The role of comparison in perceptual learning

El papel de la comparación en el aprendizaje perceptivo

Tesis doctoral de:

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The oldest and strongest emotion of mankind is fear, and the oldest and strongest kind of fear is fear of the unknown.

H. P. Lovecraft

Table of contents

Abstract

This thesis focuses on the analysis of perceptual learning from an associative framework. For this purpose we used a variety of procedures in both human and non-human animals with the aim of finding a common ground between species.

Chapter II is dedicated to experiments using visual stimuli in human participants. We demonstrated that additional exposure to the unique elements of a checkerboard only improves discrimination when it points to their location within the stimuli. Thus, the memory representation of the unique elements is not relevant to explain perceptual learning under these conditions, but rather the task can be solved focusing only on their location. We also demonstrated that explicit instructions to look for differences are needed to obtain perceptual learning, and that alternative instructions that require similar focus on the stimuli do not improve discrimination. These results suggest that perceptual learning with visual stimuli in humans is not mediated by salience modulation of the unique elements caused by mere exposure, but instead depends on a location bias and instruction-driven self-reinforcement.

In Chapter III we adapted the procedure used with humans to animal subjects. Hence, we obtained perceptual learning using a procedure with short inter-stimulus intervals, in contrast to the usual procedure with intervals of several hours. We achieved this by controlling the influence of the excitatory associations between the stimuli on the test. Furthermore, we demonstrated that adding a distractor in the middle of the exposed stimuli abolished perceptual learning, thus replicating a similar result with humans. Our results highlight the possibility that comparison might be a relevant

mechanism to explain both human and animal perceptual learning, and that there is no need to postulate separate mechanisms for different species.

Finally, in Chapter IV we replicated the standard animal perceptual learning procedure using a flavour preference conditioning paradigm. We posit that perceptual learning might be involved in human feeding behaviour, thus having several applications such as the development of effective interventions to promote healthy eating or the prevention of intake habits that can lead to obesity.

Resumen

Esta tesis se centra en el análisis del aprendizaje perceptivo desde el marco del aprendizaje asociativo. Para ello hemos empleado varios procedimientos en animales humanos y no-humanos con el objetivo de encontrar unas bases comunes entre especies.

El Capítulo II está dedicado a experimentos con estímulos visuales en participantes humanos. Demostramos que la exposición adicional a los elementos únicos de un damero sólo mejora la discriminación cuando señala su localización dentro del estímulo. Así, la representación en memora de los elementos únicos no es relevante para explicar el aprendizaje perceptivo en estas condiciones, sino que la tarea puede ser resuelta centrándose sólo en su localización. También demostramos que la presencia de instrucciones explícitas para buscar diferencias es necesaria para obtener aprendizaje perceptivo; y que instrucciones alternativas que requieren similar atención al estímulo no mejoran la discriminación. Estos resultados sugieren que el aprendizaje perceptivo con estímulos visuales en humanos no está mediado por la modulación de saliencia de los elementos únicos causada por mera exposición. Por el contrario, depende de un sesgo de localización y de auto-reforzamiento dirigido por las instrucciones.

En el Capítulo III adaptamos el procedimiento utilizado en humanos a sujetos animales. Así, obtuvimos aprendizaje perceptivo usando un procedimiento con intervalo entre estímulos corto, en contraste con el procedimiento habitual que usa intervalos de muchas horas. Logramos esto controlando la influencia en el test de las asociaciones excitatorias entre estímulos. Además, demostramos que la colocación de un distractor entre los estímulos expuestos abolía el aprendizaje perceptivo, replicando por tanto resultados similares en humanos. Nuestros resultados indican que la comparación podría

ser un mecanismo relevante para explicar tanto el aprendizaje perceptivo con animales como con humanos, y que no hay necesidad de postular mecanismos separados para diferentes especies.

Por último, en el Capítulo IV replicamos el procedimiento estándar de aprendizaje perceptivo en animales usando un procedimiento de preferencia condicionada al sabor. Proponemos que el aprendizaje perceptivo podría estar relacionado con la conducta de ingesta en humanos, teniendo múltiples aplicaciones tales como el desarrollo de intervenciones eficaces para promocionar el consumo de comida saludable o la prevención de hábitos que pueden llevar a obesidad.

Chapter I

Introduction

Chapter I: Introduction

A brief historical perspective

Perceptual learning can be broadly defined as "any relatively permanent and consistent change in the perception of a stimulus array, following practice or experience with this array" (Gibson, 1963). Whilst this may sound like a strange laboratory phenomenon that one would never see in the real world, it is, in fact, surprisingly ubiquitous. It has always been notable that some individuals can actually differentiate between things that for most people are indistinguishable. A typical example is chicken sexing. Chicken sexers are able to classify day-old chicks with an incredible accuracy and at great speed, when most of us probably could never tell the difference between males and females even with plenty of time to examine the animals (Biederman & Shiffrar, 1987). Perceptual learning can also be seen in the ability of food and beverage tasters to discriminate and to detect small differences in different varieties of, for example, wines (Bende & Nordin, 1997). But we can also assume that perceptual learning is involved in many other everyday abilities that require fine and fast discriminations: discrimination and identification of faces, identification of traffic signs and other traffic events, detection of events in radar and sonar screens, detection of anomalies on x-ray pictures or CT scan images, and the perception of different pitches and timbres in music.

The origins of the interest in perceptual learning can be traced back before the rise of psychology as an empirical science. Many philosophers tried to address the question of how we perceive the world, and if such perception perfectly reflects reality

or if it is a construction of our psyche. A rationalist view would be that perception is determined by the beholder's rational faculties or innate mental abilities. An empiricist view would hold that perception is modelled by experience and learning. In the light of evidence (for example, from early sensory deprivation experiments, e.g. Gibson & Walk, 1960), this "nativist vs. empiricism" debate would be later solved in a conciliatory way: perception may change with experience, but not all perception depends on learning (Gibson, 1963).

As perceptual learning became the focus of attention, some explanations were developed to account for this phenomenon. Early experimental psychologists such as Titchener claimed that perception arises from the association between different sensations in consciousness. Further, William James (and later Miller and Dollard, 1941) developed a related idea. Stimuli would be associated with response cues, for example verbal responses (labels). When two stimuli are associated with similar responses, they become less distinctive (equivalent), whilst when two stimuli are associated with different responses they become more distinctive. This view, named "enrichment theory", was taken to depend on associative processes, by which percepts would change with experience, becoming more complex or "rich". In this sense, perception would with time become more and more different from reality, as percept construction would be chiefly based on associations and elaborations of the perceiving individual. In contrast to this view, Gibson and Gibson (1955) proposed that changes in perception may depend on an increasing ability to detect distinctive features of the stimuli. This implies that, with experience, perception would become a more faithful representation of sensory stimulation. Thus, associations with responses would not be

the cause of the change in perception, but a consequence of the detection of new features. They called this view “specificity” or “differentiation theory”. In spite of their underlying differences, both accounts have in common that they focus on the modification of how organisms perceive the world as a result of learning. Therefore, any account of perceptual learning should be able to explain how perception of any single physical object may change as a function of experience.

Many phenomena can fit under the definition of perceptual learning described previously; that is, a change in perception as a result of experience. Research on top-down effects on perception could easily fit within this definition (Bruner, 1957), as well as some research on perceptual changes that occur during development (Gibson & Olum, 1960) and imprinting (Montuori & Honey, 2015). Such topics were of sufficient relevance to have their own fields of study, distinct from the perceptual learning framework. There are other phenomena that fit the definition of perceptual learning, such as habituation or attenuation of neophobia (Hall, 1991), discrimination learning (Sutherland & Mackintosh, 1971), acquired distinctiveness or equivalence (Honey & Hall, 1989a), or easy-to-hard effects (Scahill & Mackintosh, 2004). Many of these phenomena have been explained using associative theory, which, in terms of Gibson, could be regarded as a form of “enrichment” because new information is added to the stimuli.

A great deal of research has focused on the psychophysics of visual stimuli, and how repeated exposure to very simple stimuli (such as lines, gratings or moving dots) causes changes in the perceptual sensitivity to certain features, allowing for the

detection of previously imperceptible differences (this has been called hyperacuity, e.g., Poggio, Fahle, & Edelman, 1992). These changes are mediated by plasticity in primary brain areas, and it has been argued that they are very specific and not transferrable to other retinal locations or stimuli (Fahle, 1997, but see Dwyer, 2008). There has also been much research regarding the effects of familiarity on discrimination under more complex conditions, such as with language perception (e.g., Pisoni, Lively, & Logan, 1994) or categorical perception of faces or animals (e.g., Beale & Keil, 1995; Tanaka & Taylor, 1991). However, our current concerns are not to review all of the existing literature that could be classified under the name of perceptual learning. Instead, we are going to focus on the evidence from the associative framework, and how it attempted to accommodate some forms of learning that challenged contemporary associative theories. Following Gibson's footsteps, Goldstone (1998) specifically distinguishes between "perceptual changes", that occur in the early stages of processing, and "high-level changes", such as associative learning. It is a matter of discussion if such a distinction really exists, and one may wonder why associative mechanisms should be considered "high-level" and why we should postulate a different mechanism for "low-level" perceptual changes. In fact, there have been some recent attempts to merge both perspectives into a single framework, considering reinforcement signals as the cornerstone of perceptual changes (Seitz & Watanabe, 2005; Tsushima & Watanabe, 2009). Such an idea considers all perceptual learning as a form of "enrichement", even changes usually considered to be a product of mere exposure, since reinforcement (or "diffuse reinforcement signals", Seitz & Watanabe, 2003) is considered sufficient and necessary. However, as we will see, there are situations in which it is very difficult to

identify any differential reinforcement source, and under such conditions it is also possible to observe perceptual learning. This "differentiation" learning poses a real challenge for the classic associative models, as well as for "diffuse reinforcement" theories (Gibson, 1963). Following Mackintosh (2009) we are going to focus only on that learning which changes how individuals discriminate between similar events as a result of exposure. For this reason we are adopting a narrower definition of perceptual learning, which would be an improvement in the discrimination between two similar stimuli as a result of mere exposure to such stimuli (Mitchell & Hall, 2014).

Perceptual learning in animals

One of the first instances of the perceptual learning effect in animals was offered by Gibson and Walk (1956). They exposed one group of young rats to geometrical figures (triangles and circles) stuck on the walls of their home cages. Later, they found that these rats were faster in learning to discriminate between the figures than a non-exposed control group. Gibson (1963) drew up a non-associative explanation for this phenomenon, in terms of "differentiation". According to her, "the differentiation view holds that practice serves to reduce generalization among the stimuli, to increase precision of discrimination of variables actually present in stimulation, and to detect relevant variables or distinctive features not previously detected" (Gibson, 1963). In a further development of this idea, Gibson and Levin (1975) stated that differentiation allows for the extraction of information from the stimuli, in contrast with associative accounts, which serve to add information to the stimuli (i.e. "enrichment"). To illustrate this more clearly, we could conceptualize any stimulus (e.g. AX and BX) as a set of

unique, distinctive elements (e. g. *a* and *b*), and a set of elements in common with other stimuli (e. g. *x* see Figure 1). Exposure would extract or "pull out" the unique information, making it more salient and thus increasing differentiation. The critical idea is that this differentiation would occur due to the opportunity to compare the to-be-discriminated stimuli (Gibson, 1969). That is, both stimuli (and their mental representations) should be present at the same time. Since then, the notion of comparison has been a recurrent theme in perceptual learning research.

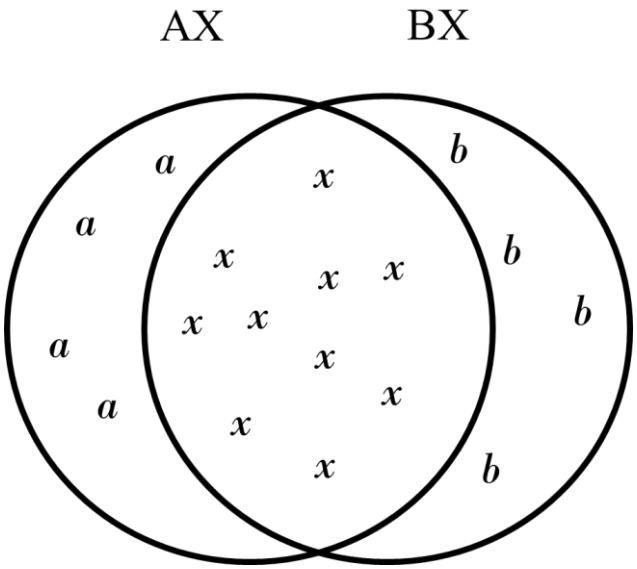

Figure 1: Schematic representation of two similar stimuli (AX and BX), with their shared unique elements (*x*) and their unique distinctive elements (*a* and *b*).

Despite Gibson's interpretation of perceptual learning being a challenge to associative theory, there has been much research attempting to accommodate such phenomena to this framework, whilst maintaining the "differentiation" concept. For example, Mackintosh, Kaye and Bennet (1991, Exp. 2) exposed one group of rats to two compound flavours (lemon-sucrose and lemon-saline), another group to the common element alone (lemon), and a third group to the unique elements alone (sucrose and

saline). Following this, they paired the lemon-saline compound with an injection of LiCl to establish an aversion, and then tested consumption of lemon-sucrose. They found that the group exposed to the unique elements alone showed a greater level of generalization to the test compound than the other two groups, which did not differ between them. They interpreted this result in terms of latent inhibition (LI), that is, the retardation of learning caused by exposure to the target stimuli. During exposure, the common element X would be exposed twice as often as the unique elements, so it should develop more latent inhibition. As generalization depends precisely on the degree of conditioning of this common element, this mechanism can elegantly explain perceptual learning within standard associative theory (McLaren, Kaye, & Mackintosh, 1989).

However, it soon became clear that LI alone was not sufficient to explain perceptual learning. Symonds and Hall (1995, Exp. 3) exposed one group of rats to two compound flavours (acid-saline and acid-sucrose) in an intermixed fashion, that is, a different compound on each session (AX, BX, AX, AX…), similar to the arrangement used by Mackintosh et al. (1991). However, they also exposed another group to the same compounds the same number of times, but in a blocked fashion (AX, AX… BX, BX…). According to the LI account, there should have been no differences between both groups, as the number of exposures to the unique and common elements is the same. However, they found that the intermixed group generalized less than the blocked group, and that the latter did not generalize less than a non-exposed group. Honey, Bateson and Horn (1994; see also Honey & Bateson, 1996) found a similar result using visual stimuli with chicks using an imprinting procedure. This observation has since

been named the intermixed-blocked (I/B) effect, and has been taken as a measure of perceptual learning in later experiments. Several models have since been developed to accommodate the I/B effect, and the most influential of these will be reviewed next.

The McLaren and Mackintosh model

McLaren and Mackintosh (2000) expanded their previous model (see McLaren, Kaye, & Mackintosh, 1989) to accommodate the I/B effect, proposing two different mechanisms. The first mechanism is unitization (already present in the first instance of the model), which refers to the forming of associations between the different features that comprise each stimulus. To understand this mechanism, it is necessary to conceptualize two very similar stimuli as a set of common and unique features. On every trial, a random subset of features will be sampled, and they will form associations with whichever features are active at the same time. But, because of their high similarity, unique features will be very scarce, and they will be sampled inconsistently. That is, it is less likely that the same unique features will be active at the same time on several successive trials. Because of this, they will initially not form strong associations with other features. Conversely, common features will be sampled very consistently on every trial, and thus they will suffer a great deal of latent inhibition due to the high level of unitization (we are also assuming a situation in which the context is familiar). As common features gain latent inhibition, it will become increasingly likely that the still highly associable unique elements will form associations between themselves. A high degree of unitization will have the consequence of spreading the activation to more features, thus increasing the number of unique features activated with each presentation

of the stimuli. This would serve to reduce generalization on a discrimination test. Further, the model proposes that this increase in unitization might in some cases outweigh latent inhibition. Since more features are sampled after unitization has taken place, this could lead to better conditioning, as more unique features are active at the same time as the US (Bennett, Tremain, & Mackintosh, 1996). To sum up, unitization can be understood as the formation of a representation of the different elements that comprise any stimulus: the higher the unitization, the better the representation. This is relevant for perceptual learning because what drives discrimination between two very similar stimuli is the representation of the elements that make them different. In a way, it could be regarded as the interpretation of the "differentiation" concept from an associative point of view.

The second mechanism proposed by McLaren and Mackintosh (2000) is the formation of inhibitory associations. Intermixed exposure would allow the formation of inhibitory associations between the unique elements of the exposed stimuli. Following standard associative theory (e. g. Wagner, 1981), some excitatory associations between the common and unique elements of each compound are expected (A-X and B-X). Once formed, these associations allow the common element X to associatively activate the representation of the non-present unique element. It is predicted that the unique element activated this way will form inhibitory associations with the unique element physically present on that trial. After conditioning AX, generalization to BX will decrease, because B is an inhibitor of A, which is a good predictor of the consequence. In intermixed exposure, A will become a predictor of the absence of B, and B will become a predictor of the absence of A. However, in blocked exposure, when the same stimulus is

presented for many days, only weak inhibitory associations, if any, will be formed. Espinet, Iraola, Bennett and Mackintosh (1995) provided the first direct evidence of inhibitory associations between the unique elements after intermixed exposure, a phenomenon that has since been termed the "Espinet effect". Bennett, Scahill, Griffiths and Mackintosh (1999) demonstrated the relevance of such inhibitory links in a perceptual learning procedure. In their Experiment 2 they used three different groups: one with blocked exposure, other in which AX was followed by BX (AX->BX), and a last one with the reverse arrangement (BX->AX). The idea is that presenting AX immediately followed by BX will lead to unidirectional inhibitory links from B to A, while using the reverse arrangement will cause inhibition from A to B. After conditioning AX, we should only expect less generalization in the AX->BX group. According to such a prediction, group AX->BX showed less generalization, while group BX->AX showed equivalent generalization to the blocked group.

McLaren and Mackintosh (2000) do not directly propose that unitization plays a role in the I/B effect. However, there are some ideas that can be drawn from their model. First, intermixed exposure makes sampling of the unique features even more variable. This might lead to faster unitization of the common features and more latent inhibition. Artigas and Prados (2014) provided some evidence of this possibility, since they found that after intermixed exposure to AX and BX and conditioning to a novel compound ZX, there is less generalization to another novel compound NX. In this case, the higher the associability of X, the more generalization would be expected. Second, for the same reasons, the intermixed exposure pattern could also affect unitization of A and B. If during intermixed exposure X acquires latent inhibition more rapidly, then A

and B should also be more unitized themselves. Thus, in addition to inhibitory links, the representation of the unique elements could play a role in the I/B effect. This could potentially account for some results where inhibitory links cannot be operating, although it would have problems to explain the results of experiments using within-subject designs (e.g., Blair & Hall, 2003; Blair, Wilkinson, & Hall, 2004). In this case, when intermixed exposure to AX and BX is followed by further exposure to CX in a single block, C should be more unitized, since the common elements would have suffered a lot of LI.

The model developed by McLaren and Mackintosh (2000) is sufficiently powerful to explain many instances of perceptual learning, including the basic I/B effect. Some of their predictions have been confirmed independently, such as the Espinet effect. However, there are some results that the model has some trouble explaining, and these will be described next.

Hall's salience modulation model

A few years after McLaren and Mackintosh published their model, Hall (2003) proposed another explanation for the I/B effect. He accepts that during exposure excitatory associations are formed between the features of the compounds, and does not argue against the existence of inhibitory links. However, he deemed this process insufficient to explain perceptual learning, and thus proposed a rather different effect for the associative activation of the unique elements. He also adopted the notion of differentiation and attempted to integrate this into the associative framework, but without turning to the concept of comparison. He pointed out that repeated exposure

causes habituation of the stimuli presented. However, the associative activation has the effect of reversing or attenuating this habituation process. Hence, as a consequence of the associative activation of the unique elements during intermixed exposure, these will suffer less habituation and will be more salient than the common elements (they will be "pulled out", in terms of Gibson). Blocked exposure would not allow this process to act optimally, and thus less salience modulation would be expected (see Figure 2). Blair and Hall (2003) found compelling evidence in favour of this account. They exposed AX and BX intermixed and CX blocked in a within-subjects design. After that, they conditioned a new flavour Y, and tested generalization to BY and CY. With this manipulation, they intended to eliminate any possible source of conditioned inhibition. According to their predictions, rats generalized less to BY than to CY, which indicates that the unique elements were more salient after intermixed exposure. Blair, Wilkinson and Hall (2004) presented more direct evidence of this higher salience by directly assessing the UR to the flavours and their relative associability.

The predictions of this proposal are very similar to those from the unitization account discussed earlier. However, most of the assumptions made by McLaren and Mackintosh (2000) regarding unitization are based mainly on plausibility, and not on direct evidence. The merit of Hall's proposal is that it requires fewer assumptions to explain the same results. Probably because of this last reason most of the literature on perceptual learning have avoided discussing the unitization mechanism, and simply adopted the inhibitory link formation as the hallmark of the McLaren and Mackintosh (2000) model (e.g., Blair & Hall, 2003; Hall, 2003). As a corollary for this, it has been shown that both Hall's (2003) salience modulation mechanism and McLaren and

Mackintosh's (2000) inhibitory associations proposal can underlie perceptual learning, and which one prevails depends on procedural variables such as the length of the preexposure phase (Artigas, Sansa, Blair, Hall, & Prados, 2006).

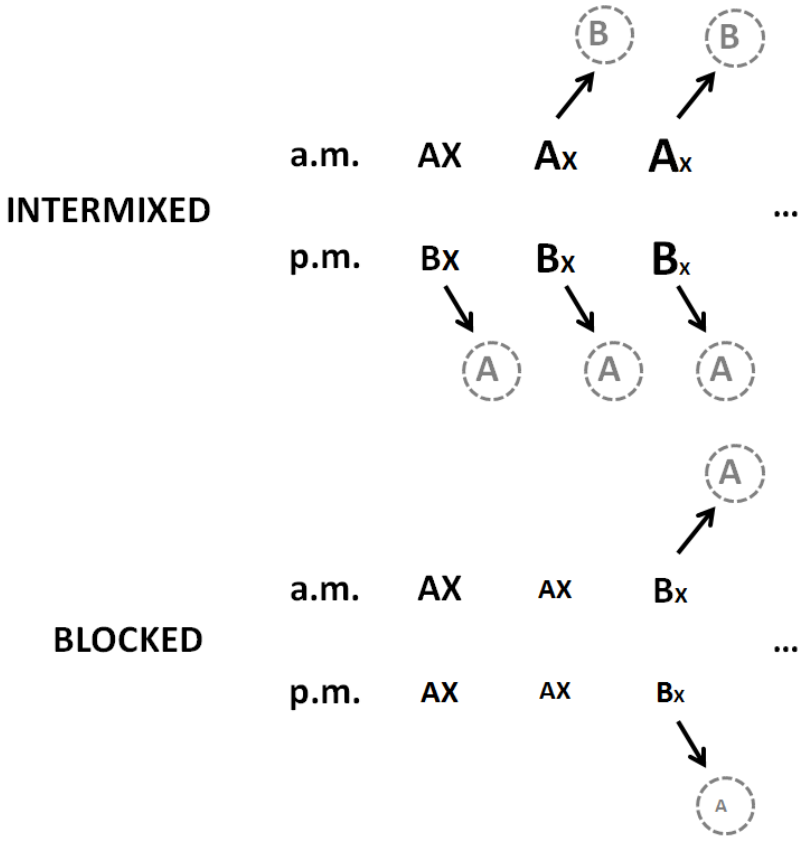

Figure 2: Representation of Hall's model (2003) with a between groups procedure similar to Symonds and Hall (1995). The circles represent associative activation of the unique elements, which would restore their salience. Adapted from Mitchell and Hall (2014).

We should note, however, that direct assessments of changes in salience caused by associative activation have not always yielded positive results (Dwyer & Honey, 2007; but see Hall & Rodriguez, 2009). For instance, Dwyer and Honey (2007) exposed rats to AX and BY, after which they prompted the associative activation of B by exposing Y alone. They then conditioned AB. If associative activation caused higher salience of B, we should expect greater overshadowing of A in comparison with a

control group without associative activation. They found no such difference, thus disconfirming a strong prediction of Hall's model. In summary, the proposal of Hall (2003) can explain many instances of perceptual learning that are beyond the McLaren and Mackintosh model, but there is no strong direct confirmation of these predictions. This, together with the results of human experiments (which we are going to review next) seems sufficient to raise doubts about the general applicability of this model.

Perceptual learning in human experiments

The previous models were based mainly on data from animal research, but there are some effects in human perceptual learning that appear to be beyond the scope of the McLaren and Mackintosh (2000) and Hall (2003) proposals. At first sight it seems that the same basic effects are obtained with humans. For example, Lavis and Mitchell (2006) exposed participants to four coloured checkerboards. All of them shared the same background (the common element), but had unique features as unique elements (clusters of coloured squares). After exposing two of them in an intermixed fashion and the remaining two in blocks, they conducted a same-different test, asking participants if pairs of checkerboards were identical or different. Participants discriminated better between the checkerboards previously exposed in alternation. This experiment was the first replication of the I/B effect in humans, and was followed by many more (de Zilva & Mitchell, 2012; Lavis, Kadib, Mitchell, & Hall, 2011; Mitchell, Kadib, Nash, Lavis, & Hall, 2008; Wang, Lavis, Hall, & Mitchell, 2012).

However, procedural differences make a direct implementation of the previously described models difficult. Usually, experiments with humans use complex visual

stimuli such as coloured checkerboards or faces (but see, Dwyer, Hodder, & Honey, 2004; Mundy, Dwyer, & Honey, 2006, for examples of perceptual learning in humans using flavours). The stimuli are variations of the same prototype that include some unique features, such as a cluster of coloured squares in the case of checkerboards. Exposure takes place at a very fast pace, and usually the stimuli remain on the screen for less than a second, with an interval of little more than a second between trials. The test is also different: instead of a generalization test, it is commonplace to use discrimination (same-different) tests. Under these conditions, a comparison-like process seems likely to occur, as the representation of one stimulus is presumably still active when the next appears. This very fact is unlikely in most experiments with animals, as there is usually a gap of several hours between presentations of the stimuli. It is difficult to see how a model such as Hall's (2003) could operate here, because with such a short interval between stimuli, associative activation is unlikely. For example, according to Wagner's SOP model (Wagner, 1981), when a given stimulus is presented its constituent elements will be activated in the A_1 state, which is a state where they receive maximum processing but has limited capacity. Those elements will quickly decay to the A_2 state, which is a state of marginal processing. Associative activation is also assumed to proceed in the A_2 state. Further decaying to the long-term memory inactive (I) state will be slow. Central to the model is the assumption that inactive elements could be activated to A_1 state or to A_2 state, but elements in A_2 cannot pass directly to A_1 state (see Figure 3). Thus, if the unique elements of a stimulus are active in A_1 or A_2 state because they have been recently presented, they cannot be activated associatively and thus no salience modulation would take place. As for McLaren and Mackintosh (2000),

there is evidence that this mechanism is not involved in perceptual learning with visual stimuli (Lavis & Mitchell, 2006; Mitchell et al., 2008; however, see Mundy et al., 2006, for support of this model using flavors).

