1), 1. https://doi.org/10.1037/h0033333

Robinson, J. S. (1955). The effect of learning verbal labels for stimuli on their later discrimination. *Journal of Experimental Psychology*, 49(2), 112. https://doi.org/10.1037/h0042117

Rodríguez, G., & Alonso, G. (2004). Perceptual learning in flavor-aversion learning: Alternating and blocked exposure to a compound of flavors and to an element of that compound. *Learning and motivation*, 35(3), 208-220. https://doi.org/10.1016/j.lmot.2003.12.002

Rodríguez, G., & Alonso, G. (2008). Stimulus comparison in perceptual learning: Roles of sensory preconditioning and latent inhibition. *Behavioral Processes*, 77(3), 400-404. https://doi.org/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. https://doi.org/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. https://doi.org/10.1037/xan0000333

Sánchez, J., González, A., & de Brugada, I. (2023). Intermixed rapid exposure to similar stimuli reduces the effective salience of their distinctive features. *Journal of Experimental Psychology: Animal Learning and Cognition*, 49(3), 151. https://doi.org/10.1037/xan0000355

Spector, A. C., Klumpp, P. A., & Kaplan, J. M. (1998). Analytical issues in the evaluation of food deprivation and sucrose concentration effects on the microstructure of licking behavior in the rat. *Behavioral neuroscience*, 112(3), 678. https://doi.org/10.1037/0735-7044.112.3.678

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. https://doi.org/10.1016/0023-9690(95)90005-5

Symonds, M., Hall, G., & Bailey, G. K. (2002). Perceptual learning with a sodium depletion procedure. *Journal of Experimental Psychology: Animal Behavior Processes*, 28(2), 190. https://doi.org/10.1037/0097-7403.28.2.190

Titchener, Edward B. (1890). *Lectures of the Experimental Psychology of Thought Processes*. New York, Macmillian.

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. 5–47). Hillsdale, NJ: Erlbaum.

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

Wang, T., Lavis, Y., Hall, G., & Mitchell, C. J. (2012). Location and salience of unique features in human perceptual learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 38(4), 407. https://doi.org/10.1037/a0029733

Wang, T., & Mitchell, C. J. (2011). Attention and relative novelty in human perceptual learning. *Journal of Experimental Psychology: Animal Behavior Processes*, 37(4), 436. https://doi.org/10.1037/a0023104

Westbrook, R. F., Homewood, J., Horn, K., & Clarke, J. C. (1983). Flavor-odor compound conditioning: Odor-potentiation and flavor-attenuation. *The Quarterly Journal of Experimental Psychology Section B*, 35(1b), 13-33. https://doi.org/10.1080/14640748308400911

Wickelgren, W. A. (1972). Trace resistance and the decay of long-term memory. *Journal of Mathematical Psychology*, 9(4), 418-455. https://doi.org/10.1016/0022-2496(72)90015-6