Investigating Perceptual Learning with Textured Stimuli in Rats

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DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is being submitted concurrently in candidature for any degree or other award.

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Acknowledgements

To sufficiently recognise all those who have contributed in some small part to this final work would be a task almost as herculean as this thesis, or maybe that's an overstatement that people use to avoid having to actually do it. That said, the signing of the required declaration feels in some ways to be dishonest, given that in light of their contributions this work is the result of many peoples' efforts alongside my own. To say that these past 4 years have been the most difficult of my life would not be an exaggeration, and the personal challenges alone have provided more learning material than the content of the research degree could entail. I am grateful to all who have been involved in this journey, both your professional contributions and how you've provided me with the opportunity for extensive personal growth.

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"You must understand the whole of life, not just one little part of it. That is why you must read, that is why you must look at the skies, that is why you must sing and dance, and write poems and suffer and understand, for all that is life." - Jiddu Krishnamurti

Publications

Some of the research and ideas presented in Chapters 2 and 3 have previously been presented at conferences and are described in two recent papers. Experiments presented in Chapter 2 have been described in depth in a recently submitted paper by Montuori and Honey (2015), and the ideas presented in Chapters 1 and 2 contributed to a previously published publication by Montuori and Honey (2015).

Conference presentations:

- Montuori, L. M., & Honey, R. C. (2014, April). Perceptual learning with textured stimuli in rats. Paper presented at the Gregynog Associative Learning Symposium, Wales, United Kingdom.

- Montuori, L. M., & Honey, R. C. (2013, September). Perceptual learning with textures in rats. Paper presented at the International Congress of the Spanish Society for Comparative Psychology, Donostia-San Sebastian, Spain

Peer-reviewed papers:

- Montuori, L.M., & Honey, R.C. (2015). Representation in development: From a model system to some general processes. *Neuroscience and Biobehavioral Reviews, 50,* 143-149.

- Montuori, L.M., & Honey, R.C. (in press). Perceptual learning with tactile stimuli in rats: Changes in the processing of a dimension. *Journal of Experimental Psychology: Animal Learning and Cognition*

Summary

In this thesis I present a series of experiments that aimed to examine the effect of experience on the subsequent discriminability of similar stimuli. It has oft been observed that preexposure to stimuli enhances the rate at which a discrimination with similar stimuli will progress, or will reduce the amount of generalisation that occurs to similar stimuli following training. In animals, this effect has typically been studied using the conditioned taste aversion paradigm. Here, I describe a novel experimental method whereby animals learn to discriminate between textured stimuli, and do so differentially based on their previous experience with textures. In Chapter 2, the basic perceptual learning effect is found using this novel experimental method, along with some novel findings. In Chapter 3 I sought to extend the use of this method to the investigation of preexposure schedule, which has been observed affect perceptual learning. This effect was not found using textures. In Chapter 4 I replicated a basic finding from chapter 2, that preexposure to a midpoint stimulus facilitated the discriminability of stimuli that lay on either side of that stimulus on a texture continuum. Chapter 4 also featured an observation that changing the context in between preexposure and discrimination training has an effect on behaviour (although not the extent to which a perceptual learning effect may be observed). These experiments are first demonstrations that perceptual learning can be reliably studied using textured stimuli in rats. Given there is a growing body of literature dedicated to investigating the way in which texture information is encoded using the rat's whisker system, this experimental method provides a unique opportunity to combine theoretical accounts of behaviour with the biological underpinnings of sensory perception.

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"All our knowledge has its origin in our perceptions."

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Chapter 1: Introduction

1. Adapting to a changing environment

Upon entering the world an organism is faced with a set of challenges and pressures to which it must be able to respond appropriately in order to survive. Very crudely, the organism must be capable of identifying and avoiding threats to its existence in the form of predators or general environmental dangers, and must also be able to satisfy its own biological needs, and respond to homeostatic pressures by seeking out resources or favourable environmental conditions. These demands must be met in an environment that may not necessarily be consistent, where the contingencies between events are not necessarily static, and must be discerned in the presence of potentially irrelevant stimuli or events. What seems like an insurmountable task is mitigated by the organism's access to a variety of sources of information that can be used to maximise its chances of survival. This information is made available to the organism via multiple channels, and biological adaptations that provide different organisms with the capacity to process different, and differentially relevant, types of information. However, across different organisms, the information that is available can be grouped into conceptually distinct categories.