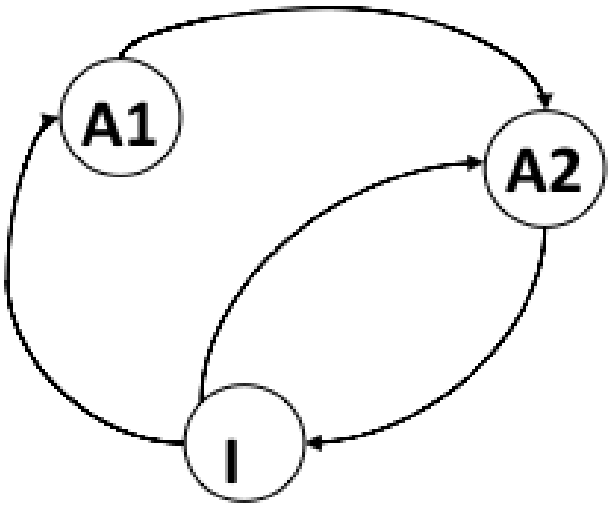

Figure 3: Diagram showing the activation flow of an element according to Wagner (1981, adapted from Brandon, Vogel, & Wagner, 2003)**.**

Because the experimental paradigm used humans, and the results it yielded did not fit well with salience modulation models, some alternative explanations were developed. For example, Lavis et al. (2011) included exposure to the unique features alone on a blank screen mixed with an alternate exposure to two checkerboards. They found that this additional exposure further increased discrimination in comparison with a standard intermixed group. Furthermore, additional exposure also increased accuracy on a colour matching task, showing that the memory of the unique features was better under such conditions. This led to a proposed explanation of human perceptual learning in terms of better memory representation. Intermixed exposure would result in higher salience of the unique elements, which would command more attention and then be better represented in memory. However, further experiments raised doubts about some

of the results obtained using visual stimuli in humans. For instance, Jones and Dwyer (2013; see also, Wang et al., 2012) showed that the memory of the unique elements was irrelevant for solving the same-different task. They gave their subjects intermixed exposure to AX and BX, and then tested CX and DX, where C and D were new features placed in the same spot as A and B had been located. They found that under those circumstances the improvement in discrimination was transferred to the new unique elements, contrary to the predictions of Lavis et al. (2011). They also tested participants with A'X and B'X, being A' and B' the same unique elements previously exposed but located in a different position, and they found no improvement in discrimination. In the face of such results, Jones and Dwyer (2013) concluded that the better discrimination after intermixed exposure was based only on an attentional bias, at least when using stimuli such as checkerboards.

In spite of such problems, research with humans brought back the old idea of comparison to perceptual learning research. Many pioneering experiments used comparison as a framework (e.g., Honey et al., 1994; Symonds & Hall, 1995), although it lost importance in favour of more elaborate associative accounts. The fact that results with animals were readily explained in associative terms, and that results with humans seemed to contradict such models, led Mitchell and Hall (2014) to state that "[it] appears then that humans, but not rats, can benefit from the opportunity to compare the stimuli very directly during preexposure". The evidence for this suggestion will be reviewed next.

The role of comparison in perceptual learning

In the previous sections we have seen how associative learning researchers have tried to solve the issue of perceptual learning. First, they attempted to rely only on well established associative mechanisms such as latent inhibition or conditioned inhibition (Mackintosh et al., 1991). Later, some models were developed that included some form of mechanism of salience modulation, by which the unique elements gained salience (Hall, 2003; McLaren & Mackintosh, 2000). This was a return to the concept of differentiation proposed by Gibson (1963). However, the idea of comparison did not feature in any of these models. This is not surprising, bearing in mind that such a concept was ill-defined and Gibson did not propose any underlying mechanism for it. In spite of this, there have been several attempts to test the idea of comparison in human and animal research.

Many of those attempts found results that run counter to the idea of comparison. Honey and Bateson (1996), using chicks, found that reducing the interval between presentations of the stimuli increased generalization between them. Bennett and Mackintosh (1999), using rats, found that intermixed exposure was better than a rapid alternation procedure, and that the shorter the interval between presentations of the flavours, the greater the generalization. Alonso and Hall (1999) and Rodríguez and Alonso (2008), also with rats, even found that the simultaneous presentation of two flavours produced more generalization than blocked exposure. In all of these experiments, the results can easily be explained: the simultaneous or close exposure causes excitatory associations to be formed between the flavours presented, which

increase generalization (Honey & Bateson, 1996). Thus, on the one hand, if AX activates B during conditioning, it is likely that it will also be associated with the unconditioned stimulus. On the other hand, when presenting BX during test it will retrieve A, which will in turn activate the representation of the unconditioned stimulus. Thus, mediated conditioning and sensory preconditioning are both possible when the unique elements are linked. To control this, Rodriguez, Blair and Hall (2008) conditioned a new flavour Y after intermixed, blocked or concurrent exposure to AX and X, and then they tested AY. Direct associations between the preexposed compound flavours should not have any influence with such a procedure, but salience modulation of the unique elements should still exert an effect. Their results showed that concurrent exposure produced less generalization than blocked exposure, but did not differ from spaced intermixed exposure. If comparison had any involvement with perceptual learning, then we should have expected better discrimination under concurrent conditions. As this effect was not found, they concluded that comparison does not exist in animals.

However, the results of research with humans have yielded a rather different picture. Despite our earlier criticisms of human research, experiments using faces have been of particular interest to the study of comparison. Mundy, Honey and Dwyer (2007; see also, Mundy, Honey & Dwyer, 2009) showed that simultaneous exposure to a pair of faces produced better discrimination than successive intermixed exposure. In a further set of experiments, Dwyer, Mundy and Honey (2011) found that a visual distractor placed between two different faces presented successively decreased later discrimination between them. This interference was greater when the distractor was

similar to the target stimuli (another face) than when it was quite different (a checkerboard). These results clearly support the notion that comparison is important in perceptual learning with humans.

Honey and Bateson (1996) proposed an explanation based on short-term habituation or sensory adaptation. The fact that the representation of one stimulus is active when the other stimulus appears (that is, the conditions that allow comparison) means that the elements they have in common will be habituated. This would lead to an increased effective exposure to the unique elements, which could affect later learning in several ways. Perhaps such a process improves memory encoding of the unique elements (Mitchell, Kadib, et al., 2008) or their unitization (McLaren & Mackintosh, 2000), thus making them more effective. Montuori and Honey (2015, see also Dwyer et al., 2011; Honey & Ward-Robinson, 2002) suggested that when a compound stimulus is presented, the node corresponding to each element is linked to a hidden unit, which at the same time is linked to an outcome unit. The expected result of exposure is that both compound stimuli (e.g. AX and BX) are linked to the same configural hidden unit by mediation of the common element (X). However, because of the short-term habituation of X more resources will be allocated to the processing of A and B, which will affect how the information related to the stimuli is stored in memory. This processing bias of the unique elements might increase the likelihood that the nodes of the unique elements will be linked to different hidden units. As each hidden unit can be linked to different outcome units, a reduction in generalization is expected. The idea that short-term habituation somewhat improves the processing of the unique elements can explain some animal experiments as well as most of the experiments with humans, including the

effect of distractor placement. Dwyer et al. (2011) proposed that the distractor would disrupt short-term habituation of X, possibly displacing the stimuli from short-term memory, and thus it would neutralize the processing bias in favour of the unique elements.

In contrast to the idea that a processing bias might increase the effectiveness of the unique elements, Artigas, Contel, Sansa and Prados (2012) found evidence that better processing might actually be reducing this effectiveness. Thus, they found that when the habituation of X allows for better processing of the unique elements, these elements acquire less of an aversion in a later conditioning phase. They suggested that better processing of the unique elements caused by short-term habituation of the common elements would lead to increased latent inhibition. It remains a matter of discussion whether more latent inhibition necessarily implies worse discrimination. In fact, perceptual learning is precisely that: it is easier to discriminate between familiar than between novel stimuli, even though it might be harder to learn about the former.

Throughout this thesis we are going to try to confront some of the issues we have raised in this introduction. First, we are going to present some experiments with human participants, in which we will address some of the problems with the standard experimental paradigms. Second, we are going to demonstrate perceptual learning in rats using a procedure that allows comparison, that is, where the representations of two stimuli are active at the same time. We are going to test whether disrupting such comparison will exert an effect on discrimination. Finally, we will outline the basis of some applied research that can be drawn from the perceptual learning framework.

Chapter II

Perceptual learning in humans

Chapter II: Perceptual learning in humans

Research on perceptual learning in humans from an associative framework has begun relatively recently. In the introduction, we described some of the experiments carried out with human participants, in which most of them used visual stimuli, specifically coloured checkerboards, which were presented consecutively in an intermixed or blocked fashion. Checkerboards are usually composed of a common background, often named X, and some unique element formed by a cluster of squares of the same colour. The unique elements are named A, B, C, etc., so whole checkerboards are usually referred to as AX, BX, CX, etc. (see Figure 1). After exposure, participants were usually required to perform a same-different task or a discrimination learning task (Carvalho & Albuquerque, 2012; Lavis et al., 2011; Lavis & Mitchell, 2006; Mitchell, Kadib, et al., 2008; Wang et al., 2012; Wang & Mitchell, 2011). The usual result was better discrimination after intermixed presentation (the intermixed-blocked effect, or I/B). Even though it would be tempting to interpret such results using associative models (Hall, 2003; McLaren & Mackintosh, 2000), they do not fit well with the particular methodological features of these tasks. There are also reasons to think that the same principles we are about to detail apply to all experiments on perceptual learning in humans using visual stimuli, be it faces (Dwyer, Mundy, & Honey, 2011; Mundy, Honey, & Dwyer, 2007, 2009); figure matrices (de Zilva & Mitchell, 2012); or Arabic characters (Angulo & Alonso, 2012).

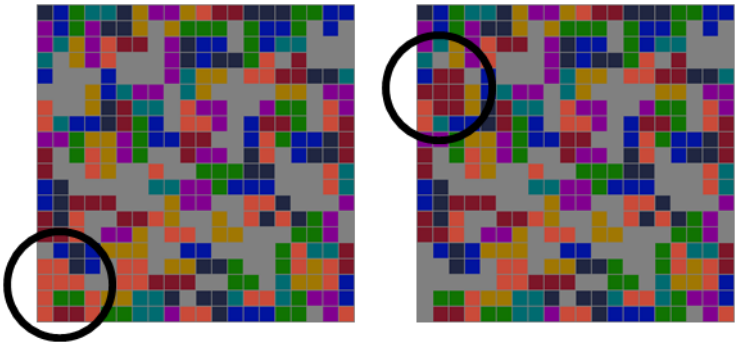

Figure 4: Example of two checkerboards (AX and BX). The common background is the same for both checkerboards, while the unique element is surrounded by a circle.

McLaren and Mackintosh (2000) proposed that inhibitory associations formed between the unique elements after intermixed exposure could explain the subsequent enhancement in discrimination. It is easy to see how this would affect a discrimination learning test, but it is not clear how it would explain the results on a same-different task. Inhibitory associations are expected to influence generalization tests where there is an inhibitory relationship between the conditioned stimuli and the test stimuli. However, in a same-different, generalization is not being evaluated, and the fact that one unique element inhibits the other should not have any influence on their detection. In addition to this, there is some direct evidence that inhibitory associations are not involved in the results observed in humans with visual stimuli. For example, Lavis and Mitchell (2006) exposed humans to six different checkerboards, two intermixed pairs and one blocked (AX/BX_CX/DX_EX_FX). According to McLaren and Mackintosh (2000), we should expect the formation of inhibitory links between A and B and C and D, but not between A and C or B and D because they are presented in different blocks. Thus, we should expect increased discrimination between AX and BX, but not between AX and CX. However, there is also increased discrimination between pairs of checkerboards exposed in an intermixed manner, but in different blocks, relative to the blocked pairs. Mitchell

et al (2008) obtained more direct evidence of perceptual learning without involvement of inhibitory connections. They found increased discrimination after intermixed exposure to AX and X alone, where there is no unique element B with which A could form reciprocal inhibitory links. In contrast, there is evidence that inhibitory associations actually play a role in human perceptual learning with flavours (Mundy et al., 2006).

As a complementary model, Hall (2003) proposes that associative activation of the unique elements during intermixed exposure should disrupt their (long term) habituation, thus making them more salient relative to the common element. This increased salience could then explain the improved discrimination on test relative to stimuli presented in blocks. The idea of increased salience of the unique elements can be accommodated with the results of a same-different test, in which a more salient unique element would make it easily detectable. However, it has problems when it comes to the preexposure schedule itself. Stimuli are presented for less than a second with inter stimulus intervals of around one second, usually with multiple repetitions. Following Wagner (1981), under such conditions a recently presented stimulus would have its elements active in either A_1 or A_2 states, thus making associative activation impossible. Furthermore, many of the experiments of this sort used within-subjects designs, in which all the participants received presentations of different checkerboards with the same common element both intermixed and blocked. We should expect Hall's mechanism to operate more readily when the intermixed pairs are presented first, as further associative activation would occur with the blocked pair. Further, when the blocked pair is presented first, we might expect that the common element would be

highly habituated by the time the intermixed pair is presented, so no intra-stimulus associations should be formed and thus no associative activation should take place. The lack of evidence of this predicted asymmetry can be taken as suggestive that the mechanism proposed by Hall (2003) may not be necessary to explain perceptual learning in humans (Mitchell, Kadib, et al., 2008).

In the face of such problems, specific models were developed to explain the results obtained with humans. Lavis et al (2011; see also, Mitchell, Nash, & Hall, 2008) proposed that the better a feature is "remembered" (recently presented), the less processing resources it demands. Because with intermixed exposure the common element is presented on every trial and the unique elements only once every two trials, this means that the former will be "remembered" and thus will receive less processing resources. On the other hand, the unique elements will receive more processing resources, which would lead to better memory encoding. This more detailed encoding will mediate the increased discrimination on test. A related account was proposed by Mundy et al. (2007, see also Dwyer et al., 2011). They suggest that the common elements will accrue more short-term habituation than the unique elements, which would lead to a switch in the attentional weighting towards the unique elements. The increased attentional resources devoted to the unique elements would affect how these unique elements are stored, for example allowing them to be linked to different hidden units instead of sharing one (Honey & Ward-Robinson, 2002).

The previous accounts can satisfactorily explain the results found with human participants, perhaps opening a breach between perceptual learning in humans and other

animals (Mitchell & Hall, 2014). However, before fully considering these models we need to address some issues that can be raised from the research detailed earlier. First, one of the critical pieces of evidence for these models comes from the experiment of Lavis et al. (2011, Experiment 2), in which they presented the participants with additional exposure to the unique elements alone. This should lead to better memory encoding of the unique elements, and thus better discrimination. This was exactly what they found after randomly exposing participants to four checkerboards differing only in their unique elements, interspersing trials with two of those unique elements presented alone. This result offers support to the previously described models, since both of them depend on better memory encoding of the unique elements. However, there is an obvious caveat in the design: The unique elements were presented in the same position as they appear in the checkerboard. This would give the participants information regarding the location of these unique elements inside the checkerboard, facilitating their detection and allowing perfect discrimination without the need for any perceptual learning (Jones & Dwyer, 2013). If memory representation is critical for perceptual learning, we should see increased discrimination after additional exposure to the unique elements regardless of their position. To ascertain this, in our Experiments 1a we replicated Lavis et al. (2011) Experiment 2. Critically, in our Experiment 1b we presented the unique elements alone centered on the screen, an arrangement that would not allow the participants to find them immediately based only on their location (Recio, Iliescu, Bergés, Gil, & de Brugada, 2016).

Second, and more important, is the suggestion made by Mackintosh (2009) that perceptual learning in humans is not unsupervised, and thus it could be considered an

instance of discriminative learning. According to him, exposure to the stimuli does not occur passively. Participants receive instructions to attend to the images and to look for differences. Even though they do not receive feedback during that stage of the experiment, the question arises as to whether they might not be receiving some sort of reinforcement after detecting a difference. Because the goal of the task is explicit (finding differences) participants can be "self-reinforced" upon detecting elements that are perceived as different. Furthermore, what might be reinforced is the most obvious feature of the unique elements: location (Jones & Dwyer, 2013; Wang et al., 2012). That is, participants might simply be learning to look at a specific location of the stimuli, which would allow them to solve the discrimination without any need to appeal to memory encoding or other more complex mechanisms. In our Experiments 2a and 2b we try to manipulate instructions, which are the main source of this self-supervising learning. If there are no specific instructions to look for differences, then self-reinforcement when detecting differences would be less likely (Navarro, Arriola, & Alonso, 2016; Recio, Iliescu, Mingorance, et al., 2016). Under such conditions, if perceptual learning occurs it could be considered truly unsupervised, and it could be explained by the mechanisms described previously.

Experiments 1a and 1b: The effect of additional exposure to the unique elements

These experiments are a replication of Lavis et al. (2011, Experiment 2), in which we randomly presented four checkerboards which consist of the same background and a feature unique to each one of them. In addition, we also randomly interspersed two of the unique elements alone. In Experiment 1a, those unique elements

were located in the same position as the checkerboard. That is, if the feature was located in the top right corner of the checkerboard, it would also be located in the top right corner of a blank square of the same size as the checkerboard. In Experiment 1b, the unique elements alone were always presented on the centre of the screen. If the results of Lavis et al. (2011) are to be explained in terms of a better memory representation of the unique elements, then we should not see differences between both experiments, or at least we should see increased discrimination in both of them. If the results were caused by a location bias, then we should not see any effect at all when additional exposure is given centrally.

Method

Participants: 48 psychology students from the University of Granada (8 male) agreed to participate in the experiments in exchange for course credit. The mean age was 21 (range from 18 to 31). 26 participated in Experiment 1a, and the remaining 22 in Experiment 1b. All of the participants had normal or corrected to normal vision. The Research Ethics Committee of Granada University approved the experimental protocol.

Apparatus and stimuli: The stimuli consisted of eight different 20x20 square checkerboards, with a size of 321x321 pixels. Each checkerboard shared the same common structure (X), which was created by colouring 298 of the 400 squares with 8 easily distinguishable colours. The remaining squares were grey. Each colour had between 35 and 39 squares, which did not form clusters of more than 4 squares. A unique element was included in each checkerboard, consisting of clusters of 7 squares of the same colour. Each unique element was different in shape, colour and position

within the checkerboard. For each participant, four stimuli (AX, BX, CX and DX) were randomly selected from the eight different checkerboards. Additionally, two more stimuli were added, consisting of two of the selected unique elements alone (A and B) superimposed over a grey square of the same size as the other stimuli. In Experiment 1a, the figures were positioned in the same location as that when presented together with the common element. In Experiment 1b, the figures were located in the centre of the square. During the practice block, eight checkerboards with similar features but completely different common and unique elements were created, and four were randomly chosen for each participant. During the procedure, all the stimuli were presented centrally on the screen over a black background.

The experiment was written with e-Prime software (v 2.0.10), and the program was run on a PC with a 17' screen. The participants were sitting in front of the screen and they interacted with the program using a Spanish qwerty keyboard.

Design and procedure: All the procedures used here were approved by the Ethics Committee of the University of Granada. All of the participants were required to sign a consent form before carrying out the task, and were then assigned to one of the two experimental conditions. The participants sat in front of the computer in an adjustable chair, at approximately 1 m from the screen, in a small isolated room. The participants were verbally required to read the instructions carefully and to ask the experimenter any questions they may have had before the start of the experiment.

The design of both experiments is summarized in Table 1. The experiment consisted of 3 different parts: practice, preexposure, and test. Before the task began, the

participants received written instructions in which they were explicitly asked to look for differences, stating that these differences would be important for a subsequent task. All participants were required to push the spacebar when a checkerboard appeared on the screen, in order to maintain attention to the stimuli. The response did not affect the pace of the task.

Experiment	Preexposure	Test
1a	AX/BX/CX/DX/A/B	AX-AX, BX-BX (SAMEPRE) AX-BX, BX-AX (DIFPRE)
1b	AX/BX/CX/DX/A'/B'	CX-CX, DX-DX (SAMENOP) CX-DX, DX-CX (DIFNOP)

Table 1: Designs of Experiments 1a and 1b. AX, BX, CX and DX refer to different checkerboards. A and B refer to the unique element alone in the original position, while A' and B' refer to the unique element alone centered. "/" indicates random alternation. In the test phase, DIF and SAME refer to test trial type, while PRE and NOP refer to the presence or absence of additional exposure.

In the practice block, 4 random checkerboards were presented for a total of 8 trials. Each trial began with a fixation point on the centre of the screen for 300 ms, followed by a checkerboard. The checkerboard remained on the screen for 480 ms, and this duration was independent of the response of the participants. After this interval, a blank screen appeared for 1000 ms. Finally, the participants received feedback about their response for 1000 ms. The inter-trial interval was therefore 2000 ms long. This same trial structure was used in the preexposure phase, with the exception that feedback was not provided, and the blank screen appeared for 2000 ms.

When the practice phase ended, participants received a brief reminder of the instructions before the preexposure began. Stimuli were selected randomly without

replacement. Each selection cycle included 10 trials, 2 of each complete checkerboard (AX, BX, CX and DX) and 1 of each unique element (A and B, see Figure 5). Thus, the participants received additional exposure to the unique elements of AX and BX. The preexposure continued for 10 cycles, for a total of 100 trials.

Figure 5: Example of additional exposure. The left panel shows the unique element in its original position, the right panel shows the unique element centered.

At the end of the exposure block, participants received new instructions about the same-different test. They were told that two checkerboards will be presented consecutively, and they have to push the "k" key if they think the stimuli were the same, or the "a" key if they were different. There were 4 types of trials in this phase: DIFPRE (AX-BX or BX-AX), DIFNOP (CX-DX or DX-CX), SAMEPRE (AX-AX or BX-BX), and SAMENOP (CX-CX or DX-DX). A total of 40 trials were presented, 10 of each type, and they were selected randomly, with the constraint that there could not be two identical consecutive trials. Every trial in this phase began with a fixation point in the centre of the screen that remained for 1000 ms. After this interval, a checkerboard appeared for 800 ms, followed by a blank screen for 3000 ms, and then by another checkerboard with the same duration as the previous one. Finally, a fixed screen with a reminder of the instructions appeared until the participant emitted a response. No feedback about the response was provided.

Statistical analysis: The analyses were conducted on sensitivity scores (*d'*) and the proportion of correct responses for each type of trial. In this sort of task, same trials usually elicit a higher proportion of correct responses. Since the stimuli are difficult to discriminate, the complete failure to do so would give results approaching 100% correct responses for the same trials, and 0% correct responses for the different trials. A proportion of correct responses close to 0.5 on same trials would imply responding by chance and thus not following instructions. Bearing this in mind, we used as an a priori exclusion criterion a mean proportion of correct responses on same trials lower than 0.6[1]. Following this, 4 participants were excluded from further analysis (3 from Experiment 1a and 1 from Experiment 1b). Because of the presence of extreme values, d' was calculated using a log-linear correction, as indicated in Stanislaw and Todorov (1999). This approximation consisted of adding 0.5 to the number of hits and false alarms and adding 1 to the total number of trials, before calculating the hit and false alarms rate[2].

General linear model analyses were conducted, adopting a critical *p* value of 0.05. Greenhouse-Geisser correction was chosen for the within-subjects analysis. In addition, we conducted Bayesian analysis, using the Jeffrey-Zellner-Siow (JZS) prior and the default *r* scale size, as recommended in Rouder, Speckman, Sun, Morey and Iverson (2009) and Rouder, Morey, Speckman and Province (2012). We used JASP

[1] Analyses were also conducted without excluding any participant for proportion of errors and *d'*. The results were the same. We decided to keep this exclusion criterion because it was decided a priori, and its logic applies.

[2] Bias (*c*) analyses were also conducted, but there were no significant differences in any of the experiments. They do not add relevant information and are therefore not included in this thesis.

software to perform the analysis (Love et al., 2015). We interpreted the results following the guidelines of Jarosz and Wiley (2014). Thus, a Bayes factor (B_{01}) higher than 3 can be interpreted as support for the null hypothesis, with higher values indicating stronger support. On the other hand, values lower than 1/3 can be interpreted as support for the alternative hypothesis, with lower values indicating stronger support. As B_{01} is the odds ratio for the null hypothesis, to obtain the odds ratio for the alternative hypothesis (B_{10}) the inverse must be calculated (1/ B_{01}).

Results

Experiment 1a: The sensitivity scores showed a clear pattern of results (see upper panel of Figure 6). The within-subjects ANOVA, with Additional exposure (NOP/PRE) as the independent factor, revealed a significant effect of this factor, $F(1, 22) = 7.38$, $\eta^2_p = 0.25$. The Bayesian *t* contrast also showed support in favour of the alternative hypothesis, $B_{01} \approx 0.25$. With the accuracy data (lower panel of Figure 6) we ran a within-subjects 2x2 ANOVA with Additional exposure (NOP/PRE) and Test trial (DIF/SAME) as independent factors. This analysis revealed significant effects of Test trial, $F(1, 22) = 71.82$, $\eta^2_p = 0.77$; and Additional exposure, $F(1, 22) = 6.33$, $\eta^2_p = 0.22$; although the interaction did not reach statistical significance, $F(1, 22) = 2.43$, $p = 0.13$, $\eta^2_p = 0.1$. Nevertheless, we ran a planned contrast with different trials only, that showed a significant difference between PRE and NOP trials, $t(22) = -2.05$, $d = -0.43$. The Bayesian ANOVA showed that the model including the interaction is $\approx 9.5 \times 10^6$ times more likely than the null hypothesis, $B_{01} \approx 1.05 \times 10^{-7}$. It is also ≈1.4 times more likely than the next preferred hypothesis including the factors Test trial and Additional

exposure. The Bayesian *t* test, however, showed only marginal support in favour of the alternative hypothesis, $B_{01} \approx 0.78$.

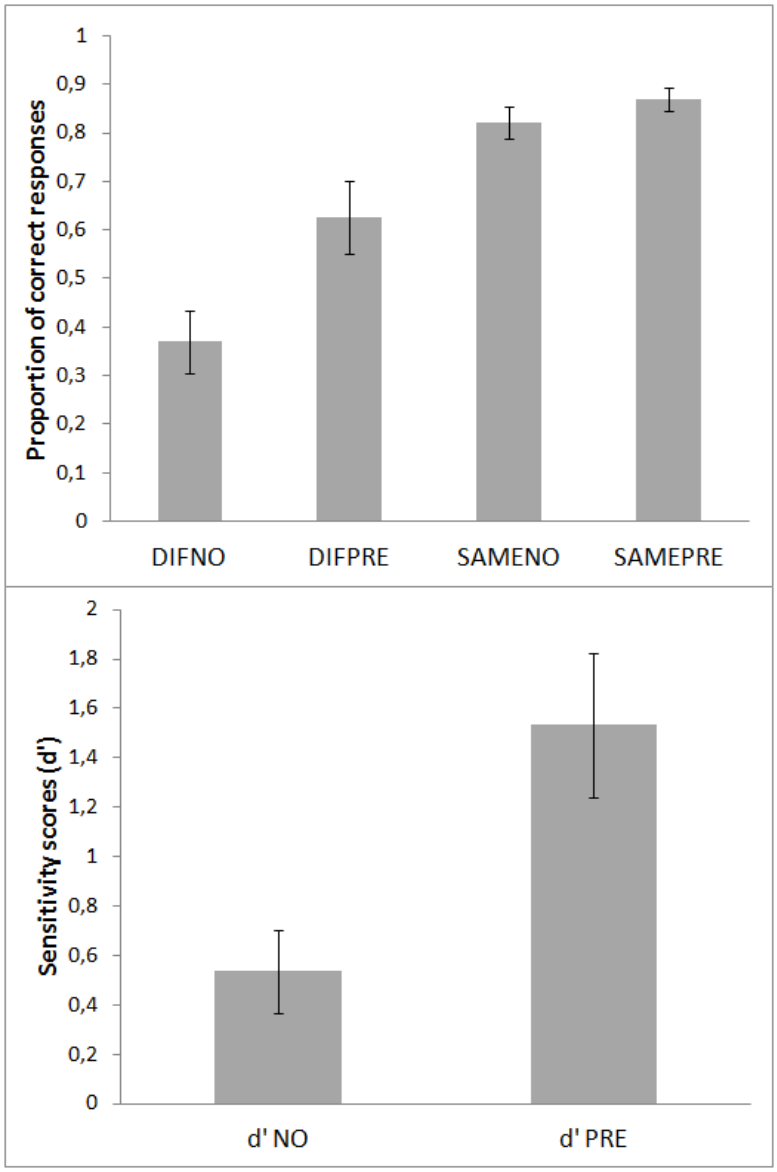

Figure 6: **Results of Experiment 1a (original position). Lower panel:** mean (±SEM) sensitivity scores during the discrimination test**. Upper panel:** mean (±SEM) proportion of correct responses during the discrimination test. On the *x*-axis, DIF and SAME refer to test trial type, while PRE and NO refer to the presence or absence of additional exposure.

Experiment 1b: The sensitivity scores did not show any apparent differences between conditions (upper panel of Figure 7). The within-subjects ANOVA with Additional

exposure (NOP/PRE) as independent factor confirmed there to be no significant differences, $F< 1$. The Bayesian *t* contrast showed support in favour of the null hypothesis, $B_{01} \approx 4.3$. A 2x2 ANOVA conducted with the accuracy data (lower panel of Figure 7) showed a significant effect of Test trial, $F(1, 20) = 38.68$, $\eta^2_p = 0.66$; but no effects of Additional exposure, or an interaction between these factors (Fs< 1). The Bayesian ANOVA further confirmed this negative result, as the most likely model was the one including only Test trial, $B_{01} \approx 1.25\text{x}10^{-8}$. It was $8\text{x}10^{7}$ times more likely than the null, and also roughly 4 times more likely than the next preferred model including Test trial and Additional exposure.

Discussion

The results of this experiment are clear-cut: The effect of additional exposure on subsequent discrimination is only evident when the unique elements are presented in the same position as in the whole checkerboard. The most straightforward interpretation is that the results of our Experiment 1a, and of Lavis et al. (2011), reflected the effect of a location bias. The additional exposure guided the participants towards looking to fulfil the instructions given ("look for differences"). Finding some unique elements would bias the participants' attention towards the location where they were found, thus hindering the detection of the unique elements of those checkerboards that were not additionally exposed. The central position would give no hint of the location of the unique elements, so no bias would be expected. However, it should improve their memory representations, so according to Lavis et al. (2011) they should be more easily detected on the common background.

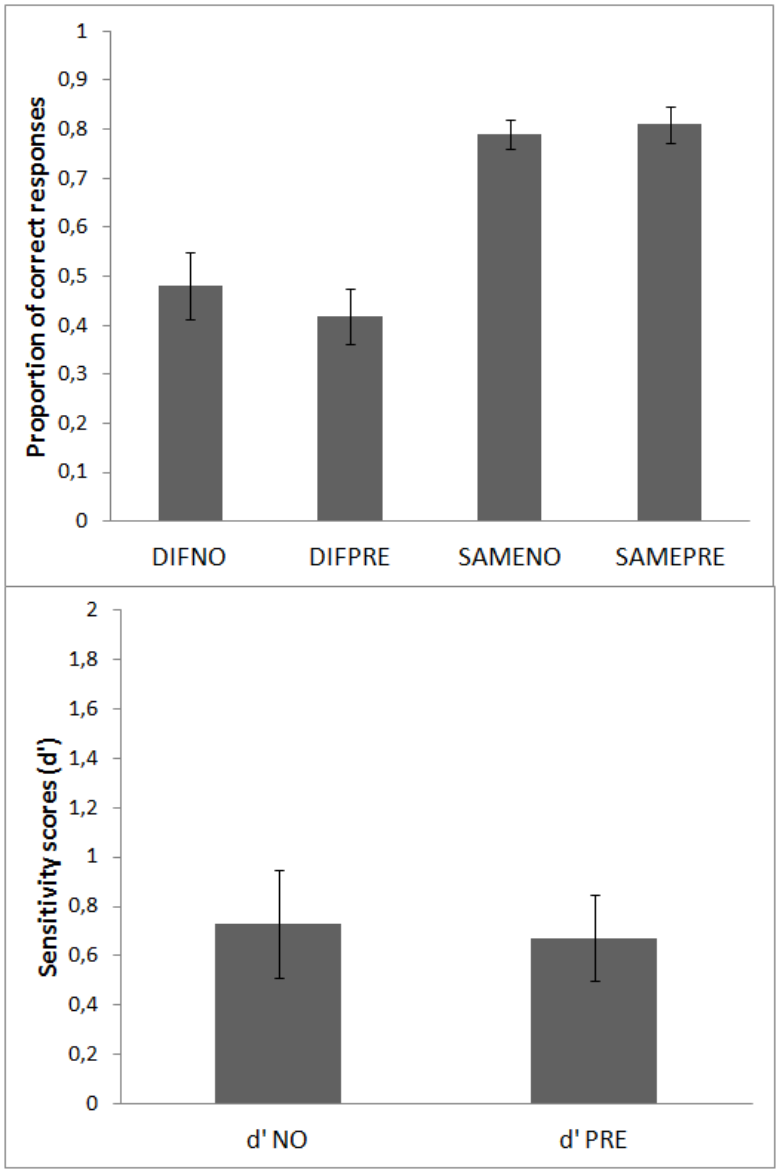

Figure 7: **Results of Experiment 1b (central position). Lower panel:** mean (±SEM) sensitivity scores during the discrimination test. **Upper panel:** mean (±SEM) proportion of correct responses during the discrimination test. On the *x*-axis, DIF and SAME refer to test trial type, while PRE and NO refer to the presence or absence of additional exposure.

However, there are other interpretations that need discussion. First, it is possible that the centrally positioned exposure could have biased attention of the participants towards the centre of the screen, thus hindering detection of the unique features on every checkerboard. It is difficult to see how this could have been the case, since

reinforcement is needed for such a bias to occur. That is, presenting the unique elements in their original position causes participants to focus around that location because they were later detected within the full checkerboard, thus fulfilling the task and receiving reinforcement (Mackintosh, 2009). However, the central presentation of the unique elements does not lead to an immediate detection based on location, so the strategy to focus on that place would not be reinforced. Participants would have needed to keep looking, and had memory representation played a key role, they should have detected those unique elements more easily within the checkerboard.

A second possibility is that additional exposure actually increases habituation of the unique elements, thus reducing their salience. Lavis et al. (2011) acknowledge this possibility, but they dismiss it based on their results. However, our experiments seem to indicate that their results were based entirely on a location bias. Thus, it remains a possibility that a better memory representation of the unique elements plays a role in perceptual learning, but in the case of central additional exposure this role was overshadowed by habituation. This idea is supported by the results of Lavis et al. (2011, Experiment 1), where they expose participants to two pairs of checkerboards, two intermixed and two blocked. Later, participants had to solve a colour matching task in which they received only the shape of every unique element, and had to choose the colour in which it had been during preexposure. As predicted, participants were better able to identify the colours of the unique elements from the checkerboards presented in an intermixed schedule. Even though this result doubtlessly supports the notion that their memory representation was better, it does not indicate the direction of the causality. It is perfectly possible that the unique elements, when presented intermixed,

were better represented in memory because they were more easily detected, instead of being detected more readily because they were better represented.

In fact, there are reasons to believe that intermixed exposure can actually lead to easier detection of the unique elements for reasons other than perceptual learning. For example, one possibility is that the rapid succession of the checkerboards during intermixed preexposure could have caused the unique elements to *pop-out*, thus making detection trivial. Even though the length of the inter-stimulus intervals was sufficient to prevent the influence of a visual trace, informal comments from the participants in our experiments suggest that it might have played a role (many of them commented that something was "appearing and disappearing on every trial"). Another possibility was proposed by Jones and Dwyer (2013), who pointed out that during intermixed exposure the critical difference is present on every trial, and thus detection caused by deliberate searching can be thoroughly checked (and reinforced). However, during blocked exposure there is only a single transition, and any possible detection of the unique elements would have little opportunity to be reinforced.

To sum up, the outcome of our experiments strongly indicate that the results of Lavis et al. (2011) can be explained by a location bias, instead of a better memory representation. Even though we cannot compellingly claim that the formation of a better memory representation of the unique elements does not play any role in human perceptual learning, there are reasons to doubt that there is a casual relationship between memory representation and increased discrimination. The key element to explain the results of experiments using visual stimuli with humans seems to be what Mackintosh

(2009) referred to *self-supervised* learning. Our next experiments will try to ascertain the role of such a mechanism in human perceptual learning.

Experiments 2a and 2b: The effect of instructions on perceptual learning

Mackintosh (2009) proposed that some instances of human perceptual learning might not be the product of mere exposure, but a form of discriminative learning. If the goal of the task is made explicit (looking for differences) and if the achievement of this goal is easily determined (even in the absence of external feedback) we could expect a form of self-supervising learning. In many of the experiments using visual stimuli in humans, the participants receive explicit instructions to look for differences during preexposure, making them aware of the goal. Furthermore, during intermixed exposure it is very easy to check if this goal has been achieved, as there is opportunity to do so on every trial. The differences between stimuli are easily isolated features (a cluster of coloured squares, a row of shapes, a particular anatomical feature in a face) that can be remembered from one trial to the next and whose presence can be checked. Every time a difference is detected in this way, the participant is being (self) reinforced. Specifically, it seems that what is being reinforced is the action of attending to a specific location on the stimulus (Jones & Dwyer, 2013; Wang et al., 2012). This can hardly be considered to be within the scope of perceptual learning as we have defined it in the introduction.

However, all the arguments we have just presented are speculative. One way to truly confirm that self-reinforcement is responsible for the results found with humans is to create conditions in which it is less likely to occur. One possibility is to create stimuli that have no easily separable unique features, such as colour variations along a

continuum of saturation. This strategy is challenging to pursue, as it would require creating pairs of colours that are not too difficult or too easy to discriminate, and that would have an equivalent psychological "distance" between them. A more achievable strategy would be to make the goal of the task non-explicit. That is, we would need a way of making the participants attend to the checkerboards but without explicitly making them look for differences. Under such conditions, mere exposure would be taking place, allowing any potential perceptual learning mechanism to occur. Thus, in our current experiments we tried to replicate the procedure used by Lavis and Mitchell (2006), but manipulating the instructions given to participants during preexposure to control their awareness of the goal and thus reducing or eliminating self-reinforcement (see Table 2). As long as we can reasonably ensure that participants are attending to the checkerboard, perceptual learning should take place. To accomplish this, bogus instructions about unrelated tasks requiring to attend or to visually search for the checkerboards are provided.

Experiment 2a

In this experiment human subjects were trained on a version of the task employed by Lavis and Mitchell (2006), comparing the effects of intermixed and blocked preexposure schedules with checkerboard stimuli. A within-subjects design was used, with all subjects receiving intermixed presentations of one pair of stimuli (AX/BX) and blocked presentations of another pair (CX_DX). This preexposure was followed by a same/different test. One group of participants (the INST group) received the usual explicit set of instructions, and, for these, better test performance with AX and

BX than with CX and DX can be expected. For a second group (NOINST) there were no instructions about the need to look for differences. It is possible that participants in this latter group might fail to attend to, or even look at, the stimuli, so that a reduction in the perceptual learning effect might occur simply because these subjects were not exposed to the stimuli. Accordingly, we included a third group (FAKE) given "fake" instructions that required the participants to look at and respond quickly to the stimuli, but with no requirement to look for differences among them. A reaction-time task was chosen given that it places a very low demand on cognitive resources, so that direct interference with the perceptual learning process would not be expected.

Method

Participants: The participants were 214 students[3] of psychology from the University of Granada (26 male) who agreed to participate in exchange for course credit. Their mean age was 19 years (range 19 to 36). There were 67 assigned to the INST group, 71 to the NOINST group and 76 to the FAKE group. All of the participants had normal or corrected-to-normal vision. Any participants reporting anomalous colour vision were excluded from the study.

Apparatus and stimuli: We used the same checkerboards as those described in the previous experiments. From the pool of eight different checkerboards, four were

[3] This sample is actually the product of merging two identical replications of the same experiment. In the first instance of the experiment we detected an unexpected effect (a reverse I/B effect in the group receiving fake instructions). However it was a weak effect and we were unable to replicate it a second time, and also there were no trace of it after combining the two experiments. Given its unexpectedness and the lack of theoretical sense, we decided that it was probably an artefact and reported the whole data combined.

randomly chosen for each participant (AX, BX, CX and DX). For the practice block, eight checkerboards with similar features but completely different common and unique elements were created, and four were randomly chosen for each participant. All other details not reported here are the same as in the previous experiments.

Design and procedure: All the procedures used here were approved by the Ethics Committee of the University of Granada. The participants were required to sign a consent form before carrying out the task, and were then assigned to one of the three experimental conditions. 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. For the INST group the instructions, translated from Spanish, were: "[…] Your task is to focus on the checkerboards and try to discover any difference that you can find between them. It is very important that you try to find and remember these differences, because they will be useful in a later task. […]". For the NOINST group the instructions were as follows: "[…] Your task is to look carefully at the checkerboards until you receive new instructions. […]". Subjects in the FAKE group were told: "[…] The goal of this experiment is to check how the complexity of visual stimuli affects the speed of the response. […] Your task consists of pressing the spacebar as fast as you can every time a checkerboard appears. […]". The participants in the other two groups were also required to press the spacebar when a checkerboard appeared on the screen, in order to maintain attention to the stimuli.

The experiment consisted of three phases: practice, preexposure, and test. In the practice phase, four checkerboards were used, each presented twice. Each trial began with a fixation point on the centre of the screen for 300 ms, followed by a checkerboard. The checkerboard remained on the screen for 480 ms, and this duration was independent of the response of the participants. After this interval, the participants received a feedback screen for 1000 ms, recording that the spacebar response had been made. For the FAKE group, the feedback screen also presented the reaction time (if the response was made before the end of the 480-ms duration of the display). The reaction time 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 1500 ms, during which the screen remained blank. This same trial structure was used in the preexposure phase.

Group	Preexposure	Test
INST	AX/BX_CX_DX	AX-AX, BX-BX (INT-SAME) AX-BX, BX-AX (INT-DIF) CX-CX, DX-DX (BLK-SAME) CX-DX, DX-CX (BLK-DIF)
NOINST		
FAKE		

Table 2: **Designs of Experiments 2a and 2b**. INST refers to explicit instructions, NOINST refers to non-explicit instructions, FAKE refers to instructions about an unrelated task, AX, BX, CX and DX refer to different checkerboards. "/" indicates intermixed exposure, "_" indicates blocked exposure. In the test phase, DIF and SAME refer to test trial type, while INT and BLK refer to the type of exposure received. Experiment 2b did not have a NOINST group.

The participants received a reminder of the instructions on screen before the preexposure phase began. There were 80 preexposure trials in total; 40 consisted of the intermixed exposure of AX and BX (AX/BX/AX/BX…), and 40 of the blocked preexposure of CX and DX (CX/CX…DX/DX…). The order of the type of exposure was randomized between participants.

At the end of the exposure phase, participants received new instructions about the test. They were told that two checkerboards would be presented consecutively, and that they must press the "k" key if they thought the stimuli were the same, and the "a" key if they thought them to be different. There were 4 types of trials in this phase: with different stimuli that had been presented intermixed (INT-DIF: AX-BX or BX-AX), same intermixed stimuli (INT-SAME: AX-AX or BX-BX), blocked different stimuli (BLK-DIF: CX-DX or DX-CX), and blocked same stimuli (BLK-SAME: CX-CX or DX-DX). There were 10 of each type, presented in random order, with the constraint that there could not be two identical consecutive trials. Trials began with a fixation point in the centre of the screen that remained for 1000 ms; then a checkerboard appeared for 800 ms, followed by a blank screen for 3000 ms, and then another checkerboard for 800 ms. Finally, there was a screen with a reminder of the instructions that remained until the participant had made a response. No feedback about the response was provided.

Statistical analysis: We used the same statistical analyses and parameters as in the previous experiments. Following the outlier criteria that we described previously (correct responses on same trials lower than 0.6), 25 participants were excluded from further analysis (6 from group INST, 9 from group NOINST and 10 from group FAKE)

Results and Discussion

Figure 8 (upper panel) shows the proportion of correct responses for all 3 groups and for each type of trial. As expected, participants were much more accurate on same than on different trials. Moreover, it is evident that only the participants in the INST

group benefited from the intermixed exposure. A mixed 2 x 2 x 3 ANOVA, with Preexposure (BLK vs INT) and Test trial (DIF vs SAME) as within-subjects variables, and Instructions (INST, NOINST and FAKE) as a between-groups variable was conducted. There were significant main effects of Test trial, $F(1, 186) = 367.09$, $\eta^2_p = 0.66$, and of Instructions, $F(2, 186) = 5.50$, $\eta^2_p = 0.06$. There were significant interactions between Test trial and Instructions, $F(2, 186) = 5.31$, $\eta^2_p = 0.05$ and between Preexposure and Instructions, $F(2, 186) = 3.66$, $\eta^2_p = 0.04$.The triple interaction was also significant, $F(2, 186) = 6.53$, $\eta^2_p = 0.07$. To explore this interaction further, we conducted individual 2 x 2 ANOVAs for each instruction group. For groups NOINST and FAKE only the main effect of Test trial was significant, $F(1, 61) = 166.02$, $\eta^2_p = 0.73$, and $F(1, 65) = 120.97$, $\eta^2_p = 0.65$, respectively. For group INST, the main effects of both Test trial, $F(1, 60) = 90.64$, $\eta^2_p = 0.60$, and of Preexposure, $F(1, 60) = 9.94$, $\eta^2_p = 0.14$, were significant, as was the interaction between these variables, $F(1, 60) = 10.95$, $\eta^2_p = 0.15$. Planned comparisons between INT and BLK different trials revealed a significant difference in group INST, $t(60) = -3.54$, $d = -0.45$, but not in groups NOINST and FAKE, $t(61) = 0.7$ and $t(65) = 0.89$, respectively.

The Bayesian ANOVA confirmed the same pattern of results. The model including the triple interaction was 4.8×10^{70} times more likely than the null model, $B_{01} \approx 2.08 \times 10^{-71}$, and roughly 10 times more likely than the next preferred model. Planned comparisons for each group showed that for group INST the model including the interaction between Preexposure and Test trial was 3.77×10^{16} times more likely than the null model, $B_{01} \approx 2.66 \times 10^{-17}$, and more than 60 times more likely than the next preferred model. A *t* contrast between the DIF trials showed strong support for the alternative

hypothesis, $B_{01} \approx 0.03$. However, for groups NOINST and FAKE the model including Test trial was the most likely, and at least 20 times more likely than the model including the interaction, $B_{01} \approx 1.61 \times 10^{-30}$ and $B_{01} \approx 2.57 \times 10^{-28}$, respectively.

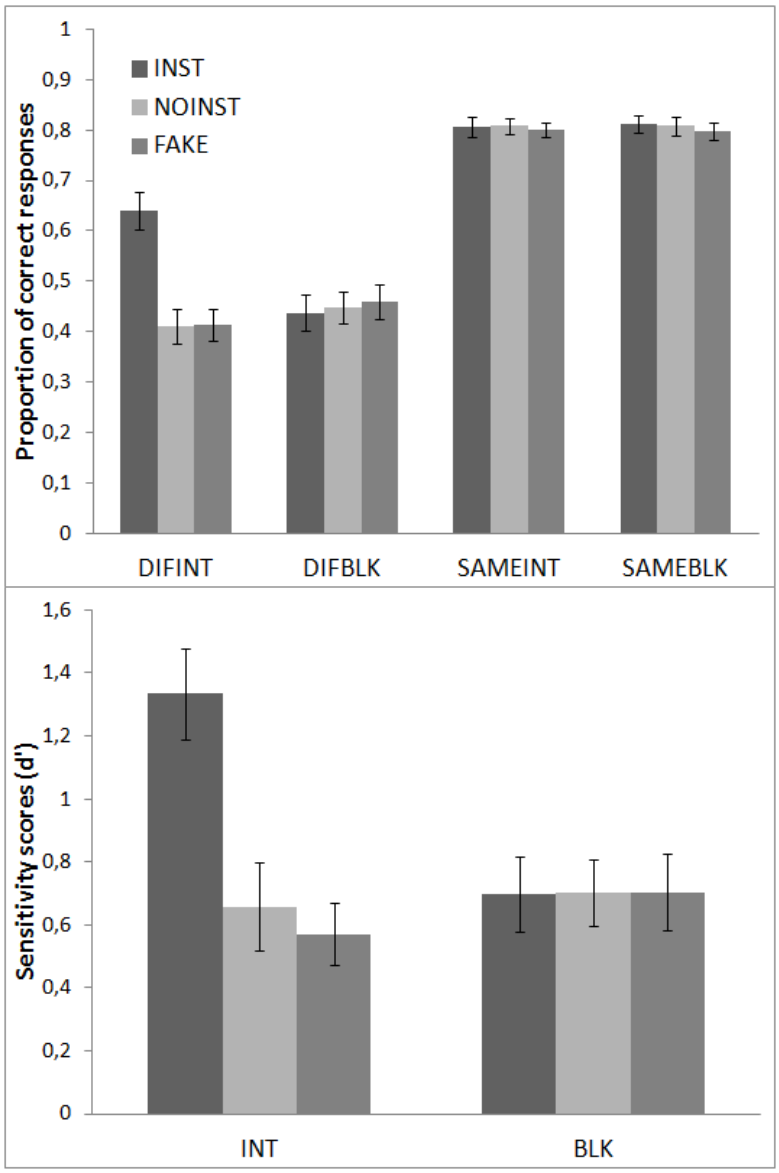

Figure 8: **Results of Experiment 2a. Lower panel:** mean (±SEM) sensitivity scores during the discrimination test. **Upper panel:** mean (±SEM) proportion of correct responses during the discrimination test. On the *x*-axis, DIF and SAME refer to test trial type, while INT and BLK refer to intermixed and blocked respectively. Different groups were instructed to look for differences (INST), given no instructions (NOINST), or instructed about a bogus task (FAKE).

Figure 8 (lower panel) shows the same results expressed as sensitivity scores (*d'*). It is evident that only group INST showed an improvement in discrimination as a result of the intermixed exposure. We conducted a 2 x 3 mixed ANOVA, with Preexposure as a within-subjects variable, and Instructions as a between-groups variable. There was a main effect of Instructions, $F(1, 186) = 5.94$, $\eta^2_p = 0.06$, and a significant interaction, $F(2, 186) = 5.52$, $\eta^2_p = 0.06$. This interaction was explored by means of planned contrasts for each instruction group. For group INST, there was a significant effect of Preexposure, $t(60) = 3.36$, $d = 0.43$. Groups NOINST and FAKE did not show any significant difference, $t(61) = -0.25$ and $t(65) = 0.89$, respectively. Similarly, the Bayesian ANOVA for sensitivity scores showed that the model including the interaction was 16 times more likely than the null model, $B_{01} \approx 0.06$, and almost 6 times more likely than the next preferred model. Bayesian paired samples *t* tests for each group showed support for the alternative hypothesis in group INST, $B_{01} \approx 0.05$, and support for the null hypothesis in groups NOINST and FAKE, $B_{01} \approx 7$ and $B_{01} \approx 5.53$, respectively.

These results show that the superiority of intermixed over blocked preexposure emerges only when participants have been given instructions to look for differences. This finding appears to challenge any proposal that mere exposure to intermixed presentations of the stimuli should be enough to produce a perceptual learning effect. But before accepting this conclusion, we should acknowledge the possibility that the null result for the participants without instructions might simply reflect the fact that the preexposure procedure failed to allow adequate exposure to the stimuli. It is true that participants in the NOINST condition were required to press the spacebar when a checkerboard appeared, and did so reliably; it is also true that the instructions in the FAKE condition kept the

participants involved with the task, and forced them to look at the checkerboards. Given that the inter-stimulus interval was variable, it was necessary for subjects to detect presentation of the stimuli in order to press the spacebar appropriately, and accuracy for spacebar pressing was >0.9 for all groups, with no differences among them. This could be taken as an indication that most of the participants were actively attending to the task; but it is none the less possible that subjects in the NOINST and FAKE conditions failed to focus on the stimuli reliably, in which case the importance of the instructions for the INST group could merely be that they ensured full exposure to the stimuli. To address this issue requires a further experiment.

Experiment 2b

In this experiment we compared two groups, one given the same training as the INST group of Experiment 2a, and a second given a new version the FAKE task, with instructions designed to force participants to attend to the stimuli, thus guaranteeing exposure. In this latter task, the subjects were not told to look for differences, but were instructed to look at and remember all the different colours presented in the checkerboards. These instructions were justified by the inclusion of a brief colour recognition test given immediately after preexposure. The critical results came, however, from a final same/different task for which the FAKE instructions were, indeed, irrelevant.

Method

Subjects: The subjects were 75 students of psychology from the University of Granada (9 male) who agreed to participate in exchange for course credit. Their mean age was 19 years (range 18 to 34). Of these, 46 were randomly assigned to the INST

group and 29 to the FAKE group. All of the participants had normal or corrected-to-normal vision.

Apparatus and stimuli: In addition to the usual checkerboards, we constructed sixteen different single-colour squares, with a size of 321 x 321 pixels, to use in the colour recognition test. Eight of these were colours that were presented in the checkerboards; the remaining eight were easily distinguishable variations of the same colours, so that each checkerboard colour had its non-presented pair. All the remaining details were the same as those described for Experiment 2a.

Design and procedure: The procedure was the same as that used for Experiment 2a, with the following exceptions. The instructions for the INST group were slightly modified so as to match those given to the FAKE group. Translated from Spanish, they were: "[…] Your task is to focus on the checkerboards and try to discover and remember all the differences that you can find between them. You will need this information in a later task. […]". For the FAKE group, they were: "[…] Your task is to focus on the checkerboards and try to detect and remember all the different colours you can find in them. You will need this information in a later task. […]". No spacebar pressing was required during preexposure trials.

A colour recognition test was conducted immediately after the preexposure phase. After the instructions, participants were presented with a coloured square in the centre of the screen. They had to press the "z" key if they thought that the colour was new or the "m" key if they thought it had been presented previously. A reminder of the significance of the keys was displayed at the bottom of the screen throughout this.

Every trial was preceded by a fixation point for 500 ms, and the stimuli remained on the screen until a response was given. The subjects were tested with 8 of the 16 coloured squares. These were selected randomly with the constraint that there should be 4 of each type, and were presented in a random order. At the conclusion of this test all subjects were given the same-different task, as described in Experiment 2a.

Results and Discussion

Using the criteria described in the previous experiments, we eliminated 10 participants, 7 from the INST group and 3 from the FAKE group.

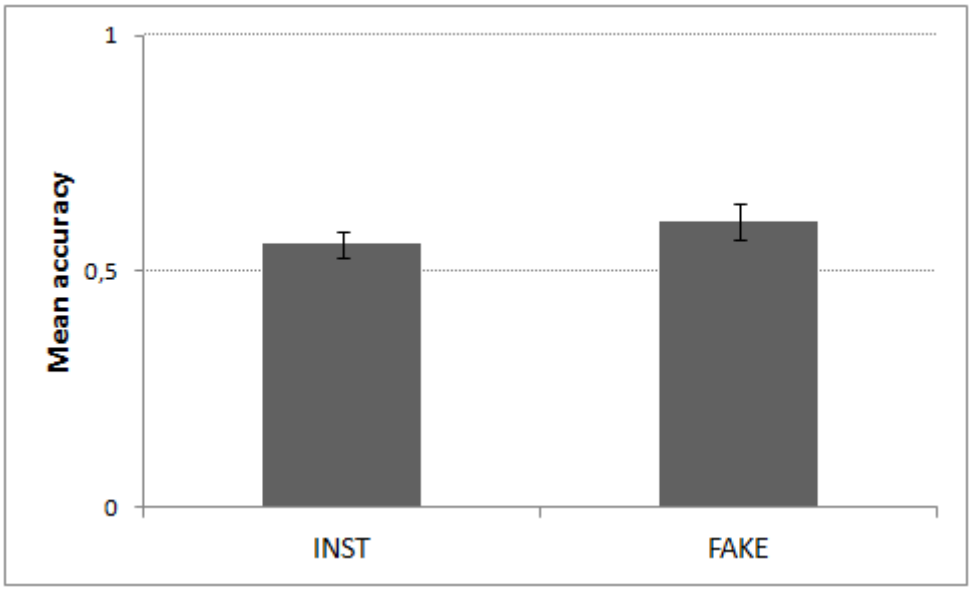

Figure 9: **Results from the colour test of Experiment 2b.** Different groups were instructed to look for differences (INST), or required to look for all the different colours present (FAKE).

The results of the colour recognition test provide indication that participants given the FAKE instructions had been attending to the checkerboards. The mean accuracy score for the INST group was 0.56; that for the FAKE group was higher at 0.61 (see Figure 9). Although the evidence in favour of the alternative was anecdotal, $B_{01} \approx 0.40$, it is worth

noting that 46% of the participants in the INST group obtained a score above chance level, in contrast with 62% of the participants in the FAKE group. For each group we ran a one-sample Bayesian *t* test against the chance value 0.5. For group the INST there was marginal support for the alternative, $B_{01} \approx 0.89$, whereas Group FAKE showed a significantly higher than chance accuracy, $B_{01} \approx 0.25$.

Figure 10 (upper panel) shows the results of principal interest, the proportion of correct responses for groups INST and FAKE on the same/different test. The results mirrored those of Experiment 2a. Both groups were more accurate on the same than on the different trials, but only group INST showed a difference according to the schedule of exposure. We confirmed this by running a mixed 2 x 2 x 2 ANOVA, with Preexposure (BLK vs INT) and Test trial (DIF vs SAME) as within-subjects variables, and Instructions (INST and FAKE) as a between-groups variable. We found a significant effect of Test trial, $F(1, 63) = 72.09$, $\eta^2_p = 0.53$, and also an interaction between test Trial and Preexposure, $F(1, 63) = 3.72$, $\eta^2_p = 0.06$. More importantly, the triple interaction was also significant, $F(1, 63) = 4.22$, $\eta^2_p = 0.06$. We analysed this interaction with pairwise contrasts between INT and BLK different trials for each group. In the INST group we found a significant difference, $t(38) = -3.33$, $d = -0.53$; while in the FAKE group the difference was not significant, $t(25) = -0.08$.

The Bayesian ANOVA showed that the model with the interaction between Test trial and Preexposure was 5.5×10^{13} times more likely than the null model, $B_{01} \approx 1.81 \times 10^{-14}$. It was also more likely than any model including the factor Instructions or any interaction with it, and was ≈20 times more likely than the model including the triple

interaction ($B_{01} \approx 3.66x10^{-13}$). In spite of this, pairwise contrasts between INT and BLK different trials showed strong support for the alternative model in the INST group, $B_{01} \approx 0.06$; and moderate support for the null model in the FAKE group, $B_{01} \approx 4.81$.

Figure 10 (lower panel) shows the sensitivity score results. As in Experiment 2a, only in group INST was there a difference between intermixed and blocked exposure. A 2 x 2 ANOVA with Preexposure as a within-subjects variable, and Instructions as a between-groups variable showed that the effect of preexposure approached significance, $F(1, 63) = 3.36$, $p=0.07$, $\eta^2_p= 0.05$, whilst the interaction was not significant, $F(1, 63) = 2.39$, $p = 0.12$, $\eta^2_p= 0.04$. However, based on the sensitivity results of Experiment 2a, and the fact that in this experiment we obtained an interaction using raw accuracy data, we thought it appropriate to run planned contrasts between INT and BLK different trials. These analyses showed a significant effect of Preexposure for group INST, $t(38) = 2.85$, $d= 0.46$. In contrast, for group FAKE there was no significant difference, $t(25) = 0.17$.

The Bayesian ANOVA with sensitivity scores showed that the model including Preexposure was 2.5 times more likely than the null model, $B_{01} \approx 0.4$, with all the other models being less likely than the null, lowest $B_{01} \approx 1.65$. Planned contrasts for each group showed that the data supported the alternative hypothesis for group INST, $B_{01} \approx 0.18$; while supporting the null for group FAKE, $B_{01} \approx 4.76$.[4]

[4] Note that the lack of strong support for the interaction model in the Bayesian ANOVAs for both accuracy and sensitivity data might mean that the design was underpowered for this type of analysis. However, the results from the planned contrasts show moderate to strong support for either the null or the alternative hypotheses, and further analyses suggest that those results are robust.

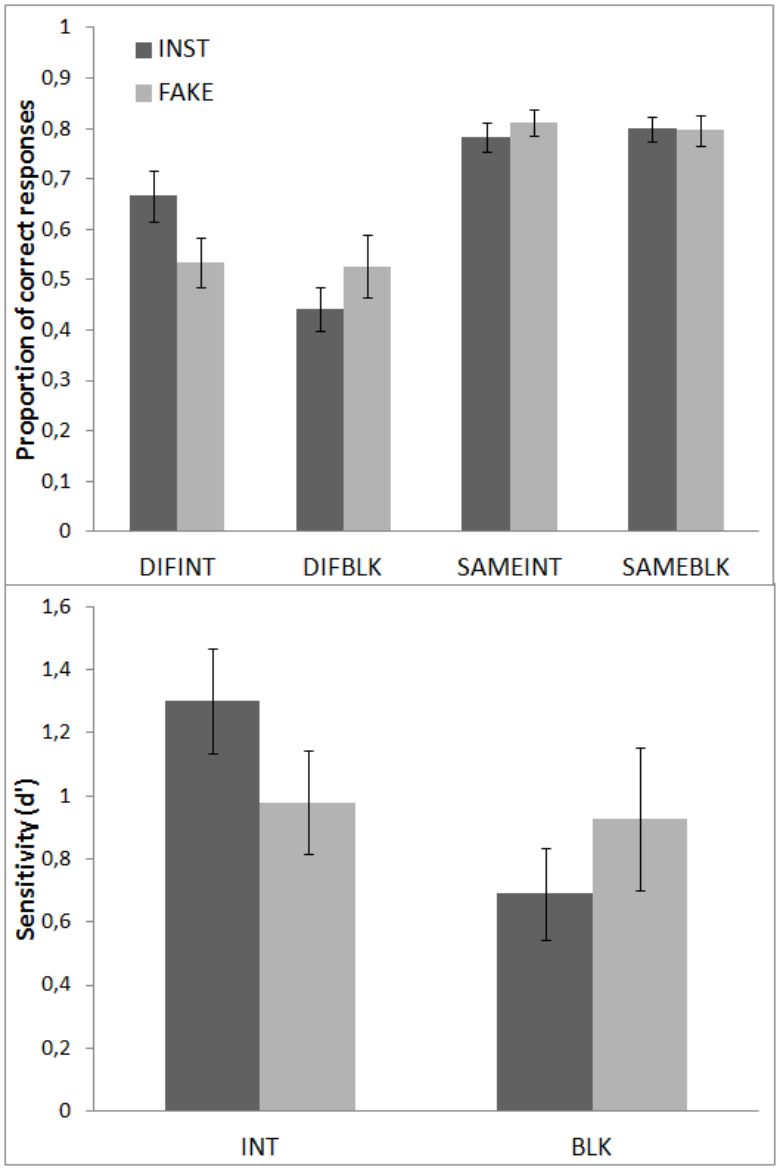

Figure 10: **Results of Experiment 2b. Lower panel:** mean (±SEM) sensitivity scores during the discrimination test. **Upper panel:** mean (±SEM) proportion of correct responses during the discrimination test. On the *x*-axis, DIF and SAME refer to test trial type, while INT and BLK refer to intermixed and blocked respectively. Different groups were instructed to look for differences (INST), or instructed about a bogus task (FAKE).

The results of Experiment 2b further confirmed the findings of Experiment 2a. That is, explicit instructions to look for differences are needed so the intermixed exposure can actually improve discrimination on test. Even though the same previously described criticisms can be applied to this experiment, we believe that the instructions

used in the FAKE group reasonably ensure attention to the stimuli and active visual searching through such cues. Thus, awareness of the goal, and not mere exposure, would be key to explain perceptual learning using visual stimuli in humans.

A further criticism that Dwyer (2016) pointed out is that the FAKE instructions have the effect of diverting the attention to the common features alone. For example, Navarro et al. (2016) asked the participants on their masking task condition to focus on features that only appear in the background (dark-blue splotches). Such instructions might encourage participants to focus on the background, preventing them to detect the unique elements and thus abolishing the I/B effect. This analysis might be valid for the results of Navarro et al. (2016) but cannot be extended to our procedure, as the FAKE instructions of our Experiment 2b direct the attention to features that are also included in the unique elements. We should thus expect any perceptual learning process to take place regardless of the lack of reinforcement. A much broader criticism would be that the lack of explicit instructions would require a much longer exposure for perceptual learning to emerge. This might indeed be true, however it does not contradict the fact that goal awareness and self-reinforcement seem to be important under the conditions present in our experiments and in other similar studies. We cannot, with any certainty reject the idea that other mechanisms might be mediating perceptual learning in their absence, but our results suggest that they are not manifest with this kind of procedure. Under the conditions imposed in the visual perceptual learning tasks we described, increased discrimination can be explained by the sort of self-supervised learning described by Mackintosh (2009).

General discussion

The four experiments described in this chapter highlight some important caveats of the research on human perceptual learning with visual stimuli. Experiments 1a and 1b showed that the effect of additional exposure on discrimination was probably mediated by a location bias, and not by a better memory representation of the unique elements. The scope of this result might seem limited to a refutation of Lavis et al. (2011). However, it can also be broadly interpreted as evidence of self-supervised learning (Mackintosh, 2009). In this case, in Experiment 1a participants received a clear hint of the location of the unique element, which led to its detection and the consequent improvement in discrimination during test. Presumably, as the order of the stimuli was random, participants had many chances to check the reliability of the hint. Once detection took place they kept looking at the place where they knew there was a relevant feature, this strategy probably involving self-reinforcement. On the other hand, Experiment 1b showed that central additional exposure did not improve discrimination at all. It could have been the case that the presentation of the unique elements alone facilitated their detection in the checkerboard, regardless of the position. The lack of such facilitation can be taken as evidence against the suggestion that better memory representation of the unique elements mediates perceptual learning (Lavis et al., 2011; Mitchell, Nash, et al., 2008).

Experiments 2a and 2b showed that instructions that make the goal explicit are necessary for perceptual learning to emerge. We cannot rule out the possibility that perceptual learning would appear with more extensive exposure regardless of

instructions, thus indicating the presence of different mechanisms. For instance, it is perfectly possible that a mechanism based on short-term memory such as the one proposed by Dwyer et al. (2011) allows easier detection of the unique features during intermixed exposure. But, because of their irrelevance (and thus the lack of reinforcement), they are ignored and not remembered later during test. However, we can say that, at the very least, self-reinforcement is sufficient to explain our results under these specific conditions. Even though our experiments used checkerboards, we believe that it makes sense to extend these conclusions to all of the research in humans using visual stimuli. We have explained previously that two things are necessary for self-supervising learning to take place: awareness of the goal and easily separable features. Any of the stimuli used in visual perceptual learning in humans have those qualities. Perhaps the only stimulus that can be considered different is human faces. Checkerboards, foreign graphemes or abstract figures are relatively novel to participants, whereas faces are strongly familiar and thus processed in a different way (e.g., Gauthier & Tarr, 1997). One could expect a more configural type of processing to occur with faces, without isolation of the different features. However, to solve the task it is still perfectly possible (and indeed likely) for the participants to adopt a strategy based on attention to specific features of the face. For example, to assign two very similar faces to a different category (left-handed or right-handed), participants may be paying attention to specific features such as the distance between the eyes or the curvature of the lips in order to perform the discrimination (Mundy et al., 2007).

Very recently, Dwyer (2016) demonstrated perceptual learning without explicit instructions using faces, claiming that "[…] the challenge of Mackintosh (2009) has

been met: unsupervised learning does contribute to exposure schedule effects in human perceptual learning". However, it is possible to argue that such a claim might be rushed. Dwyer (2016) asked one group of participants to look for differences (as usual), and a second group to consider the attractiveness of the faces, insisting that in both cases such information would be useful in a later task. Unexpectedly, both groups discriminated the faces better following intermixed exposure in comparison with blocked exposure. The issue here is that participants are indirectly encouraged to look for differences. Attractiveness is based on features of the face, and different degrees of attractiveness are based on differences in those features of the face. It is likely that the finding of such differences in similar faces was self-reinforced, and such a finding would be easier with intermixed exposure.

All our previous arguments apply to the body of human research with visual stimuli in humans — specifically to those studies attempting to determine the effects of the schedule of exposure. However, we are not suggesting that perceptual learning does not exist under such conditions. Controlling the influence of task demands and hypothesis speculation with human participants is indeed a challenge, but it can be done. It is perfectly possible that such processes are competing with more basic mechanisms shared with animals. To detect the latter, we need to find a way to control the former. An elegant example of this was provided by Dwyer, Hodder, and Honey (2004), using a conditioned taste aversion procedure in humans, who found a dissociation between two different dependent variables (reported preference and discrimination) depending on the feedback provided. On the one hand, participants that received feedback showed improved discrimination between flavours after intermixed

exposure compared to blocked exposure, but there were no differences in the evaluations of preference after the aversion was established. On the other hand, participants that did not receive feedback did not show differences in discrimination, but they showed higher generalization of the aversion after blocked exposure.

Nonetheless, contrary to our hope of finding truly unsupervised perceptual learning, there have been some attempts to incorporate reinforcement as a necessary element. For example, Watanabe, Náñez and Sasaki (2001) found perceptual learning in the direction of coherent motion of task-irrelevant background moving dots. The movement exposed was under the detection threshold (5% of the dots showed coherent motion in the same direction, the rest moving randomly), and it was irrelevant to the main task (a letter identification task); but exposure to it improved later discrimination when it was above detection threshold (10% of the dots). Later, Seitz and Watanabe (2003), using the same task, found that no perceptual learning was found for a particular movement direction when it was uncorrelated with the reinforcement of the main task. Perceptual learning was only observed for the specific direction that was presented when reinforcement took place. Based on this result, and on the ubiquitous presence of reinforcement in the perceptual learning literature, Seitz and Watanabe (2003; see also, Seitz & Watanabe, 2005) proposed that all perceptual learning is controlled by "diffuse reinforcement-learning signals" that might not be related to the particular to-be-discriminated stimuli. It is certainly easy to see how this would affect perceptual learning in rats using flavours (e.g., Symonds & Hall, 1995), as they are thirsty and the ingestion of any liquid may be considered reinforcing. It could also be extended to the classical experiments with imprinting in chicks (e.g., Honey, Bateson, & Horn, 1994).

However, it is more difficult to see how it would apply to other experiments, such as the study by Gibson and Walk (1956). There is also no obvious explanation for the effects of schedule (the I/B effect), or even with the effects of distractor placement (Dwyer et al., 2011). As Mackintosh (2009) pointed out: “That there are other processes going on as well it would be foolish to deny. Perceptual learning, like virtually every other interesting example of a psychological phenomenon, is surely multiply determined.”

Chapter III

Perceptual learning and comparison in rats

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We have highlighted in Chapter II the problems inherent in human research on perceptual learning. We claimed that the failure to find convincing evidence of mere exposure perceptual learning does not mean that such a thing does not exist in humans. Other processes related to the structure of the task, as well as to other human specific attributes, might be overshadowing perceptual learning. Researchers must continue to pursue ways to control such problems in order to find procedures equivalent to animal research in humans. Some attempts have had some success using flavours (Dwyer, Hodder, & Honey, 2004; Mundy, Dwyer, & Honey, 2006), which contribute to close the gap between human and non human subjects. A complementary strategy is to modify animal procedures to make them more similar to human research. This will be the focus of the present chapter.

Since Gibson and Walk's (1956) pioneering experiment, one of the most pervasive explanations of perceptual learning has been comparison. Even though Gibson did not propose any specific mechanism to explain comparison, it can just be regarded as an indeterminate process that happens when the representations of two similar stimuli are active at the same time that causes their unique elements to become more salient. In spite of the problems with human research, its results are quite consistent with this idea. For example, Mundy, Honey and Dwyer (2007) found that simultaneous presentation of a pair of faces increased discrimination between them more than intermixed exposure. It would be reasonable to assume that with simultaneous presentation the representations of the two faces will be more likely to be

active at the same time. Later, Dwyer, Mundy and Honey (2011) conducted another experiment in which they exposed several pairs of faces in rapid alternation, but they introduced a distractor in between some of the pairs. The distractor could be either another face or a checkerboard. Any sort of distractor is expected to impair comparison, as it would be disrupting the representation of the first member of the pair. This disruption would be greater when the distractor is a face, which would be more effective in masking a stimulus with the same identity. As expected, they found that the introduction of a distractor impaired perceptual learning, and that this impairment was greater when the distractor was a face. Again, these results can be taken as evidence of comparison. In fact, any perceptual learning in humans can be explained in terms of comparison as we defined it previously, because they all share the same key feature: stimuli are presented with very brief intervals between them.

In contrast, experiments with animals do not fit well with the idea of comparison. The standard perceptual learning procedure in rats involves inter-stimulus intervals of several hours (e.g., Mackintosh, Kaye, & Bennett, 1991; Symonds & Hall, 1995), which make it hard to figure out how comparison might be acting. Usually, under such conditions, associative models are a good option to explain the results (Hall, 2003; McLaren & Mackintosh, 2000). There are some examples of perceptual learning in animals with short inter-stimulus intervals. For example, Honey and Bateson (1996; see also, Honey, Bateson, & Horn, 1994) found perceptual learning in chicks using an imprinting procedure with visual stimuli, where the inter-stimulus intervals were relatively short and several trials took place during the same session. Similarly, Bennett and Mackintosh (1999, see also Bennett, Scahill, Griffiths, & Mackintosh, 1999) found

perceptual learning using alternating presentation of two flavours, with a short interval between them. However, in both examples discrimination was found to be worse when reducing the inter-stimulus interval. This finding is unexpected, since we should expect easier comparison with shorter inter-stimulus intervals. One possible explanation to this increased generalization is the formation of excitatory associations between the flavours presented close in time, which might increase generalization via sensory preconditioning or mediated conditioning (Honey et al., 1994).

Further attempts to provide evidence for the role of comparison while trying to control the influence of such excitatory associations has also yielded unsatisfactory results. Alonso and Hall (1999) tried to present both target flavours (A and B, no introduced common element) concurrently, and after conditioning one of them they found similar levels of generalization than after blocked exposure, and in both cases lower than in a control non-preexposed group. To ascertain if excitatory associations played a role in this effect, Alonso and Hall (1999) also tried to extinguish these associations after preexposure, finding that this procedure that should increase discrimination had only a very limited effect. However, the results of these experiments must be interpreted with caution, as the flavours used had very little in common. McLaren and Mackintosh (2000) suggested that the stimuli cannot be too similar or too different for perceptual learning to occur. Furthermore, they did not use an intermixed group to check if they could successfully find perceptual learning with that procedure, so their results could be based entirely on latent inhibition to the preexposed flavours. Rodríguez and Alonso (2008) tried again to ascertain the role of comparison with a between-groups design, with one group receiving concurrent exposure to compound AX

and X alone, and two further groups receiving either intermixed or blocked exposure to those same flavours. They found that after conditioning X discrimination was at its worse after concurrent exposure, finding also that intermixed exposure improved discrimination relative to blocked exposure. Despite the lack of a unique element B to form excitatory associations with A, the results can be explained if we consider that such associations can also be formed between the configuration of AX and X alone.

Finally, Rodríguez, Blair, and Hall (2008) replicated the experiment of Rodríguez and Alonso (2008), but instead of conditioning X they conditioned a new flavour, Y. With this manipulation, the influence of excitatory associations is controlled, as no sensory preconditioning or mediated conditioning can influence generalization. Thus, if the salience of the unique elements is higher, then they should find less generalization to AY. According to this, they found that both concurrent and intermixed groups had similar levels of generalization, in both cases lower than the blocked group. They interpreted this as evidence that comparison did not play a role in perceptual learning, as otherwise they should have found better discrimination after concurrent exposure, where comparison is more likely to act optimally. However, it is unlikely that the same mechanisms explained their results after both intermixed and concurrent exposure. A mechanism based on the associative activation of the unique elements, such as the one proposed by Hall (2003), can hardly occur with concurrent exposure. The unique element A should not be associatively activated when it is already physically present, and thus no salience modulation should take place. Moreover, a mechanism based on short-term habituation such as the one proposed by Montuori and Honey (2015) cannot easily explain the results when there are several hours between

presentations of the flavours. Thus, we think it is plausible to assume the existence of different mechanisms to explain perceptual learning depending on the particular conditions of the experimental procedure.

Thus, even though associative salience modulation models disregarded the concept of comparison (Hall, 2003; McLaren & Mackintosh, 2000), our goal in this chapter is to further explore how perceptual learning occurs under conditions where it is likely. Instead of concurrent exposure, we used serial exposure to two compound flavours (AX and BX) with a brief inter-stimulus interval between them. In our Experiment 3 we are going to use a rapid succession procedure with the typical procedure of conditioning AX and testing BX. In this case, we expect the formation of excitatory associations between the unique elements that should increase generalization in the intermixed group. In order to control the influence of those excitatory associations, we adopted the same procedure as Rodríguez et al. (2008), conditioning a new flavour Y and then testing generalization to AY. In Experiment 4a we sought to obtain the basic intermixed/blocked (I/B) effect with this rapid succession procedure. In Experiment 4b we introduced a distractor in between the two target stimuli. With this manipulation, we expect comparison to be disrupted, and thus we should abolish the I/B effect. Finally, in Experiment 5 we tried to further confirm our results by comparing two intermixed groups, one of them with the distractor placed in a way that it should disrupt comparison, and the other with the distractor placed elsewhere. We anticipate our results to replicate those of Dwyer et al. (2011) with humans, thus potentially providing evidence for the role of comparison in animal perceptual learning.

Experiment 3: evidence of excitatory associations with a rapid succession procedure

The experiments reported in this chapter intend to be an adaptation of the procedure usually employed with human participants (e.g., Lavis & Mitchell, 2006), where stimuli are presented in rapid succession with a brief interval between them. Clearly, we have several constraints such as the rats motivation to drink or the time it takes them to consume the fluid available, and our procedure must be adapted to deal with these limitations. This first experiment is a preliminary attempt to develop a procedure of rapid succession. The design is summarized in Table 3. Rats were given limited access to a compound flavour for enough time to enable them to consume it. Immediately after that, rats had limited access water for a brief period. After that period expired, rats again had limited access to another compound flavour. Even though comparison should be possible under such conditions, so are excitatory associations between the unique elements. Because we are conditioning AX and then testing BX, the consumption during test is susceptible to being affected by sensory preconditioning or mediated conditioning, thus increasing generalization. In this situation, according to previous evidence, we expect to find increased generalization in the intermixed group (Alonso & Hall, 1999; Bennett & Mackintosh, 1999; Honey & Bateson, 1996) .

Method

Subjects and apparatus: 16 naïve Wistar rats with ad libitum mean weight of 517 g (range: 460-585 g) were used in this experiment. They had previous experience with a flavor preference conditioning procedure, but were naïve to the flavors used in

this experiment. The rats were individually housed in translucent plastic cages measuring 35x22x18 cm, with wood shavings as bedding. They were maintained on a 12-h light/dark cycle (starting at 8:00 a.m.). These same housing conditions apply to the rest of the experiments detailed in this chapter.

Group	Preexposure	Conditioning	Test
INT	AX/W/BX_D		
		AX+	BX?
BLK	AX/W/AX_D		

Table 3: Design of Experiment 3. INT refers to intermixed exposure, BLK refers to blocked exposure. W refers to water and D refers to a distractor. A, B and X are different flavors, + indicates an i.p. injection of LiCl. "/" indicates rapid succession, "_" indicates different session.

All of the flavored solutions used were prepared with tap water on the day of each experimental session, and were administered in the home cage using inverted 50 ml centrifuge tubes with stainless steel, ball-bearing-tipped spouts. Fluid consumption was calculated by weighing the tubes before and after the drinking sessions. AX and BX were 0.05% v/v caramel or hazelnut (counterbalanced) flavor solutions (Manuel Riesgo, Madrid) with a 9 g/l commercial sodium chloride solution. The distractor was a solution of 20 g/l commercial sucrose. For conditioning, intraperitoneal injections of 0.15 M LiCl were administered at a volume of 1% of body weight.

Procedure: All the procedures explained here were approved by the Animal Research Ethics Committee (CEEA) from the University of Granada. Rats were divided into two groups (INT and BLK) with equivalent weights (means 519 g and 514 g, $F<1$). All rats were deprived by restricting the water availability to two daily sessions of 30 min, at 2:00 p.m. and 7:00 p.m. Rats received three baseline days where water

consumption was measured only during the morning session, since no relevant manipulations were conducted during the afternoon session. No differences were found between groups (last day means 11.4 ml and 10.8 ml, $F<1$).

The preexposure stage lasted four days (Days 1-4). During the first session, at 2:00 p.m., all rats received access to three different solutions. The INT group received 6 ml of solution AX for 10 min, followed by 4 ml of water for 5 min, and finally 6 ml of solution BX for 10 min. The order in which AX and BX were presented was alternated across days. The BLK group received the same schedule, but they received presentations of AX during the first two days, with water in between, and BX during the last two days. Both groups received 5 minutes of the distractor on the second session at 7:00 p.m. All rats received ad lib access to water for 30 min immediately after the afternoon session to keep them hydrated.

The prexposure stage lasted four days (Days 1-4). During the first session, at 2:00 p.m., all rats received access to three different solutions. The INT group received 6 ml of solution AX for 10 min, followed by 4 ml of water for 5 min, and finally 6 ml of solution BX for 10 min. The order in which AX and BX were presented was alternated across days. The BLK group received the same schedule, but they received presentations of AX during the first two days, with water in between, and BX during the last two days[5]. Both groups received 5 minutes of the distractor on the second session at

[5] We did not counterbalance the blocked groups, as previous literature shows that it should not affect the I/B effect (cf. Symonds & Hall, 1995; Mondragon & Hall, 2002).

7:00 p.m. Also, all rats received ad lib access to water for 30 min immediately after the afternoon session to keep them hydrated.

On the following 4 days (Days 5-8) rats received two conditioning trials (on Days 5 and 7) and two recovery days (on Days 6 and 8). On each conditioning trial rats had constant access to 10 ml of AX for 30 min, immediately followed by an i.p. injection of LiCl. On recovery days, rats had free access to water for 30 min at 2:00 p.m. During the next three test days (Days 9-11), rats received ad lib access to BX for 30 min at 2:00 p.m.

Statistical analysis: We used general linear model contrast to analyze our data. We adopted a critical *p* value of .05, and we used Greenhouse-Geisser corrections when needed for the within-subjects ANOVAs. Partial eta squared (η^2_p) and Cohen's *d* were used to measure effect sizes. We also used Bayesian contrasts, choosing the Jeffrey-Zellner-Siow (JZS) prior and the default *r* scale size, as recommended in Rouder et al. (2009) and Rouder, Morey, Speckman and Province (2012). We used JASP software to conduct the analysis (Love et al., 2015). For the interpretation and reporting of Bayesian contrasts we followed Jarosz and Wiley (2014) guidelines. Thus, a Bayes factor (B_{01}) higher than 3 can be interpreted as support for the null hypothesis, with higher values indicating stronger support. On the other hand, values lower than 1/3 can be interpreted as support for the alternative hypothesis, with lower values indicating stronger support. As B_{01} is the odds ratio for the null hypothesis, to estimate the odds ratio for the alternative hypothesis (B_{10}) the inverse must be calculated (1/ B_{01}). The same analyses were used throughout this chapter.

Results

During preexposure, aside from some neophobia on the first day, rats drank virtually all the fluid available on all of the sessions; and the mean consumption of AX decreased between the first to the second conditioning trials in both groups: from 8.1 ml to 2.9 ml in group INT, and from 8.6 to 3.9 in group BLK. A mixed ANOVA with Preexposure and Trial as factors revealed a significant effect of Trial, $F(1, 14) = 33.83$, $\eta^2_p = 0.7$. There were no significant effect of Preexposure and no interaction between these factors, highest $F(1, 14) = 1.38$, $p > .26$.

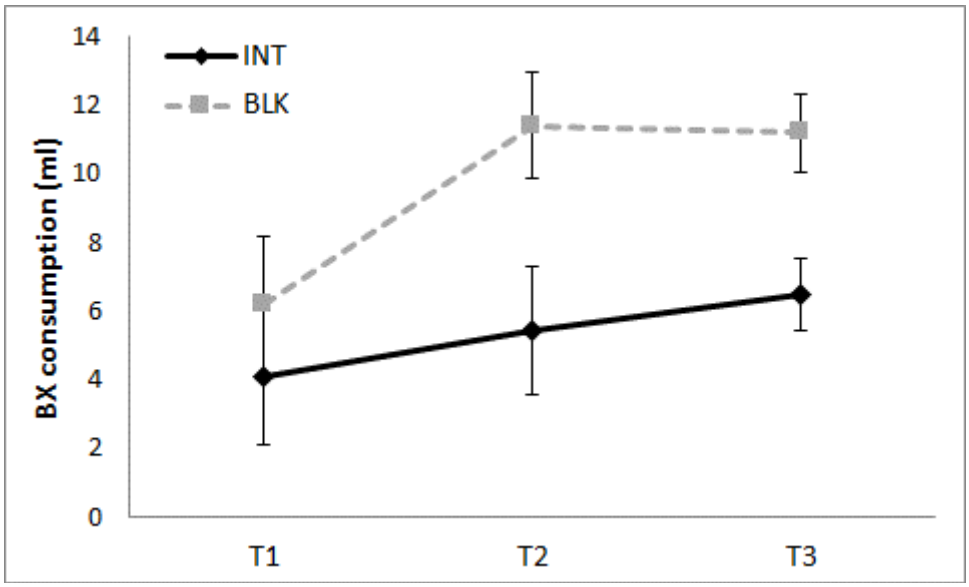

Figure 11: **Results of Experiment 3.** Mean consumption (±SEM) of BX after pairing AX with LiCl. INT refers to rapid intermixed exposure with water in between AX and BX and the distractor in the afternoon. BLK refers to blocked exposure.

Figure 11 shows consumption of BX during the three test trials. Inspection of the figure reveals that consumption increased across trials, but was consistently lower in group INT than in group BLK. A mixed ANOVA with Preexposure and Trial as factors yielded significant effects of Test, $F(2, 28) = 3.75$, $\eta^2_p = 0.21$ and Preexposure, $F(1, 14) = 7.20$, $\eta^2_p = 0.34$, with no significant interaction between these factors ($F<1$). The

Bayesian ANOVA with the same factors showed that the model including Trial and Preexposure was 6 times more likely than the null model, $B_{01} \approx 0.17$, and more than twice more likely than the next preferred hypothesis including the interaction.

Thus, our results are consistent with the proposal that presenting two compound solutions in alternation close in time allows the formation of excitatory links between their unique elements. Such associations would increase generalization of a conditioned aversion, as observed in our results. This could be masking any effect of comparison that might be taking place, so our next step would be to modify this rapid succession procedure in a way that renders those excitatory associations irrelevant.

Experiments 4a and 4b: the effect of distractor placement on perceptual learning with a rapid succession procedure

The design of Experiments 4a and 4b is summarized in Table 4. We adopted the strategy used by Rodríguez et al. (2008) to control sensory preconditioning and mediated conditioning caused by the excitatory associations between the unique elements. Thus, we conditioned a new flavour Y and then tested it in compound with a unique element. Any change in the effectiveness or salience of the unique elements should be easily detectable with this test. Thus, less generalization in the intermixed group on Experiment 4a could be interpreted as being caused by a comparison process since, according to our definition, the representation of both fluids should be active at the same time. Associative activation could be possible, but according to standard associative theory it would be unlikely even though the first fluid is not physically present (Wagner, 1981). In Experiment 4b we added a distractor in between the stimuli

instead of water. Such a distractor should interrupt comparison, potentially displacing the memory trace of the first fluid out from the limited capacity short term memory. Hence, if perceptual learning in Experiment 4a was indeed caused by comparison, we should not see this effect in Experiment 4b.

	Group	Preexposure	Conditioning	Test
Experiment 4a	INT_W	AX/W/BX_D	Y+	AY?
	BLK_W	AX/W/AX_D		
Experiment 4b	INT_D	AX/D/BX_W		
	BLK_D	AX/D/AX_W		

Table 4: **Designs of Experiments 4a and 4b.** INT refers to intermixed exposure, BLK refers to blocked exposure. W refers to water and D refers to a distractor. A, B, X and Y are different flavors, + indicates an i.p. injection of LiCl. "/" indicates rapid succession, "_" indicates different session.

Method

Subjects and apparatus: 16 naïve Wistar rats with ad libitum mean weight of 296g (range: 263-393g) were randomly allocated to Experiment 4a. A second group of 16 naïve Wistar rats with ad libitum mean weight of 329 g (range: 286-386 g) were allocated to Experiment 4b. The housing conditions and apparatus were the same as in Experiment 3. The only changes were the introduction of the new flavor Y, consisting on a solution of 0.5 g/l citric acid, and the increase in concentration of sucrose of the distractor, from 20 g/l to 40 g/l. This latter change was made to ensure that the distractor was salient enough to interrupt comparison.

Procedure: Rats in each experiment were divided into two groups (INT and BLK) with equivalent weights (Experiment 4a: means 296 g and 299 g, $F<1$; Experiment 4b: means: 329 g and 331 g; $F<1$). All rats were deprived by restricting the water availability to two daily sessions of 30 min, at 9:45 a.m. and 4:00 p.m. Rats received three baseline days where water consumption was measured only during the morning session, since no relevant manipulations were conducted during the afternoon session. No differences were found between groups (Experiment 4a: last day means 12.03 ml and 12.51ml, $F<1$; Experiment 4b: last day means: 11.7 ml and 11.3 ml; $F<1$).

The prexposure stage lasted four days (Days 1-4), and was identical to Experiment 3 except for one detail. Rats in Experiment 4a received water between AX and BX at 9:45 a.m. and the distractor in the afternoon at 4:00 p., but rats in Experiment 4b instead received the distractor in between the compound stimuli and water in the afternoon.

On the following 4 days (Days 5-8) rats received two conditioning trials (on Days 5 and 7) and two recovery days (on Days 6 and 8). Conditioning proceeded as in Experiment 3, but rats had access to Y instead of AX. During the next five test days (Days 9-13), rats received ad lib access to AY for 30 min at 9:45 a.m.

Results

Experiment 4a: Rats consumed all of the fluid available during the preexposure sessions; and the mean consumption of Y decreased across the two conditioning trials in both groups: from 6.4 ml to 3.4 ml in group INT, and from 7.8 ml to 4.0 ml in group BLK. An ANOVA conducted on these data confirmed that there was an effect of Trial,

$F(1, 14) = 15.37$, $\eta^2_p = 0.52$, but no effect of Preexposure and no interaction between these factors, largest $F(1, 14) = 2.51$, $p > .14$.

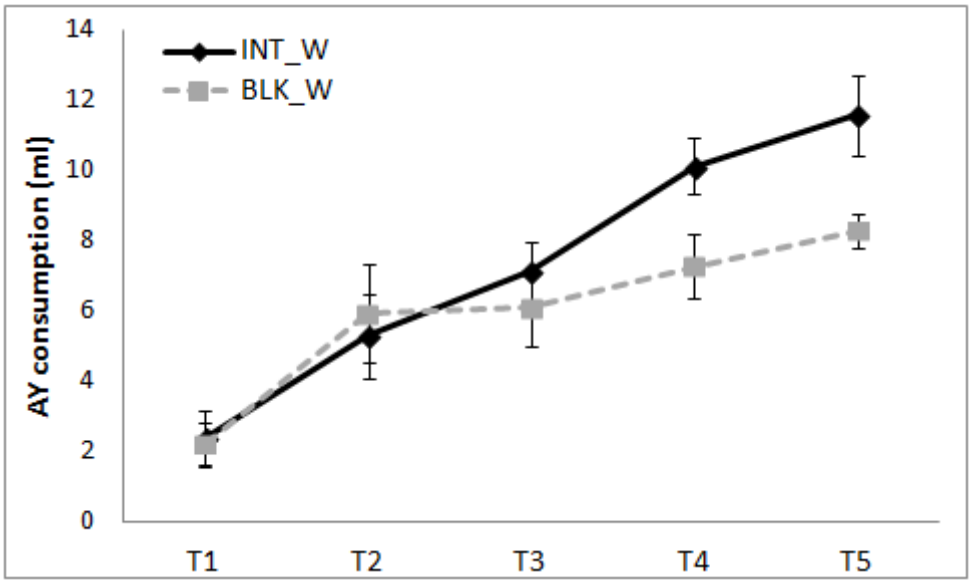

Figure 12: **Results of Experiment 4a.** Mean consumption (±SEM) of AY after pairing Y with LiCl. INT_W refers to rapid intermixed exposure with water in between AX and BX and the distractor in the afternoon. BLK_W refers to blocked exposure.

Figure 12 shows consumption of AY across the five test days in Experiment 4a, and inspection of this figure shows that consumption is similarly low on the initial test trials but lower in group BLK than in group INT on the later test trials. An ANOVA conducted on these data with Group and Trial as factors yielded significant effects of Trial, $F(4, 56) = 34.38$, $\eta^2_p = 0.71$, no effect of Group, $F(1, 14) = 1.57$, $p > .23$, and an interaction between these factors, $F(4, 56) = 2.96$, $\eta^2_p = 0.17$. Pairwise comparisons confirmed that there were differences between groups on days 4 and 5, $t(14) = 2.35$, $d = 1.18$ and $t(14) = 2.60$, $d = 1.30$, respectively. Confirming these results, a Bayesian ANOVA with the same factors showed that the model including the interaction is 3.5×10^{11} times more likely than the null model, $B_{01} \approx 2.8 \times 10^{-12}$, and 1.63 times more likely than the next preferred hypothesis including the factor Trial. Bayesian *t* contrasts

showed marginal support for the alternative hypothesis on day 4, $B_{01} \approx 0.44$, but moderate support on day 5, $B_{01} \approx 0.32$.

Experiment 4b: As in Experiment 4a, rats consumed the fluids that were available during the preexposure sessions, and the mean consumption of Y decreased across the two conditioning trials in both groups: from 6.9 ml to 3.1 ml in group INT and from 7.7 ml to 2.5 ml in group BLK. An ANOVA conducted on these data confirmed that there was a significant effect of Trial, $F(1, 14) = 114.45$, $\eta^2_p = 0.89$, no significant effect of group and no interaction between these factors, largest $F(1, 14) = 1.88$, $p > .19$.

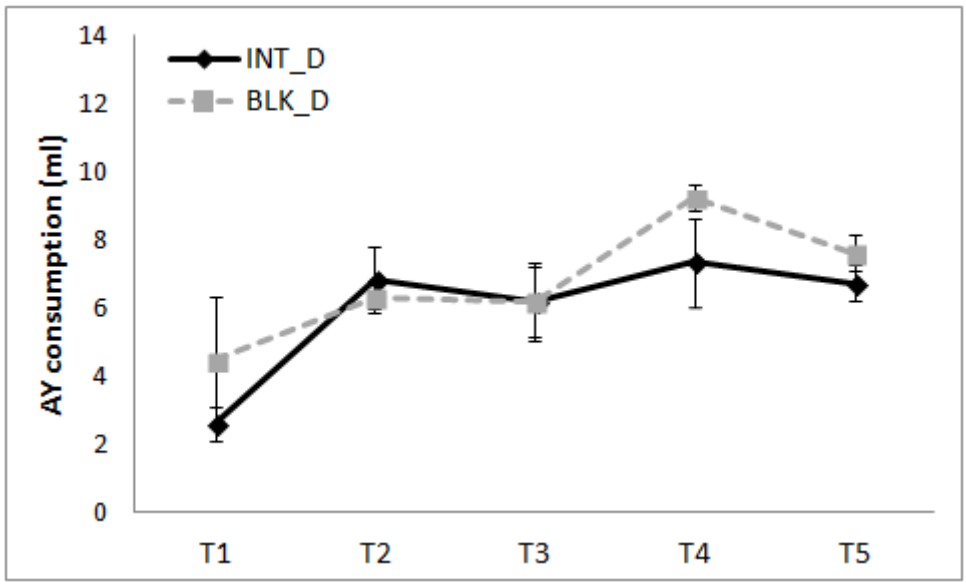

Figure 13: **Results of Experiment 4b.** Mean consumption (±SEM) of AY after pairing Y with LiCl. INT_D refers to rapid intermixed exposure with the distractor in between AX and BX and water in the afternoon. BLK_D refers to blocked exposure.

Figure 13 shows consumption of AY in Experiment 4b. Inspection of this figure shows that, in contrast to Experiment 4a, there was little difference in consumption of AY between groups INT and BLK across the extinction trials. That is, in this case, the ability of A to disrupt the aversion to Y was equivalent in the two groups. An ANOVA

confirmed that there was an effect of Trial, $F(4, 56) = 10.08$, $\eta^2_p = 0.42$, but no effect of Preexposure and no interaction between these factors (Fs < 1). The Bayesian ANOVA showed that the model including the factor Trial was roughly 12,000 times more likely than the null model, $B_{01} \approx 7.8 \times 10^{-5}$. This model was 1.8 times more likely than the next preferred model including the factor Group, and more than 8 times more likely than the model including the interaction.

Discussion

Our results support the idea that comparison plays a role in perceptual learning with this procedure. In Experiment 4a we found the I/B effect with a rapid succession procedure, in which only a brief gap separates both target compound solutions. The presence of water in between is not expected to disrupt the representation of the first flavour, as it is extremely familiar and does not have a strong taste. It can even have beneficial effects, as it would be clearing the mouth of residual aftertaste from the first solution that might alter the perceived flavor of the second compound, making it different from presentations during conditioning or test (Mackintosh, 1987). Note that in human experiments participants are also required to clear their mouths with water after tasting each flavor (e.g., Mundy et al., 2006). The introduction of a salient distractor instead of water, as in our Experiment 4b, abolishes the I/B effect. This suggests that it is disrupting comparison, probably displacing the representation of the first compound solution from short-term memory.

However, there are other ways in which the distractor could be disrupting perceptual learning (Artigas, Sansa, & Prados, 2012). It is possible that the sucrose

distractor aftertaste is affecting perception of the second compound flavor, thus having a proactive effect. In this case, there would be generalization decrement of the acquired long-term habituation between the flavor presented during exposure (and whose flavor would have been altered) and the same flavor presented later in the procedure (Kaye, Swietalski, & Mackintosh, 1988; Mackintosh, 1987). There is also some evidence that the placement of a distractor might disrupt habituation of the flavor presented before it. In this case, the distractor would be interrupting the processing of the first flavor, and less processing would lead to less habituation (Artigas, Sansa, et al., 2012; Kaye et al., 1988; Robertson & Garrud, 1983). If habituation is somehow disrupted in our Experiment 4b, this could explain the lack of perceptual learning regardless of comparison, as it would eliminate any salience modulation effect that might have taken place. Such effect could not have happened on Experiment 4a, as none of the compound flavors were either followed or preceded by the distractor. To check for any unspecific effect of the distractor, we could compare both BLK groups from Experiments 4a and 4b[6]. For none of these groups comparison should have any influence, but differences in habituation should affect generalization, as A should be more salient in Experiment 4b. The ANOVA 5x2 with Trial and Experiment as factors, showed only an effect of Trial, $F(4, 56) = 13.51$, $\eta^2_p = 0.49$, but no other effect or interaction, highest $F(4, 56) = 1.23$. The Bayesian ANOVA shows that the model including Trial alone is ≈ 240000 times more likely than the null model, $B_{01} \approx 4.2 \times 10^{-6}$, and almost 5 times more likely than the

[6] Despite being unorthodox, this comparison should be acceptable as all the rats were from the same batch and had similar previous experience and baseline water consumption. The only difference between experiments is that 1b was started a week later than 1a.

model including the interaction. Thus, the lack of differences in test for groups BLK with and without a distractor rules out any unspecific effect on habituation or aftertaste.

In spite of this comparison, we acknowledge that our interpretation relies on a negative result from Experiment 4b and on a comparison between different experiments. In our Experiment 5 we sought to further replicate the results by comparing two intermixed groups, one with a distractor placed in between the compound stimuli and the other with the distractor placed immediately after the second compound. This manipulation allows us to directly check whether the distractor must be placed in a way that interrupts comparison or if any unspecific backward processing interruption is enough to disrupt perceptual learning.

Experiment 5: Replication of the effect of distractor placement

The design of Experiment 5 is depicted in Table 5. It allows direct examination of the effect of placing a distractor during intermixed preexposure, contrasting the effect of placing the distractor between presentations of AX and BX (for group distractor or DIS) with the effect of placing the distractor after AX and BX had been presented (for group control or CNT). It can be predicted that if the placement of the distractor between AX and BX is critical, then A should be less effective in interfering with the processing of Y during the test in group DIS than in group CNT.

Method

Subjects and apparatus. 16 naïve Wistar rats that were used, with an ad libitum mean weight of 279 g (range: 258-301 g). The rats were maintained in the same way as in the previous experiments, using the same apparatus.

Group	Preexposure	Conditioning	Test
DIS	AX/D/BX/W		
		Y+	AY?
CNT	AX/W/BX/D		

Table 5: **Design of Experiment 5.** DIS refers to the group with distractor between the target stimuli, and CNT refers to the group with the distractor after the stimuli. W refers to water and D refers to a distractor. A, B, X and Y are different flavors, + indicates an i.p. injection of LiCl. "/" indicates rapid succession.

Procedure: Rats were divided into two groups (DIS and CNT) that were matched in weight (282 g and 278 g, $F<1$) and baseline water consumption (last day means 11.94 ml and 12.08 ml, $F<1$). Both groups received intermixed preexposure to AX and BX. However, for group DIS, the distractor was placed between presentations AX and BX, and water was given immediately after the second compound of the pair, whereas for group CNT water was presented between AX and BX and the distractor was presented after the second compound. The volumes of AX and BX were reduced to 5 ml and the volumes of W and D were reduced to 3 ml to ensure that the rats consumed all of the substances that were presented. Details of the procedure that have not been specified were the same as in the previous experiments.

Results and Discussion

The rats again consumed the fluids that were available to them during the preexposure stage, and the mean consumption of Y decreased across the two conditioning trials in both groups: from 9.21 ml to 6.98 ml in group DIS and from 8.73 ml to 6.73 ml in group CNT. An ANOVA conducted on these data confirmed that there was a significant effect of Trial, $F(1, 14) = 15.62$, $\eta^2_p = 0.53$, but no effect of Group and no interactions between these factors (Fs<1).

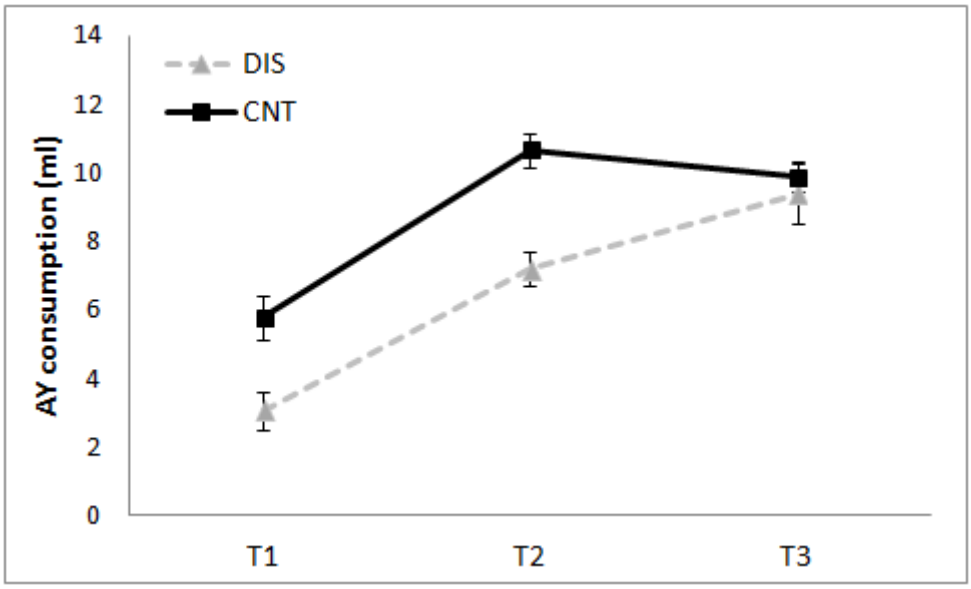

Figure 14: **Results of Experiment 5**. Mean consumption (±SEM) of AY after pairing Y with LiCl. DIS refers to rapid intermixed exposure with the distractor in between AX and BX, and water immediately after BX. CNT has water in between and the distractor after BX instead.

Figure 14 shows consumption of AY during the test in Experiment 5. It is clear that consumption of AX increased across extinction trials and that the level of consumption was lower in Group DIS than in Group CNT. An ANOVA confirmed that there were significant effects of both Trial, $F(2, 28) = 95.81$, $\eta^2_p = 0.87$ and Group, $F(1, 14) = 9.91$, $\eta^2_p = 0.42$, and a significant interaction between these factors $F(2, 28) = 7.30$, $\eta^2_p = 0.34$. Pairwise comparisons showed that there was a difference between groups on Day 1, $t(14) = -3.22$, $d = -1.61$, and Day 2, $t(14) = -4.92$, $d = -2.50$. The Bayesian ANOVA showed that the model including the interaction was 3.5×10^{11} times more likely than the null model, $B_{01} \approx 2.9 \times 10^{-12}$, and more than 11 times more likely than the next preferred model including both simple effects of Trial and Group. Pairwise comparisons showed strong support for the alternative hypothesis on Days 1 and 2, $B_{01} \approx 0.14$ and $B_{01} \approx 0.01$, respectively.

To summarize, Experiment 5 confirmed that the effectiveness of the distractor was dependent on it being presented between successive presentations of AX and BX. It also rules out a possible explanation in terms of backward interruption of processing. If the distractor affected the processing of the preceding flavour or its storage in memory, we should expect less long-term habituation of that flavour (Artigas, Sansa, et al., 2012; Kaye et al., 1988; Robertson & Garrud, 1983). However, in both groups any of the compound solutions were followed by the distractor the same number of times, so we should expect the same degree of processing interruption. There is a last possibility that we need to point out. In group DIS both flavour compounds were preceded by the distractor on some trials, while in the CNT group none of them were ever preceded by the distractor. This leaves open the possibility that the distractor had some sort of proactive effect on the second flavour that affected habituation, such as the reduction in generalization (Kaye et al., 1988). We have previously conducted some experiments trying to place distractors before and after the compound stimuli, but because of the high volume of flavours needed to implement such a design, the rats did not consume all of the fluid available, thus rendering the exposure ineffective.

General discussion

The four experiments described in this chapter aimed to investigate the effects of stimulus comparison with a similar procedure to the one used with human participants (e.g. Dwyer et al., 2011). For this, we used two different strategies: an exposure with short inter-stimulus intervals and the introduction of a distractor.

The strategy of presenting the stimuli close in time has been used before, and the usual result was worse discrimination than after spaced intermixed exposure (Alonso & Hall, 1999; Bennett & Mackintosh, 1999; Honey & Bateson, 1996; Rodríguez & Alonso, 2008). The reason why in those experiments the concurrent or rapid exposures have increased generalization relative to the usual intermixed exposure (or even the blocked exposure) could be the formation of excitatory associations between the compound flavours. If such associations are formed, then after acquiring an aversion to one of the compounds it would generalize to the other by means of sensory preconditioning or mediated conditioning. Our Experiment 3 confirmed such an idea, showing more generalization after intermixed exposure. After controlling the influence of such associations by conditioning a new flavour, thus rendering the excitatory associations irrelevant, Rodríguez et al. (2008) found equivalent levels of discrimination after concurrent than after spaced intermixed exposure, in both cases better than after blocked exposure. We replicated this result in our Experiment 4a, finding less generalization after serial intermixed than after blocked exposure.

Following standard associative theory (e.g. Wagner, 1981) it seems unlikely that those results are caused by a mechanism dependent on associative activation of the unique elements (Hall, 2003). The short inter-stimulus interval means that the representation of the first flavour would have most of its elements already active in A_1 or A_2 states by the time that the second one appears. An extremely rapid pace of decay would be required to allow a significant number of elements to be in I state, so they could be associatively activated. However, in our experiments we counterbalanced the order of the flavours each day. This would potentially allow associative activation of the

unique elements of the second compound solution when the first one is presented, once intra-compound associations have been formed between common and unique elements. This could happen only once or twice in our procedure, assuming that strong enough associations are formed on only one trial. Although unlikely, this possibility cannot be ruled out. For this reason, we sought a more direct way to assess the role of comparison.

The introduction of a distractor between the to-be-discriminated stimuli is a manipulation that directly affects comparison, and thus it is suitable to investigate its role in perceptual learning. It has been used previously with human participants, showing that impaired perceptual learning is found if comparison is disrupted (Dwyer et al., 2011). In our Experiment 4b we replicated such results, finding that the placement of a distractor between the compound solutions abolishes the I/B effect seen in Experiment 4a. Furthermore, in our Experiment 5 we compared two groups with intermixed exposure, one of them with a distractor interrupting comparison and the other with a distractor placed elsewhere, and the former group showed worse discrimination than the latter. Together, those results support the role of comparison in animal perceptual learning. Hall's salience modulation model would have problems explaining the effect of the distractor in our experiments. If the distractor is displacing the representation of the first compound solution from short-term memory, then it should allow enhanced associative activation of the first unique element when the second compound appears. According to Hall (2003), this should have increased salience of the unique elements, and thus reduced generalization.

The effect of a distractor placement has been previously tested in animals, but not in the context of perceptual learning. It has been found that the positioning of a distractor after or before a target stimulus might disrupt long-term habituation (Artigas, Sansa, et al., 2012; Kaye et al., 1988; Robertson & Garrud, 1983). This could potentially explain our results, since a disruption of habituation could eliminate any salience modulation of the unique elements relative to the common elements, and thus abolish the difference between intermixed and blocked exposure. However, a comparison between Experiments 4a and 4b do not support this idea, since the distractor does not seem to have any influence on the salience of the unique elements in the blocked groups. Our Experiment 5 also rules out any explanation in terms of backward processing interruption. For example, it could be that the distractor was preventing the formation of within-compound associations between common and unique elements, thus impeding associative activation and salience modulation. However, the placing of a distractor immediately after the second compound means that for both groups, all the solutions were followed by the distractor the same number of times. Therefore, the critical manipulation seemed to be the placement of the distractor in a way that could interrupt comparison.

Dwyer et al. (2011) made an interpretation of their finding that is also valid to explain our current results. According to them, the comparison process would affect how the stimuli are represented by means of short-term habituation or adaptation. Short-term habituation means that a stimulus recently presented would be less processed when it is presented a second time. Thus, if we present AX and shortly after BX, the common element X would be habituated, and thus there would be a bias to allocate more

processing resources to B alone. This could, for example, increase the chance that B becomes linked to a separate hidden unit, instead of to a configural unit together with X, thus reducing generalization mediated by X or increasing its relative salience (Montuori & Honey, 2015). An explanation in terms of unitization would also be possible (McLaren & Mackintosh, 2000). A processing bias towards the unique elements would increase the chance of intra-element associations, thus improving their memory representation (see also, Mitchell, Nash, & Hall, 2008).

Nonetheless, better processing could also be paradoxically interpreted as a way to increase long-term habituation and latent inhibition, hence impairing perceptual learning. For example, Artigas, Contel, Sansa, & Prados (2012) also used a serial preexposure procedure, manipulating the order of presentation of two consecutive flavor compounds (AX->BX, forward; or BX->AX, backwards). In their Experiment 1, they paired A with LiCl and then tested A. Their results showed that the unique element A was more associable (i.e. yielded better conditioning) in the forward than in the backward condition. According to them, in the forward condition A and X would compete for processing resources while in the backward condition X will be habituated (i.e. already active in A_2 state) and thus A will be fully processed. This would cause more latent inhibition and (or) long-term habituation of A, reducing its associability or effectiveness (see also, Artigas, Sansa, et al., 2012). Their idea is further supported with the results of their Experiments 2 and 3. There, they employed the same serial exposure condition as in Experiment 1, but after conditioning AX, they tested X in compound with a new flavor, N. They found less generalization in the forward group, which is consistent with a more associable A, overshadowing conditioning to X.

This apparent contradiction could be solved if we propose a distinction between associability (the ease with which a stimulus is associated with other stimuli) and effectiveness (the ease with which a stimulus is recognized and processed)[7]. Although these terms have usually been used interchangeably, our proposal here is that they can make reference to different properties of the stimulus. It is not at all counterintuitive to suppose that a very familiar stimulus will be easily located, identified or recognized over a noisy background, and there is indeed some experimental evidence for this notion (Honey & Hall, 1989b; Lubow & Kaplan, 1997; Lubow, Rifkin, & Alek, 1976). Further, this fact is not necessarily at odds with latent inhibition affecting associability. That is, it might be difficult to learn new information about a familiar object, in spite of it being easily recognized. In their paper, Artigas, Contel, et al. (2012) are evaluating associability, as the critical phase of their experiments is conditioning. Better processing could lead to more latent inhibition, and hence less conditioning (Experiment 1) or less overshadowing of X (Experiments 2 and 3). In contrast, in our current experiments we are conditioning a new flavour Y, so latent inhibition of the unique elements should be irrelevant. On the other hand, if unique elements are better represented, they should be more effectively processed. According to McLaren and Mackintosh (2000), a more unitized A should cause more external inhibition of Y during test, because more of its features will be retrieved from memory.

[7] It has been suggested (Prados, personal communication) that a difference in length of preexposure can account for the discrepant predictions, as we used only four exposures to each compound compared to the eight or twenty-four used by Artigas, Contel, et al. (2012). However, both accounts rely on short-term habituation of the common element to affect processing of the unique elements (Wagner, 1981), which should not be affected by exposure length. Furthermore, better processing of the second unique element should have caused faster latent inhibition which would, in turn, increase processing of X as training advances.

In sum, our experiments are a replication of the results of Dwyer et al. (2011) using humans. Whilst the evidence is neither conclusive or strongly in favour of any specific model, it suggests that comparison (understood as any process that requires the representation of the two stimuli to be active at the same time) might play a role in animal perceptual learning.

Chapter IV

Perceptual learning and flavour preference

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In previous chapters, we have focused on methodological and theoretical aspects of perceptual learning, setting aside any practical implication of this phenomenon. We have already mentioned in the introduction some possible everyday situations where perceptual learning might be involved (e.g., Bende & Nordin, 1997; Biederman & Shiffrar, 1987), but aside from that we never pointed out any practical implication of the ideas we are discussing here. This is not to say that perceptual learning is a laboratory-confined phenomenon. Far from it, it has many potential applications to real life situations. In this chapter, we are going to focus on one such application In particular, we are going to discuss the issue of flavour perception, and how it could affect food intake.

Recently, an increasing level of interest has emerged in the topic of food consumption and obesity, mainly because of its epidemic proportions (e.g. Caballero, 2007). People in the developed countries live in what can be considered an "obesogenic environment", where they have easy access to a great variety of highly palatable high energy-dense foods and sedentary lifestyles (Birch, 1999; Lake & Townshend, 2006). In addition to this, the human species has developed through evolution many mechanisms to promote energy intake and storage, useful in times of deprivation but hardly adaptive in our current conditions (King, 2013). There are a large number of intake control mechanisms, both to foster consumption and to inhibit it, that are based on many internal and external cues (Berridge, 2004; Morton & Schwartz, 2006). One of the most important factors that regulates nutrient intake is flavour, with sweet and salty tastes

being innately preferred, whilst sour and bitter tastes are rejected. However, other learned processes might alter these preferences or extend them to initially neutral flavours (Myers & Sclafani, 2006).

For example, much research has focused on promoting the consumption of healthier food. One of the problems that must be dealt with is that healthy food is usually not as palatable as other less healthy alternatives. Thus, one obvious strategy to increase its consumption would be to increase its palatability. A possibility would be to pair healthy food with palatable tastes or with high caloric density, to promote flavour-flavour or flavour-nutrients preference learning (cf. Myers & Sclafani, 2006). For instance, de Wild, de Graaf and Jager (2013) tried to increase infants' preference for two varieties of vegetable soup. The children received one of the soups including high caloric density, while the other had low caloric density. If flavour-nutrient learning is involved in preference acquisition, then they should have seen an increased consumption and preference of the soup paired with high caloric density relative to the other. They found an increase in consumption and preference for both soups, even after a long period of time. Even though preference was higher for the high-calorie soup early after training, such an effect disappeared during follow-up testing. Likewise, de Wild, de Graaf and Jager (2015) also tried to ascertain the role of flavour-flavour learning on the acquired preference for vegetable crisps. Thus, they gave children one vegetable crisp paired with a palatable sauce, and another crisp paired with a neutral sauce. The results showed a marked increase in consumption and preference regardless of the sauce used. Thus, it seems that mere exposure alone is enough to increase preference and

consumption of healthy, but initially unpalatable foods (see also, Birch & Marlin, 1982; Birch, McPhee, Shoba, Pirok, & Steinberg, 1987).

One criticism that might be raised regarding the previous conclusion is that studies such as the two we have just described are not drawing a clear distinction between preference and acceptance. Mere exposure should increase acceptance of a non-palatable substance because of attenuation of neophobia, thus increasing its consumption. However, pairing it with nutrients or a different palatable flavour should increase preference, that is, it should change the hedonic value of the substance. There is an abundance of evidence for such a dissociation in the animal learning literature (for a review, see Myers & Sclafani, 2006). Thus, given that in de Wild et al. (2013, 2015) an increase in preference is observed in addition to the expected increase in consumption, then perhaps mere exposure was not the only mechanism involved in their results. One possibility to explain the lack of differences between paired and unpaired foods is generalization. It is possible that the acquisition of a preference for one variety of food readily generalizes to other similar foods. This would be consistent with the initial difference in preference observed in de Wild et al. (2013), as the gradient of generalization would flatten as time passes (Bouton, Nelson, & Rosas, 1999). This possibility would be an important confound regarding the effects of mere exposure. As previous research in perceptual learning shows, discrimination is increased with exposure, and the age of the sample used (2-4 years) means that children probably have very limited experience with different foods. In fact, it has been found that in children, the increased acceptance of one food after mere exposure can generalize quite readily to other similar foods (Birch, Gunder, Grimm-Thomas, & Laing, 1998). Thus, infants in

the experiments we have just mentioned, where no differences were found between a food simply exposed and another one paired with a palatable flavour or a nutritious consequence, might just have been generalizing the acquired preference from one vegetable product to the other. If children of that age readily generalize preferences between similar foods, it remains a question if mere exposure is really enough to produce a general increase of vegetable intake, or if acquired preferences also generalize from one food to other similar foods in older populations with extensive experience with a great variety of foods and tastes. With this in mind, we designed Experiments 6-9, to explore how exposure to a variety of flavours might affect generalization of an acquired preference (see Recio, Iliescu, Honey, & de Brugada, 2016). For this we used the traditional perceptual learning paradigm (cf. Symonds & Hall, 1995), but instead of conditioning an aversion by pairing a flavour with LiCl we conditioned a preference by pairing it with a palatable taste of high nutrient content (sucrose). This modification would not only extend the phenomenon of perceptual learning to a new paradigm (flavour preference conditioning), but also allow further investigation of the processes of food preference acquisition and generalization.

Perceptual learning can affect how preferences generalize from one flavour to others, thus possibly restricting generalization of acquired preferences and limiting the potential impact of interventions to promote healthy food consumption. But perceptual learning can also affect the generalization of other learned properties of flavours. Thus, a devaluation of one flavour will generalize less to other flavours if they are readily discriminated. One flavour devaluation mechanism that many organisms share is sensory-specific satiety (SSS). SSS is a mechanism that serves to promote the intake of

a variety of foods, instead of focusing only on the most palatable one available. Hence, SSS will contribute, together with many other mechanisms, to stop consumption of a given food by decreasing its palatability (Hetherington, 1996; Rolls, Rolls, & Rowe, 1983). Repeated exposure to the same food would cause its devaluation, reducing its relative preference in relation to other foods, and in this way serving to ensure adequate intake of a variety of required nutrients (Rolls, 1986). . For example, it has been shown that increasing the variety of food over different courses of the same meal increases intake (Brondel et al., 2009). This might lead to more consumption of healthy food if, for example, we have several assortments of vegetables in a meal instead of just one (e.g., Meengs, Roe, & Rolls, 2012; Rohlfs et al., 2013). However, in our current context of easy access to lots of unhealthy foods, SSS might also increase their intake and thus contribute to obesity. This influence of variety on food consumption has been termed the "buffet effect"(Rolls et al., 1981).

In addition to this short-term effect, long-term changes in the way in which SSS operates might also promote intake, and such changes might be mediated by perceptual learning. Exposure to a high variety of palatable high-density food can increase the salience of the differences between those foods. If they are perceived as more different (assuming a differentiation process such as the one originally described by Gibson, 1963), then we should expect less generalization of the SSS. Then, a sort of learned "buffet effect" might be taking place. For example, if we have occasional access to a variety of salty snacks (such as in a party), which are relatively similar, then SSS should generalize and eventually prevent us from eating any of them. However, if we have extensive prior experience with these types of snacks, they will be perceived as more

different and SSS to one of them will not generalize to the others, thus increasing intake. In our current living conditions, with the amount of different unhealthy food to which we have access, this is likely to happen. In our Experiment 10, we try to develop a procedure to check if perceptual learning can influence SSS. We exposed one group of rats to two similar compound solutions in an intermixed fashion, while another group received blocked exposure. After that, we allowed free consumption of one of the compounds until sated, and a couple of hours later we presented the two compound flavours together in a preference test. If rats in the intermixed group are better able to discriminate between the flavours, then they should drink a lot of the non-sated compound solution. However, rats in the blocked group should drink little of any solution, as they will be perceived similar and the satiety should generalize.

It is important to note that the experiments detailed in this chapter are only a preliminary approach to the topic of how perceptual learning might affect other phenomena related to food intake, and as such we are primarily concerned with finding procedures and parameters that yield robust effects. Thus, more than strong and definitive conclusions, we expect to lay down the basis for future research on this topic.

Experiment 6: perceptual learning with flavour preference conditioning

The design of Experiment 6 is summarized in Table 6. There were two groups of rats that both received preexposure to two flavour compounds (AX and BX; caramel with quinine and chocolate with quinine) over a set of morning and afternoon sessions. Rats in Group INT received intermixed exposure to AX and BX (AX, BX, AX, BX..., counterbalanced), whereas those in Group BLK received a block of exposure to AX, for

example, followed by a block of exposure to BX (AX, AX...BX, BX..., counterbalanced). Subsequently, AX was paired with sucrose, and then the rats received a test of consumption of BX.

Group	Preexposure	Conditioning	Test
INT	AX/ BX		
		AX+	BX?
BLK	AX_BX		

Table 6: Design of Experiment 6. INT refers to intermixed exposure, BLK refers to blocked exposure. A, B and X are different flavors, + indicates pairing with sucrose. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.

Method

Subjects and apparatus: The subjects were 16 naïve male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the start of the procedure of 463g (range: 439 - 491g). The rats were individually housed in translucent plastic cages measuring 35x22x18 cm, with wood shavings as bedding. They were maintained in a 12-h light/dark cycle (starting at 8:00 a.m.). These housing conditions are the same in all of the experiments described in this chapter.

All of the solutions that were used were prepared with tap water on each day of the experiment, and were administered in inverted 50 ml centrifuge tubes with stainless steel, ball-bearing-tipped spouts in the home cage. Fluid consumption was calculated weighting the tubes before and after the drinking sessions. The flavour compounds (AX and BX) were constructed from 1% caramel or chocolate (A and B; counterbalanced) flavour solutions (Shepcote Distributors Ltd, Yorkshire, UK) with a 0.023 g/l quinine

sulphate solution. On conditioning trials the unconditioned stimulus, 50 g/l sucrose, was added to AX.

Procedure: All rats were water deprived by restricting their consumption to two daily drinking sessions of 15 minutes at 11:00 a.m. and 5:00 p.m. On the first two days (Days 1-2), in both sessions they received access to water. The two groups (INT and BLK) were matched in terms of their weights (means: 464 g and 462 g, $F < 1$). The preexposure phase, that lasted four days (Days 3-6), consisted of two daily presentations of 10 ml of the flavoured solutions, one at 11:00 and the other at 17:00. Half of the rats in Group INT received AX in the morning sessions and BX solution in the afternoon sessions over the course of four days, while the other half received the reverse order. Likewise, half of the rats in the Group BLK received AX in both sessions on the first two days and BX on the remaining days, with the other half receiving the reverse order. During the four days of conditioning (Days 7-10), all rats received 15 ml of AX together with 50 g/l sucrose in the morning session. In the afternoon sessions, rats received 15 min of water ad libitum. During test (Days 11-14), all rats received free access to BX in the morning session.

Statistical analysis: For this and the following experiments, we used a general linear model contrast to analyze our data. We adopted a critical *p* value of .05, and we used Greenhouse-Geisser corrections when needed for the within-subjects ANOVAs. Partial eta squared (η^2_p) and Cohen's *d* were used to measure effect sizes. We also used Bayesian contrasts, choosing the Jeffrey-Zellner-Siow (JZS) prior and the default r scale size, as recommended in Rouder, Speckman, Sun, Morey and Iverson (2009) and

Rouder, Morey, Speckman and Province (2012). We used JASP software to conduct the analysis (Love et al., 2015). For the interpretation and reporting of Bayesian contrasts we followed Jarosz and Wiley's (2014) guidelines. Thus, a Bayes factor (B_{01}) higher than 3 can be interpreted as support for the null hypothesis, with higher values indicating stronger support. On the other hand, values lower than 1/3 can be interpreted as support for the alternative hypothesis, with lower values indicating stronger support. As B_{01} is the odds ratio for the null hypothesis, to estimate the odds ratio for the alternative hypothesis (B_{10}) the inverse must be calculated (1/ B_{01}).

Results and discussion

Data from the preexposure phase was analyzed using a 4x2x2 mixed ANOVA, with Day and Hour as within-subject factors and Exposure as between groups factor. There were significant effects of Day, $F(3, 42) = 93.90$, $\eta^2_p = 0.87$, and Hour, $F(1, 14) = 14.12$, $\eta^2_p = 0.50$. The interactions Day x Exposure and Day x Hour were also significant, $F(3, 42) = 4.16$, $\eta^2_p = 0.23$ and $F(3, 42) = 7.93$, $\eta^2_p = 0.36$ respectively. The former interaction reflects the neophobic response of group BLK on the day the second compound was introduced. The latter interaction reflects the fact that, due to neophobia, there was no difference between morning and afternoon sessions on the first day of preexposure. No other simple effect or interaction reached significance, highest $F(3, 42) = 1.77$. Data from conditioning was analyzed using a 4x2 mixed ANOVA with Trial and Preexposure as factors. There was a significant effect of Trial, $F(3, 42) = 4.38$, $\eta^2_p = 0.24$, indicating an increase in preference. The effect of group or the interaction were not significant, highest $F(1, 14) = 2.38$.

The results of the test are depicted in Figure 15, and there seems to be no difference between groups in terms of generalization to BX. The 4x2 ANOVA with Trial and Exposure as factors revealed no significant main effects or interactions, highest $F(3, 42) = 2.31$. The Bayesian ANOVA confirmed that not a single model was more likely than the null model, lowest $B_{01} \approx 1.19$.

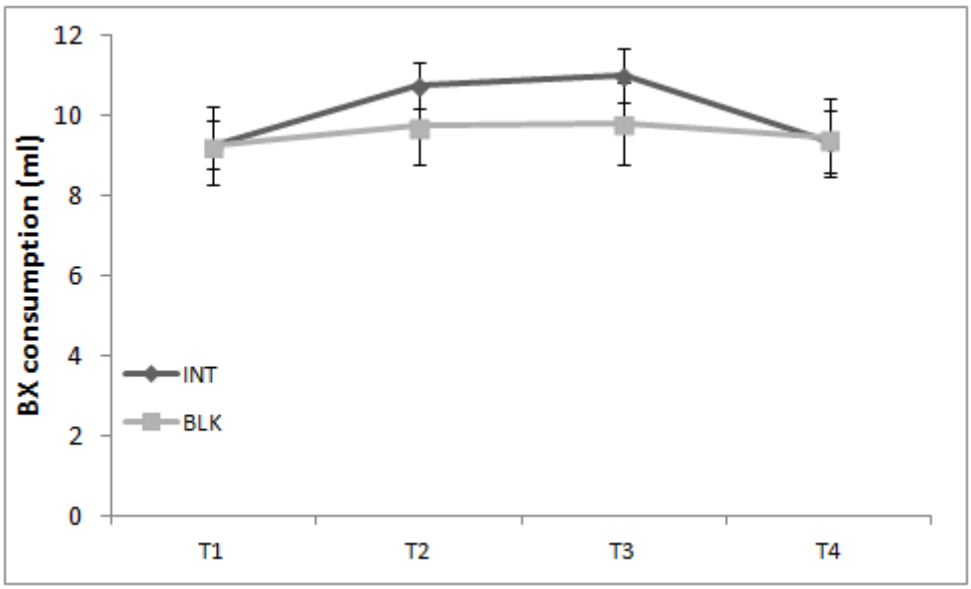

Figure 15: Results of Experiment 6. Mean consumption (±SEM) of BX. INT refers to the group that received intermixed exposure to AX and BX, BLK refers to the group blocked exposure.

Thus, there were no differences in generalization from AX to BX based on exposure. This is not necessarily indicating a lack of perceptual learning. There is good reason to think that the test we employed was not sensitive enough to detect differences in generalization. It is possible that there was a ceiling effect in consumption, as thirsty rats will probably drink any non-unpleasant solution until they are sated. In this case, we used quinine as the US, but the concentration was very low and it has been paired with sucrose, so we could expect a strong re-evaluation. This could have increased general acceptance of quinine, but possibly not to the point at which differences in

generalization are detectable in a single bottle test. Another possibility could be that the concentrations used to prepare the compound solutions were too low, thus making the tastes too similar and difficult to discriminate. The next experiment is a replica of the current experiment, but instead uses a preference test and a higher concentration of flavourings and quinine. We also manipulated the motivational state of the rats during test, as it has been shown that this might facilitate the expression of acquired preferences (Yiin, Ackroff, & Sclafani, 2005).

Experiment 7: perceptual learning with flavour preference conditioning (changing parameters)

The design of Experiment 7 is summarized in Table 7. It is essentially a replica of Experiment 6, but increasing the concentration of the solutions and changing the test. In this case, we conducted two preference tests under a motivational state of hunger: one with BX and water, and the other with BX and AX. The logic of the first one is clear, since we can anticipate that rats in the BLK group should have a higher preference for BX. In the second test, rats in the group INT, which presumably discriminate better between AX and BX, should show a clear preference for AX. However, low discrimination should lead to rats drinking AX or BX equally.

Group	Preexposure	Conditioning	Adapt	Test 1	Test 2
INT	AX/ BX				
		AX+	W	BX vs W	AX vs BX
BLK	AX_BX				

Table 7: Design of Experiment 7. INT refers to intermixed exposure, BLK refers to blocked exposure. A, B and X are different flavors, W is water, + indicates pairing with sucrose. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.

Method

Subjects and apparatus: The subjects were 16 naïve male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the start of the procedure of 286 g (range: 231–315 g). The composition of the solutions was slightly changed. A and B were 2% chocolate and caramel (counterbalanced) flavour solutions, while X was a 0.046 g/l quinine sulphate solution. The increase in the concentrations of the flavourings used was chosen to make them easier to discriminate. During conditioning, 160 g/l of sucrose was added to AX. The increase in concentration of sucrose was chosen to promote flavour-nutrient associations that could be expressed on test.

Procedure: On the first two days after water deprivation, rats received access to water for 15 min at 10:00 a.m. and 4:00 p.m (Days 1-2). Rats were divided in two groups (INT and BLK) that were matched in terms of their weights (means: 291 g and 281 g, $F < 1$) and water consumption during these 2 days (last day means: 10.58 ml and 10.50 ml, $F < 1$). The procedure during preexposure (Day 3-6) and conditioning (Days 7-10) is mostly the same as in Experiment 6, with a few exceptions. 20 ml of solution were provided during conditioning instead of 15 ml. An important change is that we added a manipulation of the motivational state. After the last day of conditioning, food was removed from the cage. The next day (Day 11) was an adaptation day, in which rats received water in the morning session and 1 h of ad libitum food and water in the afternoon. For the first test (Day 12), rats received ad libitum access to two bottles, one with water and the other with BX. The next day (Day 13), rats received again ad libitum access to two bottles, but this time they contained AX and BX. BX preference ratios for

both tests were calculated, dividing the consumption of BX by the total consumption during the session.

Results and discussion

Data from the preexposure phase were analysed using a 4x2x2 mixed ANOVA, with Day and Hour as within-subject factors and Exposure as between groups factor. This analysis revealed a significant effect of Day, $F(3, 42) = 63.24$, $\eta^2_p = 0.82$, which is consistent with an attenuation of neophobia across trials. There was also a significant Exposure × Hour interaction, $F(1, 14) = 8.59$, $\eta^2_p = 0.38$, which is consistent with the observation that Group BLK drank less fluid in the morning of the third day, when BX was presented for the first time. Analysis of the consumption scores from the conditioning stage by means of a 4x2 ANOVA, with Exposure and Trial as factors, confirmed that there was an effect of Day, $F(3, 42) = 11.54$, $\eta^2_p = 0.45$, reflecting an increase in consumption across trials, but no effect of Exposure and no interaction between these factors, Fs < 1.

The results of the first test are depicted in the upper panel of Figure 16. The one-way ANOVA revealed no significant effect of Exposure on the preference for BX, $F < 1$. A Bayesian *t* test showed marginal support for the null model, $B_{01} \approx 2.31$. It seems that rats do not show a clear preference for BX regardless of the exposure they received. Preference ratios for the second test are depicted in the lower panel of Figure 16. All rats prefer to drink AX over BX, but this preference seems lower for the rats which had blocked exposure. A one-way ANOVA confirmed this impression, $F(1, 14) = 4.33$, $\eta^2_p = 0.24$. The Bayesian *t* test showed marginal support for the alternative, $B_{01} \approx 0.62$.

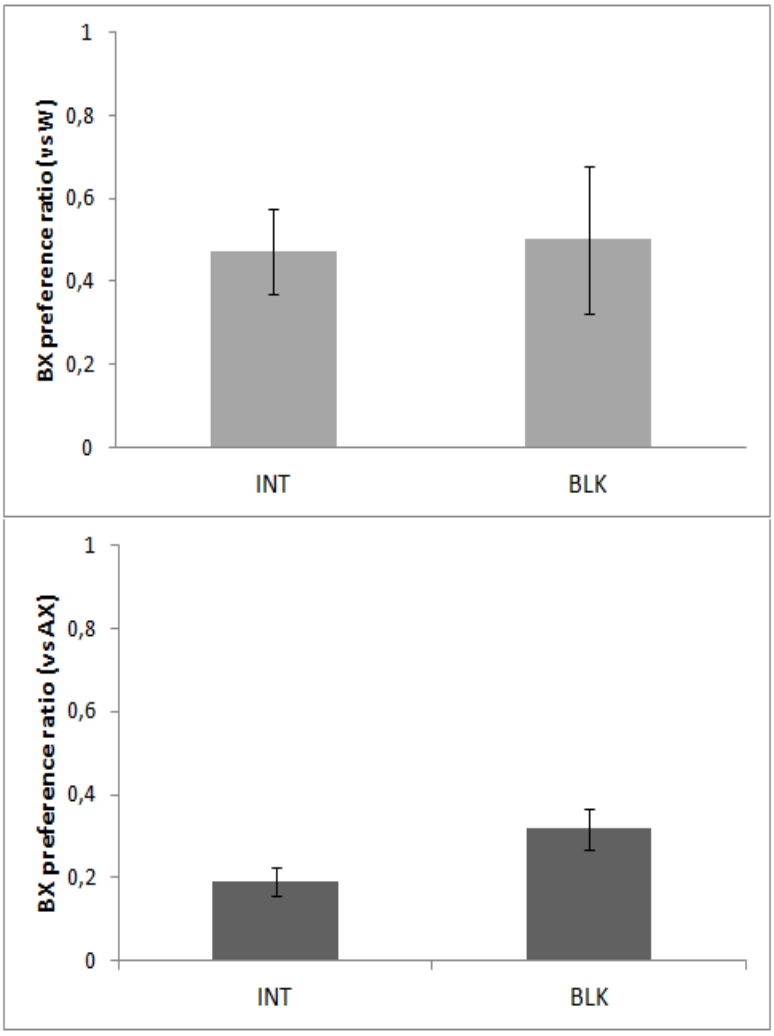

Figure 16: Results of Experiment 7. Upper panel: Mean preference ratio (±SEM) of BX over water. **Lower panel**: Mean preference ratio (±SEM) of BX over AX. INT refers to the group that received intermixed exposure to AX and BX, BLK refers to the group blocked exposure.

Bayesian analyses did not give conclusive support for the alternative hypothesis, probably because of the low amount of liquid consumed. The mean total consumptions for the first test were 4.01 ml and 3.88 ml for group INT and BLK respectively, and for the second test they were 3.41 ml and 3.72 ml. Our results also highlight that preference tests with water as a reference might not be ideal, because they are prone to ceiling and floor effects when substances with positive or negative hedonic values are used. However, we obtained some evidence that rats in the intermixed group discriminate

better between AX and BX than rats in the blocked group, based on the lower generalization of the acquired preference in the former group. To our knowledge, this is the first demonstration of perceptual learning using a flavour preference conditioning procedure. However, given the weakness of the results, we decided to replicate the experiment again using a within-subjects design.

Experiment 8: perceptual learning with flavour preference conditioning in a within-subjects design

The design of Experiment 8 is summarized in Table 8: Experimental design of Experiment 8. COND refers to the group that receives conditioning, UNP refers to the explicitly unpaired group. A, B and X are different flavors, W is water, + indicates pairing with sucrose. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.. All rats received intermixed exposure to a pair of compounds (AX and BX), and a block of exposure to a third compound (CX). After the preexposure stage, rats in Group COND received conditioning trials in which AX was paired with sucrose and those in Group UNP received unpaired presentations of AX and sucrose. Following the conditioning trials, all rats received a test in which AX and W were presented to assess the formation of a preference. We anticipated that rats in Group COND would show a more marked preference for AX than those in Group UNP. During the critical tests, all rats received a choice between BX and CX. It was anticipated that the preference in Group COND would be less likely to generalize to BX than to CX, and, to the extent that this difference reflected a difference in the

generalization of the conditioned AX preference, then it should not be evident in Group UNP.

Group	Preexposure	Conditioning	Adapt	Test 1	Test 2
COND		AX+			
	AX/ BX_CX		W	AX vs W	BX vs CX
UNP		AX/+			

Table 8: Experimental design of Experiment 8. COND refers to the group that receives conditioning, UNP refers to the explicitly unpaired group. A, B and X are different flavors, W is water, + indicates pairing with sucrose. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.

Method

Subjects and apparatus: The subjects were 16 male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the beginning of the procedure of 489 g (range: 416–536 g). The rats were previously used in a conditioned flavour aversion experiment, but were naïve with respect to all of the flavours used in this procedure. BX and CX were solutions of 2% caramel or chocolate (counterbalanced) flavouring with 0.046 g/l quinine sulphate solution. AX was a solution of 2% vanilla flavouring (Shepcote Distributors Ltd, Yorkshire, UK) with the same concentration of quinine as BX and CX. In Group COND, 160 g/l sucrose was added to AX during the conditioning trials, whereas in Group UNP, AX and sucrose were separately presented.

Procedure: In the same way as in Experiment 7, on the first two days after water restriction rats received access to water for 15 min at 10:00 a.m. and 4:00 p.m (Days 1-2). Two groups of rats (COND and UNP) were then created, counterbalanced for their previous experience. The two groups had similar mean weights (means: 494 g and 484

g, $F < 1$) and consumed similar amounts of water during the water deprivation schedule (last day means: 12.96 ml and 12.88 ml, $F < 1$). The preexposure consisted of two daily drinking sessions, and lasted for six days (Days 3-8). Half of the rats of each group received 10 ml of AX in the morning sessions and 10 ml of BX in the afternoon for four days, and the last two days received 10 ml of CX in both daily sessions. The other half of the rats received the reverse order, with the two first days having access to CX and the four following days having access to AX and BX. During the four days of conditioning (Days 9-12), group COND received 10 ml of AX mixed with 160 g/l of sucrose, while the UNP group received 10 ml of AX alone in the morning and a sucrose solution in the afternoon. Immediately after the last conditioning session (Day 12), food was removed and rats had an adaptation day as in the previous experiment (Day 13). Two tests were conducted. First, during two days rats received free access to two bottles containing either AX or water (Days 14-15). The following two days rats instead received BX in one bottle and CX in the other (Days 16-17).

Results and discussion

Data from preexposure were analysed using a 6x2x2 mixed ANOVA, with Day and Hour as within-subject factors and Conditioning as between groups factor. This analysis revealed a significant effect of Day, $F(5, 70) = 14.03$, $\eta^2_p = 0.5$, Hour, $F(1, 14) = 50.41$, $\eta^2_p = 0.78$, and also a significant interaction between both factors, $F(5, 70) = 5.38$, $\eta^2_p = 0.28$. There was no effect of group or any other interactions, highest $F(1, 70) = 1.97$. Analysis of the consumption scores from the conditioning stage by means of a 4x2 ANOVA, with Conditioning and Trial as factors, confirmed that there was an effect

of Conditioning, $F(1, 14) = 6.27$, $\eta^2_p = 0.3$, but no effect of Day or interaction between the factors, highest $F(3, 42) = 2.58$. Presumably, this reflects the higher preference for AX when it was presented together with sucrose.

Pooled data from the two sessions of the first test are depicted in the upper panel of Figure 17. It is evident that rats in the UNP group have a marked lower preference for AX than rats in the COND group. The 2x2 ANOVA confirmed this impression, showing a significant effect of Conditioning, $F(1, 14) = 8.93$, $\eta^2_p = 0.39$, but no effect of Trial nor interaction (Fs<1). The Bayesian ANOVA also showed that the model including only Group was 3 times more likely than the null model, and overall at least twice more likely than any other possible model, $B_{01} \approx 0.33$. For the second test, data from one rat was eliminated due to the leaking of one tube during one of the test sessions. In order to perform the repeated measures contrast, that cell was filled with the group average. The pooled data from the two days of this second test is depicted on the lower panel of Figure 17. Clearly, group COND shows a greater preference for CX over BX than group UNP. The ANOVA revealed a significant effect of Conditioning, $F(1, 14) = 7.56$, $\eta^2_p = 0.35$, but no effect of Trial nor interaction (Fs<1). The Bayesian ANOVA confirmed this trend by showing that the model including only Conditioning is more three times more likely than the null model, $B_{01} \approx 0.32$, and even more likely than every other possible model. However, to further confirm that the group COND has actually a preference for CX over BX, we conducted one-sample *t* tests with a criteria value of 0.5, pooling the ratios of both test days. Group COND showed a significantly higher preference for CX than expected by chance, $t(7)=2.65$, $d=0.94$, although the Bayesian analysis showed only marginal support for the alternative, $B_{10} \approx 0.38$. Group

UNP showed no significant difference from chance levels, $t(7)=-1.06$, with the Bayesian analysis showing also marginal support for the null hypothesis, $B_{10}=1.91$.

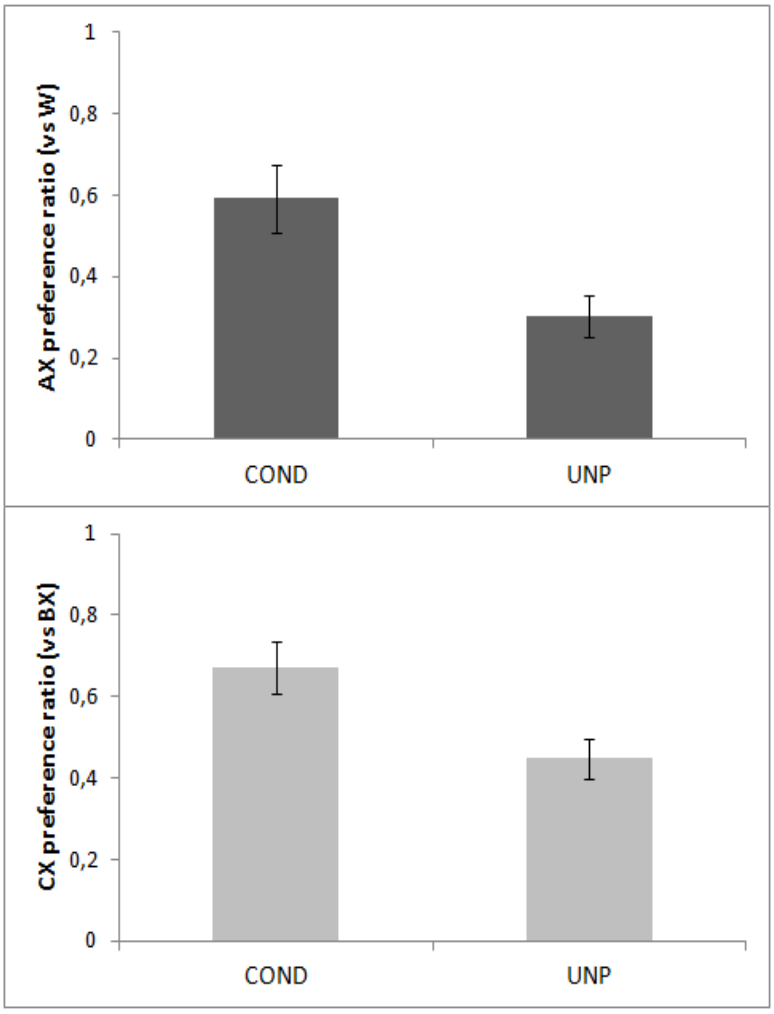

Figure 17: Results of Experiment 8. Upper panel: Mean preference ratio (±SEM) of AX over water**. Lower panel:** Mean preference ratio (±SEM) of CX over BX. COND refers to the group that received pairings of AX and sucrose, UNP refers to the group that received AX and sucrose unpaired.

The results of Experiment 8 further replicate those of Experiment 7, and are yet another demonstration of perceptual learning using a flavour preference conditioning procedure. However, as in the previous experiments, consumptions during test were also low, with mean total consumptions during the first two tests of 5.91 ml and 4.54 ml for groups COND and UNP respectively, and for the last two tests 2.23 ml and 3.29 ml.

Thus, results are weak, especially when using Bayesian statistics, as small effect sizes might mean that our design was underpowered. The fact that the rats were hungry during the test and that X was the unpleasant flavour quinine may have caused these low consumptions, and this has probably clouded the results. To avoid this, our next step was to try to replicate this same effect but using a palatable taste such as saccharin, to ensure liquid consumption in spite of the motivational state. In addition to that, given that we expect high levels of consumption due to the palatability of the saccharin, we decided to avoid introducing motivational changes so rats were hungry throughout all of the experiment.

Experiment 9: replication of the I/B effect with flavour preference conditioning using saccharin as common element

The design of Experiment 9 is depicted in Table 9. It is broadly similar to Experiment 7 in every aspect, but saccharin is used instead of quinine. With this manipulation, we intended to solve the problem posed by the low amount of liquid consumed by the rats during test. Also, we changed the test as well, trying to obtain a more direct measure of consumption. So instead of using a preference test, we again used a single-bottle test to evaluate generalization of the acquired preference from AX to BX.

Method

Subjects and apparatus: The subjects were 16 male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the beginning of the procedure of 384 g (range: 338–462 g). The rats were previously used in a conditioned flavour aversion

experiment, but were naïve with respect to all of the flavours used in this procedure. AX and BX were solutions of 0.05% caramel or hazelnut (counterbalanced) flavouring (Manuel Riesgo, Madrid) with 1 g/l sodium saccharin solution. During conditioning, 160 g/l of maltodextrin was added to AX.

Group	Preexposure	Conditioning	Test
INT	AX/ BX		
		AX+	BX?
BLK	AX_BX		

Table 9: Design of Experiment 9. INT refers to intermixed exposure, BLK refers to blocked exposure. A, B and X are different flavors, + indicates pairing with sucrose. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.

Procedure: Before the start of the procedure, food was removed from the cages and restricted to 1 hour of ad libitum access at 7:00 p.m. Water was also removed, and for three days rats (Days 1-3) received access to water for 30 min at 2:00 p.m. and 7:00 p.m. Two groups of rats (INT and BLK) were created, counterbalancing for their previous experience. The two groups had similar mean weights (means: 391 g and 377 g, $F < 1$) and consumed similar amounts of water during the water deprivation schedule (first day means: 6.11 ml and 6.41 ml, $F < 1$; the next baseline days rats barely consumed any water). The preexposure (Days 4-7) was identical to Experiment 7, save for the details that the session lasted 30 minutes instead of 15. During the four days of conditioning (Days 8-11), both groups received 10 ml of AX mixed with 160 g/l maltodextrin. On the next four days (Days 12-15), rats had free access to BX.

Results and discussion

Data from one rat of group BLK was eliminated because it refused to drink throughout the whole of the preexposure phase. The data from preexposure were analysed using a 4x2x2 mixed ANOVA, with Day and Hour as within-subject factors and Exposure as between groups factor. This showed a significant effect of Day, $F(3, 39) = 14.34$, $\eta^2_p = 0.52$, and Hour, $F(1, 13) = 11.95$, $\eta^2_p = 0.48$. There was also a significant Day x Exposure interaction, $F(3, 39) = 2.87$, $\eta^2_p = 0.18$, probably reflecting differences in neophobia when introducing BX to group BLK. No other effect or interaction were significant, highest $F(3, 39) = 1.19$. The data from conditioning were also analysed with a 4x2 mixed ANOVA, with Trial and Exposure as factors, and showed no significant effects, highest $F(3, 39) = 1.48$, as all rats drank almost all the fluid available.

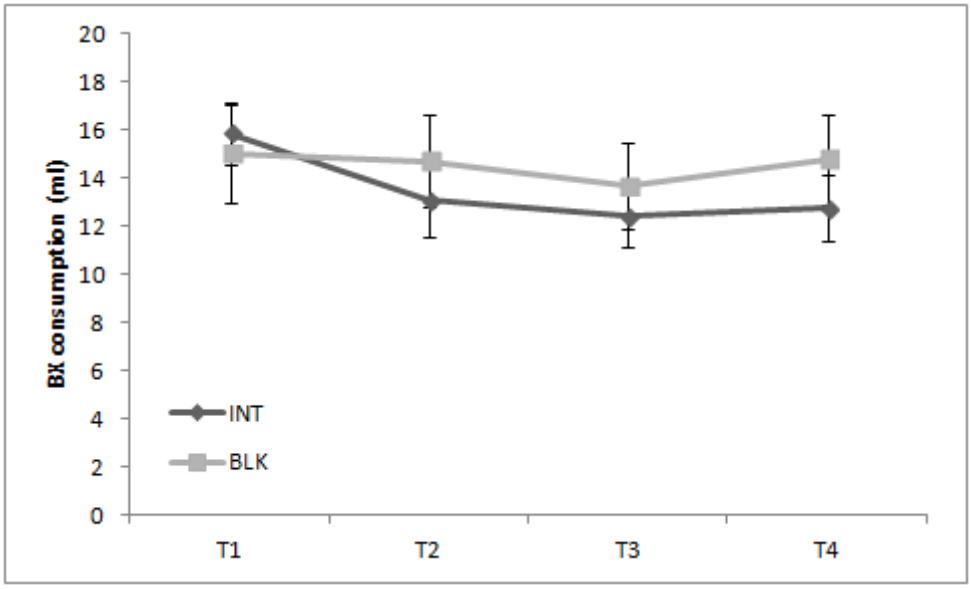

Figure 18: Results of Experiment 9. Mean consumption (±SEM) of BX. INT refers to the group that received intermixed exposure to AX and BX, BLK refers to the group that received blocked exposure.

Figure 18 shows that group BLK had a tendency to generalize more from AX to BX, reflected in their higher consumption. However, the 4x2 mixed ANOVA with Trial

and Exposure as factors did not show that difference to be reliable, as none of the effects nor the interaction were significant, highest $F(3, 39) = 2.29$. The Bayesian ANOVA confirmed this, as none of the models including any of the variables was more likely than the null model, lowest $B_{01} \approx 1.05$. In fact, the null model was 5 times more likely than the model including the interaction.

Thus, it seems that although the data shows a tendency according to our predictions, the one bottle test fails again to be sensitive enough to yield significant results. This could also be caused by a ceiling effect, as all rats are consuming great amounts of liquid. In any case, the failure to get a perceptual learning effect with this procedural variation does not undermine our previous results. Further efforts are needed to obtain a robust procedure of perceptual learning with flavour preference conditioning in order to investigate how preferences between similar flavours are generalized.

Experiment 10: an exploration of the effect of preexposure on sensory-specific satiety

This experiment is an adaptation of the standard intermixed-blocked procedure, but rather than conditioning one of the exposed flavours we devaluated it by allowing consumption until satiation occurs (see Table 10). In this experiment we have a group receiving intermixed exposure to two compound flavours, and another one receiving blocked exposure. After four days of exposure, rats are given free access to one of them and, two hours later, they receive a preference test including the previously sated flavour and the remaining one. If rats do not discriminate between them, then we expect similar low levels of consumption of both flavours. However, if the intermixed

exposure has the consequence of increasing discrimination, we should see a higher consumption of the non-sated flavour.

Group	Preexposure	Test		
		Satiety	(2 hours)	Preference
INT	AX/ BX			
		AX		AX vs BX
BLK	AX_BX			

Table 10: Design of Experiment 10. INT refers to intermixed exposure, BLK refers to blocked exposure. A, B and X are different flavours. "/" indicates intermixed exposure in different sessions, "_" indicates blocked exposure.

Method

Subjects and apparatus: The subjects were 16 male Wistar rats (supplied by the Animal Production Unit from the University of Granada), with a mean ad libitum weight at the beginning of the procedure of 350 g (range: 264–388 g). The rats were previously used in a conditioned flavour aversion experiment, but were naïve with respect to all of the flavours used in this procedure. AX and BX were solutions of 0.05% vanilla or almond (counterbalanced) flavouring (Manuel Riesgo, Madrid) with 1 g/l sodium saccharin solution.

Procedure: Before the start of the procedure, water was removed from the cages and restricted to two daily 30 minutes sessions at 9:30 a.m. and 3.30 p.m. During the next day rats received access to water ad libitum (Day 1). Two groups of animals (INT and BLK) were created, counterbalancing for their previous experience. The two groups had similar mean weights (means: 338 g and 361 g, $F(1, 14)= 2.23$) and similar amounts of baseline water consumption (means: 10.13 ml and 10.68 ml, $F < 1$). The preexposure

was similar to Experiment 6: during four days (Days 2-5), rats in the intermixed group received for 30 minutes 10 ml of either AX or BX in the morning, and the remaining solution in the afternoon; while rats in the blocked group received either AX or BX for two days and the remaining solutions the next two days. The test phase consisted of two days with two sessions each (Days 6-7). In the first one, at 9:30 a.m., rats received ad libitum access to AX for 30 minutes (satiety session). Two hours after the end of the first session, at 12:00 p.m., rats received 15 minutes of ad libitum access to two tubes, containing AX and BX (preference session). In the afternoon all rats received free access to water.

Results and discussion

We conducted a 4x2x2 mixed ANOVA with Day, Hour and Exposure as factors for the preexposure data. It showed only a significant Hour x Exposure interaction, $F(1, 14)= 5.72$, $\eta^2_p= 0.29$, reflecting less consumption in the afternoon after the change of flavour in group BLK caused by neophobia. No other effect or interaction was significant, highest $F(3, 42)= 2.00$.

For the test, we first analysed if there were any differences in ad libitum consumption of AX during the satiation session. The mixed ANOVA with Day and Exposure as factors did not show any significant effect, highest $F(1, 14)= 1.77$. Thus, both groups drank similar amounts of liquid until sated. We also analysed the total amount of liquid consumed on the preference sessions. The mixed ANOVA also did not show significant differences (Fs < 1). Bayesian analyses confirmed these results. For the satiation session, the null model had more support than any other model, lowest B_{01}

≈ 1.49. For the preference session the results were the same, lowest B_{01} ≈ 1.57. Thus, the schedule of preexposure did not affect the amount of liquid consumed. However, there was a decline in liquid consumption from the satiety session to the preference session (see Figure 19). We analysed the mean consumption over the two days with a mixed ANOVA, with Session and Exposure as factors, and this analysis revealed a significant effect of Session, $F(1, 14)= 28.27$, $\eta^2_p= 0.67$, but no other effect or interaction (Fs < 1). The Bayesian ANOVA confirmed this result, showing that the model including Session was almost 600 times more likely than the null model, B_{01} ≈ 0.002, and more than twice more likely than the next preferred model. Thus, our procedure was successful in obtaining satiety, but we still have no information of the degree of generalization.

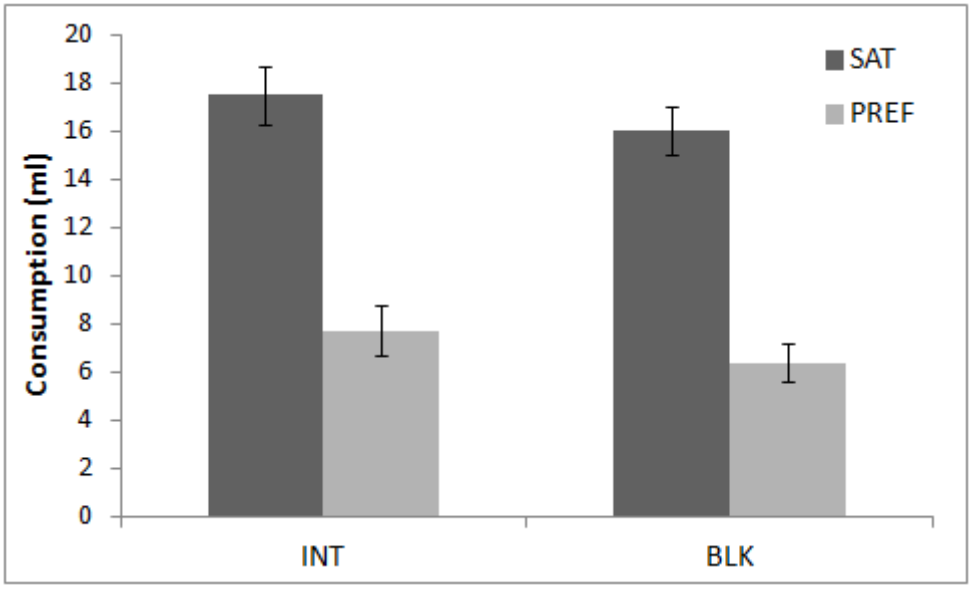

Figure 19: Results of Experiment 10. Mean total consumption (±SEM) for the satiety session (SAT) and the preference session (PREF) during the two test days. INT refers to the group that received intermixed exposure to AX and BX, BLK refers to the group that received blocked exposure.

The mean preference ratios of the non-sated compound BX are represented in Figure 20, and it is apparent that there are no differences between groups. We ran a

mixed ANOVA, with Day and Exposure as factors. None of the factors or the interaction had significant effects, highest $F(1, 14) = 2{,}28$. The Bayesian ANOVA confirmed this lack of differences, showing that the null model is almost twice more likely than the next preferred one, lowest $B_{01} \approx 1.73$.

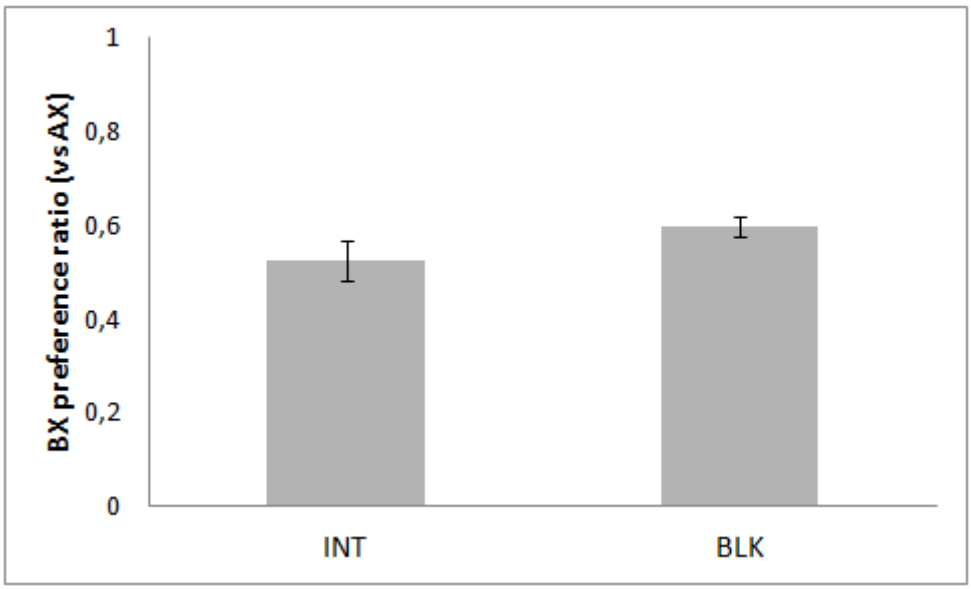

Figure 20: Results of Experiment 10. Mean preference ratio (±SEM) of BX during the two test days. INT refers to the group that received intermixed exposure to AX and BX, BLK refers to the group that received blocked exposure.

Thus, our results show that there is indeed satiety from the first session to the second. However, we cannot say whether it is sensory-specific or if rats are just no longer motivated to drink. The absence of a preference for the non-sated solution indicates either that rats cannot discriminate between the flavours, or that the lack of motivational drive prevents the expression of SSS. In any case, this first unsuccessful approach points out to some procedural changes that might be worth trying. First, it could be useful to limit the amount of liquid available in the satiation session. A limited amount (e.g. 10 ml) should be enough to cause SSS of a flavour, thus making the non-sated flavour preferred. Also, the ingestion of a smaller amount of liquid would prevent

other satiation mechanisms such as volumetric (based on guts mechanoreceptors) to interfere with further consumption (Powley & Phillips, 2004). Further, a strategy to ascertain whether the absence of effect has been caused for the inability of the rats to discriminate between the flavours would be to use pairs of solutions that are more easily discriminated. For example, Reichelt et al. (2014) used compounds of kool-aid flavouring and either sucrose or maltodextrin, which would give the solutions a distinctive and easily discriminable flavour. Thus, the comparison of a group exposed to solutions with or without an explicit common element could provide more hints as to what is necessary to obtain SSS. If satiety is not expressed because the compound flavours are too similar, perhaps more exposure is needed for this effect to emerge.

General discussion

The results described in this chapter provide a basis for further experiments on the issue of how changes in flavour perception could affect food intake.. Although more parametric refinement is needed, some conclusions can be safely drawn, and some speculation can be presented.

In Experiments 6-9, we (tried to) demonstrate perceptual learning using a flavour preference conditioning procedure. In Experiments 7 and 8 we found evidence of this effect, although the results were weak because of the low consumption of liquid during test. What we can interpret from this is that acquired preferences to one flavour generalize less to other similar flavours after intermixed exposure. In the introduction, we discussed some experiments that attempted to investigate ways of improving healthy food consumption in children (de Wild et al., 2015; de Wild et al., 2013). They found

that mere exposure appeared to be enough to increase such consumption, and that acquired preferences via associations with a palatable flavour or nutrients were irrelevant. However, their results might be the consequence of strong generalization to similar flavours caused by the scarce experience of infants with the food used (Birch et al., 1998). There is some evidence to suggest that older children might not generalize their acquired preferences to other similar foods (Sullivan & Birch, 1990). Our results support such an interpretation. Even though mere exposure was enough to increase consumption of an unpalatable novel taste (as observed with attenuation of neophobia during preexposure), we obtained evidence of a higher preference after pairing it with sucrose, and less discrimination can be taken to imply more generalization of the acquired preference to another similar flavour.

Furthermore, our results are a replication of the basic intermixed-blocked effect (e.g., Symonds & Hall, 1995) with a new procedure. This procedure can be potentially useful to investigate the mechanisms thought to underlie perceptual learning. For example, following Hall (2003, see Blair & Hall, 2003) one might argue that presenting an aversive flavour (Y) in compound with a previously exposed flavour (A) might reduce generalization from Y more after intermixed than after blocked exposure because A is more salient. Thus, such a result would be consistent with the idea that associative activation restores salience of the unique elements. However, it is also possible that associative activation acts by reducing the neophobic response to the unique element, so after blocked exposure there would be less attenuation of neophobia and thus we should expect less consumption of AY. Our results run counter to such a possibility. Increased generalization of a conditioned preference after blocked exposure

should be reflected in an increase in consumption, while reduced neophobic attenuation should cause a decrease in consumption.

In our Experiment 10, we were unable to observe any effect of the schedule of preexposure on SSS. As we mentioned earlier, it could be that rats were too sated for SSS to emerge, because they drank a great amount of liquid during the satiation session. It is also possible that the flavours were too difficult to discriminate. Our first step, then, should be to obtain the basic SSS effect using solutions that are sufficiently different (that is, with no explicit common element). After that, we could test whether adding an explicit common element abolishes the effect. We ran a pilot study in order to test this possibility. In this study we found SSS when there was no explicit common element, and no effect emerged when we added an explicit common element. Thus, we have grounds to assume that SSS with one flavour would generalize to other similar flavours. The next step would be to ascertain if experience with those similar flavours will reduce generalization of SSS, thus increasing consumption of the new flavour. Such interference with this intake inhibition mechanism could be responsible for excessive consumption of food, and could thus contribute to obesity.

Chapter V

Conclusions

Chapter V: Conclusions

Summary of new findings

Throughout Chapters II to IV we have presented several perceptual learning experiments. The main findings of these experiments can be summarized as follows:

1. We have demonstrated that the effect of additional exposure to the unique elements described by Lavis, Kadib, Mitchell and Hall (2011) was not caused by a better memory representation of those elements. Instead, it was dependent on the additional exposure signalling the location where the unique elements could be found (Experiments 1a and 1b). This result lends further support to the idea proposed by Jones and Dwyer (2013) that perceptual learning with visual stimuli might be mediated by a bias to focus on the location where differences were found.

2. In addition to this, we have also demonstrated that explicit instructions to look for differences between the stimuli seem to be necessary for perceptual learning to emerge with visual stimuli in humans (Experiments 2a and 2b). Following Mackintosh (2009), a possible explanation for this is that instructions allow for self-supervised learning. Thus, if participants are asked to look for differences, they will be self-reinforced when fulfilling their goal. It remains an open question if perceptual learning can be obtained without explicit instructions with more extended exposure under similar conditions.

3. A third finding is that we have obtained perceptual learning in animals using a rapid succession procedure with flavours (Experiment 4a), in contrast with previous results, and similar to what is found in humans. Thus, we found that the unique elements of a pair of compounds presented intermixed with a short inter-stimulus interval between them were more salient than after blocked exposure. Our procedure was similar to the serial exposure used by Bennett, Scahill, Griffiths, & Mackintosh (1999), but in our case the results cannot be explained by the formation of inhibitory associations.

4. Adapting the procedure used by Dwyer, Mundy and Honey (2011) in humans, we found that the placement of a distractor in a position that should disrupt comparison abolishes perceptual learning in rats (Experiments 4b and 5). This finding highlights the possibility that human and non-human animals share the same mechanisms of perceptual learning, and that differences previously seen as incompatible might have been caused by procedural differences.

5. Finally, we have replicated the basic intermixed-blocked effect with a flavour preference conditioning procedure (Experiments 7 and 8). Thus, we found that intermixed exposure to a pair of flavours reduced the generalization of an acquired preference from one of these flavours to the other. Restricted generalization based on experience with flavours could have applications in the promotion of healthy foods and the prevention of obesity.

Implications of the findings

Perceptual learning in humans

The results of perceptual learning in humans have been the subject of much scrutiny since the first demonstration of the intermixed-blocked effect (Lavis & Mitchell, 2006). It has been suggested that they were not an instance of perceptual learning (Mackintosh, 2009), or that the effect can be regarded as simply reflecting a strategic effect instead of an increase in discrimination (Jones & Dwyer, 2013). We have revealed further evidence of such claims in this thesis.

Unquestionably, the experimental paradigm usually employed in humans has certain characteristics that might hinder the study of perceptual learning based on mere exposure. First, all the visual stimuli used have discrete unique features that can be easily detected and isolated, thus making the task susceptible to being solved strategically. Second, all of the experiments that found the I/B effect used explicit instructions to look for differences. Hence, the demands of the task implied that participants were being self-reinforced on successfully achieving those demands. This would be a form of (self) supervised learning, and there is no need to assume a gradual relative increase in salience, or the formation of inhibitory links between the unique elements (Mackintosh, 2009). Once detection takes place, for whatever reason, the participant can simply continue to look at where the unique element was found. Such detection is more likely to be confirmed (and thus reinforced) with intermixed exposure, where there are many transitions that allow the participant to effectively see that the unique element is only appearing on half of the checkerboards. As a consequence of

this, results during the same-different test could reflect a process where the participant was reinforced to look at one location on the stimulus. This would clearly explain the superior discrimination of the stimuli presented in an intermixed manner, as well as the effects of additional exposure found by Lavis et al. (2011), because only those checkerboards were subjected to the reinforcement of the detection. In this sense, it would not be a form of perceptual learning.

It is worth noting that to explain the difference between intermixed and blocked exposure, even assuming the presence of reinforcement, we are turning to a process that we could call "comparison". When we talk about detecting differences, we are inevitably referring to the realization that a feature that is present in one given checkerboard is absent in other, which requires both representations to be active at the same time. For the unique element to be reinforced a comparison is needed between that checkerboard and the next, because it is necessary to perceive it as a difference, more than just process the feature. The presence of many transitions during intermixed exposure indeed offers multiple opportunities for reinforcement, but self-reinforcement necessarily comes from comparison. Furthermore, in the case of visual stimuli, the best cue to find a difference is the location. The fact that additional exposure to the unique elements eliminating location cues does not improve discrimination gives strength to this claim. Perhaps we were unable to find an I/B effect without explicit instructions because the lack of demand to look for differences is actually preventing this process to occur. It may be possible to argue that the effects of reinforcement cannot be disentangled from mere exposure to visual stimuli in humans. In any case, which mechanisms underlie this "comparison" remains an open question. An explanation in

terms of short-term habituation of the common elements that bias processing towards the distinctive elements, such as the one proposed by Honey and Bateson (1996) could fulfil this role. It could explain detection, and it would still allow discrimination to be based on reinforcement.

That is not to say that perceptual learning does not exist in humans with visual stimuli, although the criticisms that we have just raised might give that impression. But now that a number of methodological issues have been identified, it should be easier to devise alternative procedures to control them. Even though we have failed to obtain perceptual learning without explicit instructions (see also, Navarro, Arriola, & Alonso, 2016), perhaps more extended exposure or other procedural changes such as increasing stimulus duration could actually give results. Designing new stimuli with differences that cannot be easily isolated could also be a fruitful approach. In any case, we must understand that research with human participants has a number of confounding variables that are not present in the research with rats, and certain adaptations are needed in order to investigate the existence of general learning principles.

Comparison and perceptual learning in rats

As we have just seen, even in the human experiments where the I/B effect can be explained by self-reinforcement, we cannot neglect the notion of comparison. Clearly with rats we do not have problems such as the influence of the demands of the task on their behaviour. We are just assuming that animals are passively exposed to certain stimuli, and that this exposure has an effect on their perception. Thus, regardless of the presence or absence of differential reinforcement in humans, it was worth trying to find

evidence of a comparison-like process in rats. We implemented a manipulation that was showed to impair conditioning, the introduction of a distractor (Dwyer et al., 2011), on a rapid succession procedure. The results showed that the presence of the distractor in a way that interrupted comparison eliminated perceptual learning.

Our results on this topic have several implications. First, they cannot easily be explained in terms of the main associative models developed for perceptual learning. The proposal of Hall (2003) cannot be implemented in a procedure where associative activation is not predicted. The rapid succession means that by the time the second compound appears, the first unique element will still be active, and thus it is impossible for it to be associatively activated (Wagner, 1981). The inhibitory associations predicted by McLaren and Mackintosh (2000) could certainly occur in a serial procedure (Bennett et al., 1999), but, with the test we are using (conditioning a new flavour Y and testing AY) they are rendered inconsequential. However, it could be possible to adapt the concept of unitization to explain our results. Honey and Bateson (1996, see also, Dwyer et al., 2011; Mundy, Honey, & Dwyer, 2007) proposed that short-term habituation of the common elements would cause better processing of the unique elements during rapid intermixed exposure. This better processing would cause higher unitization of the unique elements, thus raising their effectiveness (that is, making them better encoded in memory and processed faster) relative to when they are presented in blocks. This combination of those two proposals could also explain the effects of placing a distractor. The distractor would disrupt short-term habituation of the common elements, thus allowing them to compete with the unique elements for processing and reducing their unitization.

On the other hand, better processing and more unitization are also expected to increase latent inhibition (Artigas, Contel, et al., 2012; Artigas & Prados, 2014). One way to reconcile the increased latent inhibition with higher effectiveness (as evaluated in an external inhibition test such as the one we are using) was put forward by McLaren and Mackintosh (2000). They suggested that, assuming that two stimuli are very similar, their unique elements will be inconsistently sampled (Atkinson & Estes, 1963). Unitization will increase their sampling rate because of intra-element associations, so when a unique element is presented more of its features will be active at the same time. Because of this, it will interfere more with the processing of any accompanying stimulus. Conversely, it can be argued that because the unique elements are more unitized (and thus better encoded in memory), they would require less processing resources and thus they should interfere less with the processing of the accompanying stimulus. Anyway, because they are better processed they can also be easily detected in spite of the presence of the aversive flavour, thus becoming an effective cue that would cause generalization decrement from the conditioning to the test phase.

The research we have presented here leaves many questions open. For example, the explanation we have proposed should be susceptible to order effects such as in Artigas et al. (2012), since only the second unique element of the series should receive better processing. Our experiments are not designed to test this, since we used a fully counterbalanced arrangement on each day. Another issue that is worth investigating is the concept of unitization, because to our knowledge there is no direct evidence of such a process. We have conducted some experiments using compounds where the unique

elements are a combination of two different flavours (e.g. APX and BQX), and we have obtained some promising results.

But more importantly, our results contribute towards closing the gap between animal and human research. It is not the first time that contradictory results between species have lead to the proposal of different parallel models for our species and others (Dawson & Furedy, 1976; Shanks, 1985). Those divergences indeed stimulate research, and usually they end up being explained by a common mechanism. In the case of perceptual learning, we think that associative theory already has the tools to explain the results found both with animals and humans.

Perceptual learning and preference

The results described in Chapter IV are preliminary, and thus no strong conclusions can be drawn from them. One first implication is that Experiments 7 and 8 are the first replications of the I/B effect using a flavour preference conditioning procedure. The effects are small because of limitations of the design; however, they are robust and we were able to replicate them with both a between groups and a within-subjects designs. Further work, however, will be needed to refine the procedure.

Another implication of our results is related to the generalization of preferences. In an attempt to find strategies to increase the consumption of healthy foods in children, some results have pointed to the possibility that mere exposure is sufficient to explain increased consumption and preference of different vegetable products (e.g., Bouhlal, Issanchou, Chabanet, & Nicklaus, 2014; de Wild, de Graaf, & Jager, 2015; de Wild, de Graaf, & Jager, 2013). However, there is a critical confound in many of those

experiments. Usually they expose infants to two vegetable products, one paired with nutritional consequences or a palatable flavour and the other alone, to compare the effects of conditioning and mere exposure. But they do not control for the generalization of preferences. Mere exposure is probably enough to increase acceptance to a certain degree based on habituation of neophobia. Nonetheless, the lack of differences in preference between paired and unpaired stimuli can be caused by a strong generalization between them because of the limited experience of infants with gustative stimuli (Birch et al., 1998). Our results support this hypothesis. In all our groups of rats we can see an increase in consumption of an unpalatable flavour due to exposure, but the acquired preference is less generalized with intermixed exposure, which promotes better discrimination. It remains to be seen whether this restricted generalization also affects sensory-specific satiety. Perceptual learning might have a role to play in explaining the "buffet effect" and the increased intake of junk food when there is exposure to a wide variety of such foods (Raynor & Epstein, 2001).

Final comments

The introduction of associative theory in perceptual learning is relatively recent (Hall, 1991; Honey et al., 1994; McLaren et al., 1989; Symonds & Hall, 1995), and there is still a long way ahead. New procedures need to be developed to control confounding variables in human research, to avoid the artificial creation of a gap between species. The existence of general learning principles is in no way incompatible with the reality of unique adaptations within each species, and it is up to researchers to be able to disentangle both. Also, more work is needed to find the boundary conditions

of the different theoretical accounts that have been developed. There may be multiple mechanisms behind perceptual learning, but in order to avoid unnecessary theory proliferation it is essential to find under what conditions each one is more likely to occur. Finally, to promote research on perceptual learning it is critical to find potential applications of our basic work. We have made a preliminary attempt to address how perceptual learning might affect preferences and intake behaviour, but there are many other areas where the ability to discriminate between stimuli is critical.

We hope that the experiments reported in this thesis make a solid, albeit humble, contribution to the perceptual learning literature and to associative theory.

Resumen de los resultados

A través de los Capítulos II a IV se han presentados varios resultados sobre aprendizaje perceptivo. Se va a presentar un resumen de los principales resultados obtenidos:

1. Se ha demostrado que el efecto de la exposición adicional a los elementos únicos descrita por Lavis et al. (2011) no estaba causada por una mejor representación en memoria de los elementos únicos. En lugar de eso, se encontró que dependía de que la exposición adicional señalara la localización en la que los elementos distintivos podían encontrarse en el estímulo (Experimentos 1a y 1b). Este resultado apoya la idea planteada por Jones y Dwyer (2013) de que el aprendizaje perceptivo con estímulos visuales podría estar mediado por un sesgo a centrarse en las localizaciones en las que se previamente se han encontrado diferencias.

2. Además de esto, también se ha demostrado que proporcionar instrucciones explícitas para buscar diferencias entre los estímulos es necesario para que se produzca aprendizaje perceptivo con estímulos visuales en humanos (Experimentos 2a y 2b). Siguiendo a Mackintosh (2009), una posible explicación de esto es que las instrucciones permiten que se produzca aprendizaje auto-supervisado. Así, si los participantes reciben indicaciones para buscar diferencias, recibirán auto-reforzamiento cuando consigan su meta. Queda abierta la pregunta de si es posible obtener aprendizaje

perceptivo sin instrucciones explícitas en condiciones similares incrementando la exposición.

3. Un tercer resultado es la obtención de aprendizaje perceptivo en animales usando un procedimiento de rápida sucesión con sabores (Experimento 4a), en contraste con otros resultados previos y en concordancia con lo encontrado en humanos. Así, se ha encontrado que los elementos únicos de un par de compuestos presentados intercalados con un intervalo entre estímulos corto eran más salientes que tras exposición en bloques. El procedimiento fue similar al utilizado por Bennett et al. (1999), pero en el presente caso los resultados no pueden ser explicados por la formación de asociaciones inhibitorias.

4. Adaptando el procedimiento empleado por Dwyer et al. (2011) en humanos, se ha encontrado que la colocación de un distractor en una posición que debería interrumpir la comparación eliminaba el aprendizaje perceptivo en ratas (Experimentos 4b y 5). Este resultado destaca la posibilidad de que los animales humanos y no humanos posean mecanismos comunes para explicar el aprendizaje perceptivo, y que es posible que los resultados previamente vistos como incompatibles hayan sido causados por diferencias procedimentales.

5. Por último, se ha replicado el efecto intercalado-bloque con un procedimiento de preferencia condicionada al sabor (Experimentos 7 y 8). Se ha encontrado que la exposición intercalada a un par de compuestos de

sabores reduce la generalización de una preferencia adquirida por uno de ellos al otro. Esta restricción de la generalización basada en la experiencia previa con sabores podría tener aplicaciones en intervenciones para promocionar la comida saludable o para prevenir la obesidad.

Implicaciones de los resultados

Aprendizaje perceptivo en humanos

Los resultados de aprendizaje perceptivo en humanos han recibido muchas críticas desde la primera demostración del efecto intercalado-bloques (Lavis & Mitchell, 2006). Se ha sugerido que no son un auténtico ejemplo de aprendizaje perceptivo (Mackintosh, 2009), o que son producto que una decisión estratégica en lugar de un incremento en discriminación (Jones & Dwyer, 2013). En esta tesis hemos mostrado evidencia adicional que apoya estas afirmaciones.

Indudablemente, el paradigma experimental utilizado en humanos tiene ciertas características que podrían estar dificultando el estudio del aprendizaje basado en mera exposición. En primer lugar, los estímulos visuales utilizados poseen diferencias discretas que pueden ser fácilmente detectadas y aisladas, haciendo a la tarea susceptible de ser resuelta estratégicamente. En segundo lugar, todos los experimentos que han encontrado el efecto I/B han utilizado instrucciones explícitas para buscar diferencias. Por tanto, las demandas de la tarea implicaban que los participantes estaban siendo autorreforzados al alcanzar éstas con éxito. Esto sería una forma de aprendizaje (auto) supervisado, y no habría necesidad de asumir un aumento gradual de saliencia o la formación de conexiones inhibitorias entre elementos únicos (Mackintosh, 2009).

Una vez que la detección tiene lugar por la razón que sea, el participante puede limitarse a seguir mirando al lugar donde encontró la diferencia. Dicha detección es más probable que se confirme (y por tanto que se refuerce) con exposición intercalada, donde hay múltiples transiciones que permiten al participante ver que el elemento único sólo está presente en la mitad de los estímulos. Por ello, los resultados encontrados en una tarea igual-diferente estarían reflejando un proceso por el cual el participante fue reforzado por mirar a determinada localización del estímulo. Esto explicaría de forma trivial la discriminación superior encontrada cuando los estímulos se presentan intercalados, así como el efecto de la exposición adicional encontrado por Lavis et al. (2011), ya que sólo esos estímulos estarían sujetos a reforzamiento de la detección. En este sentido, no sería una forma de aprendizaje perceptivo.

Merece la pena comentar que para explicar la diferencia entre exposición intercalada y en bloques, incluso asumiendo la presencia de reforzamiento, estamos recurriendo a un proceso que podríamos denominar "comparación". Cuando decimos que se detectan diferencias, nos estamos refiriendo inevitablemente a que el participante se da cuenta de que un elemento está presente en un estímulo y ausente en otro, lo cual requiere que las representaciones de ambos estén activas a la vez. Para que se refuerce un elemento único se necesita una comparación entre ese estímulo y el siguiente, porque es necesario que se perciba como una diferencia, no sólo que se procese. La presencia de múltiples transiciones durante la exposición intercalada proporciona múltiples oportunidades para reforzamiento, pero éste depende en última instancia de que haya comparación. Además, en el caso de estímulos visuales, la clave más adecuada para localizar una diferencia es la localización. El hecho de que la exposición adicional a los

elementos únicos eliminando las claves de localización no mejore la discriminación apoya esta idea. Quizás no se ha encontrado el efecto I/B sin instrucciones explícitas porque el hecho de no pedir que se busquen diferencias hace que no haya comparación. Quizás no se pueden separar los efectos de la comparación del reforzamiento con estímulos visuales en humanos. En cualquier caso, queda abierta la pregunta de qué mecanismos están detrás de esa "comparación". Una explicación en términos de habituación a corto plazo del elemento común que sesgara el procesamiento hacia los elementos únicos, como la propuesta por Honey y Bateson (1996) podría cumplir este rol. Explicaría la detección, y es compatible con la idea de que la discriminación depende del reforzamiento.

Esto no equivale a decir que no existe el aprendizaje perceptivo en humanos con estímulos visuales, aunque las críticas que acabamos de detallar podrían dar esa impresión. Sin embargo, ahora que se han identificado ciertos problemas metodológicos, debería ser más sencillo diseñar procedimientos alternativos para controlarlos. Aunque no hayamos encontrado aprendizaje perceptivo sin instrucciones (ver también, Navarro, Arriola, & Alonso, 2016), tal vez una exposición más prolongada u otros cambios paramétricos como el incremento en la duración de los estímulos podrían proporcionar resultados. Diseñar estímulos nuevos donde las diferencias no puedan ser aisladas podría ser también útil. En todo caso, es necesario entender que la investigación con humanos siempre incluye ciertas variables extrañas que no están presentes en ratas, y es necesario adaptar los procedimientos para investigar la existencia de principios generales de aprendizaje.

Comparación y aprendizaje perceptivo en ratas

Como acabamos de ver, aunque el efecto I/B en humanos pueda ser explicado por auto-reforzamiento, no podemos dejar de lado la idea de comparación. Evidentemente con ratas no existen problemas como la influencia de las demandas de la tarea en la conducta. Simplemente asumimos que los animales se exponen pasivamente a ciertos estímulos, y que esta exposición tiene un efecto en su percepción. Así, independientemente de la presencia o ausencia de reforzamiento diferencial en humanos, merecía la pena tratar de encontrar evidencia de comparación en ratas. Para ello, implementamos una manipulación que ha demostrado interrumpir la comparación en humanos, la introducción de un distractor (Dwyer et al., 2011) en un procedimiento de rápida sucesión. Los resultados mostraron que la presencia de un distractor en una posición en la que interrumpía la comparación eliminaba el aprendizaje perceptivo.

Nuestros resultados sobre este tema tienen varias implicaciones. En primer lugar, no pueden ser fácilmente explicados por los principales modelos asociativos desarrollados específicamente para el aprendizaje perceptivo. La propuesta de Hall (2003) no puede ser implementada en un procedimiento donde no se produce activación asociativa. La rápida sucesión implica que cuando aparece el segundo compuesto, los elementos únicos del primero todavía estarán activos, y por lo tanto no podrán ser activados asociativamente (Wagner, 1981). Las asociaciones inhibitorias predichas por McLaren y Mackintosh (2000) podrían ciertamente producirse con un procedimiento serial (Bennett et al., 1999); pero, con el test que utilizamos (condicionar un sabor nuevo Y y probar AY) no deberían tener ningún efecto. Sin embargo, sí sería posible

adaptar el concepto de unitización para explicar nuestros resultados. Honey y Bateson (1996, ver también, Dwyer et al., 2011; Mundy, Honey, & Dwyer, 2007) propusieron que la habituación a corto plazo de los elementos comunes causaría mejor procesamiento de los elementos únicos durante un procedimiento intercalado de rápida sucesión. Este mejor procesamiento causaría mayor unitización de los elementos únicos, por tanto incrementando su efectividad (esto es, mejorando su codificación en memoria y permitiendo un procesamiento más veloz) en comparación con cuando se presentan en bloques. La combinación de estas dos propuestas podría explicar también los efectos de introducir un distractor. Éste interrumpiría la habituación a corto plazo de los elementos comunes, permitiéndoles competir con los elementos únicos por los recursos de procesamiento y reduciendo su unitización.

Por otro lado, mejor procesamiento y mayor unitización también se espera que produzcan mayor inhibición latente (Artigas, Contel, et al., 2012; Artigas & Prados, 2014). Una forma de reconciliar esta mayor inhibición latente con una mayor efectividad (evaluada en un test de inhibición externa como el que utilizamos) fue propuesta por McLaren y Mackintosh (2000). Éstos sugirieron que, asumiendo que dos estímulos son muy similares, sus elementos únicos serán muestreados de forma inconsistente (Atkinson & Estes, 1963). La unitización incrementará el muestreo a causa de las asociaciones intra-elemento, de forma que cuando un elemento único es presentado se activarán un mayor número de sus características constituyentes al mismo tiempo. A causa de esto, interferirá más con el procesamiento de cualquier estímulo al que acompañe. En contraste con esto, podría argumentarse que debido a que el elemento único está más unitizado (y por tanto mejor codificado en la memoria) requerirá menos

recursos de procesamiento y por tanto debería interferir menos con el procesamiento del estímulo al que acompaña. De todas formas, por ser procesado más fácilmente también puede ser mejor detectado a pesar de la presencia del sabor aversivo, convirtiéndose en una clave efectiva que causaría decremento de la generalización del condicionamiento al test.

La investigación que acabamos de presentar aquí deja muchas preguntas abiertas. Por ejemplo, la explicación que hemos propuesto debería ser susceptible de efectos de orden como en Artigas et al. (2012), porque sólo el segundo elemento único de la serie debería tener un mejor procesamiento. Nuestros experimentos no están diseñados para comprobar esto, ya que usamos un contrabalanceo diario. Otro tema que merece la pena investigar es el concepto mismo de unitización, porque hasta donde sabemos no existe evidencia directa de que exista tal proceso. En nuestro laboratorio hemos realizado algunos experimentos utilizando compuestos donde los elementos únicos son combinaciones de dos sabores (p. ej. APX y BQX), y hemos encontrado algunos resultados prometedores.

Lo más importante, sin embargo, es que nuestros resultados contribuyen a cerrar la brecha entre investigación animal y humana. No es la primera vez que resultados contradictorios entre especies llevan a proponer modelos diferentes (Dawson & Furedy, 1976; Shanks, 1985). Esas divergencias sin duda estimulan la investigación, y habitualmente terminan siendo explicadas por un mecanismo común. En el caso del aprendizaje perceptivo, creemos que la teoría asociativa ya posee herramientas para explicar tanto los resultados encontrados en animales tanto humanos como no humanos.

Aprendizaje perceptivo y preferencia

Los resultados descritos en el Capítulo IV son provisionales, por lo que no se pueden extraer conclusiones sólidas. Una primera implicación es que los Experimentos 7 y 8 son la primera replicación del efecto I/B usando un procedimiento de preferencia condicionada al sabor. Los efectos son pequeños por limitaciones del diseño, aunque son robustos y hemos sido capaces de replicarlos tanto con un diseño intrasujeto como con otro entre grupos. Aún así, es necesario más trabajo para refinar el procedimiento.

Otra implicación de nuestros resultados está relacionada con la generalización de preferencias. En un intento de encontrar estrategias para incrementar el consumo de comidas saludables en niños, algunos resultados han apuntado que la mera exposición es suficiente para explicar el mayor consumo y preferencia de diversos productos vegetales (p. ej., Bouhlal et al., 2014; de Wild et al., 2015; de Wild et al., 2013). Sin embargo, hay una malinterpretación crítica en esos experimentos. Por lo general se expone a niños a dos productos vegetales, uno de ellos emparejado con consecuencias nutricionales o un sabor palatable y el otro sin ello, para comparar los efectos del condicionamiento con los de la mera exposición. Pero estos estudios no controlan la generalización de preferencias. La mera exposición es probablemente suficiente para incrementar la aceptación hasta cierto punto, a causa de la habituación de la neofobia. No obstante, la ausencia de diferencias en preferencia entre el estímulo emparejado y el desemparejado puede estar causada por una fuerte generalización entre ellos debida a la limitada experiencia de los niños pequeños con estímulos gustativos (Birch et al., 1998). Nuestros resultados apoyan esta hipótesis. En todos nuestros grupos de ratas se observó

un incremento en consumo de un sabor no palatable a causa de la mera exposición, pero la preferencia adquirida posteriormente se generaliza menos tras exposición intercalada que produce una mejor discriminación. Falta por demostrar si esta restricción de la generalización también afecta a la saciedad sensorial específica. El aprendizaje perceptivo puede ser un mecanismo que contribuya a explicar el "efecto buffet" y el incremento en el consumo de comida basura cuando existe exposición a una gran variedad de la misma (Raynor & Epstein, 2001).

Comentarios finales

La introducción de la teoría asociativa en el aprendizaje perceptivo es relativamente reciente (Hall, 1991; Honey et al., 1994; McLaren et al., 1989; Symonds & Hall, 1995), y todavía queda un largo camino por delante. Es necesario desarrollar nuevos procedimientos para controlar variables extrañas en la experimentación con humanos, para evitar la creación artificial de brechas entre especies. La existencia de principios generales de aprendizaje no es incompatible con el hecho de que existan adaptaciones únicas en cada especie, y depende de cada investigador buscar la forma de separar ambas cosas. También es necesario más trabajo para encontrar las condiciones bajo las cuales serán más probables los diferentes modelos teóricos que se han desarrollado. Es posible que haya múltiples mecanismos detrás del aprendizaje perceptivo, pero para evitar la multiplicación innecesaria de teorías es esencial definir bajo qué condiciones ocurrirá cada uno. Por último, para promover la investigación en aprendizaje perceptivo es crítico encontrar potenciales aplicaciones para el trabajo básico. Nosotros hemos hecho una primera aproximación a cómo el aprendizaje

perceptivo puede afectar a las preferencias y a la conducta de ingesta, pero hay muchas otras áreas donde la habilidad para discriminar entre estímulos es crítica.

Esperamos que los experimentos referidos en esta tesis constituyan una contribución duradera, aunque humilde, al estudio del aprendizaje perceptivo y de la teoría asociativa.

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