1.1. The nature of the available information

The first type of information is external to the organism; it relates to the state of the world, the presence or absence of objects or stimuli, and the qualities that these objects in the world possess. The way in which this information is coded, as objects or qualities, is constrained by the differential sensory capabilities of the organism in question: its sensory systems translate physical stimuli that exist in the world into biological signals which can then be processed by the organism. In addition to perceiving physical stimuli in the world, it is also necessary for an organism to be able to monitor its own internal biological state. This internal information provides the organism with an indication of its biological needs, and whether or not it needs to seek out stimuli, environments, or resources that will assist in the maintenance of an appropriate level of homeostatic functioning. Notwithstanding the biological complexity involved in translating physical stimuli into biological signals, these two forms of information may be considered 'basic' when compared to the third source of information; that provided by the organism's experience with the world. At one extreme, the tendency to direct behaviour in a way that has proved to be effective in the past (avoiding dangerous stimuli or identifying resources), at the other, the ability to compare the current state of the world with previously experienced states of the world and identify the stimuli that are relevant to the organism's motivations. It is critical for survival that an organism not only perceive its external and internal states, but to be able to *behave* appropriately given the circumstances, and *adapt* to changes in the importance or relevance of the stimuli present.

1.2. Learning about contingencies in the world

A major and recurring theme in the philosophical and scientific tradition over the past (few hundred years) is the relative importance of these different sources of information. One view, expressed by philosophers such as Locke, posits that organisms, and in this case specifically, humans, are born as 'blank slates', and the sum of their tendencies, dispositions and behaviours can be reduced to their experiences. The alternative view, that organisms enter the world ready to respond to it, requires a certain consistency in the environment that is unlikely in anything but the most simple of ecological niches. Of course, environments change and do so in ways that organisms need to adapt to. These adaptations require plasticity in the systems that respond to the environment even in organisms that, quite literally, hit the ground running (Lorenz, 1937).

1.2.1. The scientific study of animal learning

Early attempts to study the interactions between the sources of information identified above, and the way in which various bits of information are processed and retained, focused on the self-reported experience of individuals (e.g., James, 1890). However, introspective analysis was largely abandoned within psychology and replaced with a focus on observable behaviour and the conditions that changed it. Two specific traditions developed that focused on how different environmental contingencies affect animal behaviour: those that were independent of the organism and involved relationships between external events (Pavlov, 1927) and those directly relating to the organism's behaviour (Thorndike, 1898). The study of Pavlovian conditioning and instrumental conditioning have dominated the scientific analysis of non-human animal learning, and generated powerful formal theories of learning (e.g., Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) that are based

on simple overarching assumption: behavioural adaptation has its origins in the development of associations.

1.2.2. Conditioning as associative learning

An association can be described as a mental link that allows activation of one representational entity to excite activity in another. While the nature of the entities that become linked in Pavlovian and instrumental conditioning has been the subject of extensive investigation, the idea that changes in behaviour reflect changes in the associative connections has not been seriously challenged (see Mackintosh, 1974, 1983). In Pavlovian conditioning there is evidence that the entities are memories of the conditioned stimulus (CS; e.g., a bell chiming) and unconditioned stimulus or reinforcer (US; e.g., the delivery of food; e.g., Holland & Straub, 1979); whereas in instrumental conditioning one relevant association is between the response (R; e.g., a lever press) and the reinforcer, or outcome of that response (O; e.g., food; for reviews, see Dickinson, 1980, 1985). Associative accounts of animal learning have proven explanatory power, especially when the idea that experience can result in the formation of excitatory associations is combined with the complimentary idea that inhibitory associations can be acquired: associations that allow one entity to reduce the likelihood that another entity will become active (see, for example, Rescorla & Wagner, 1972; see also, Konorski, 1967). It must be acknowledged, however, that the appealing simplicity of such models begins to break down under certain conditions. For example, it breaks down when the representation of patterns of stimulation can no longer be considered to be the sum of their parts, as in case of negative patterning and other configural discriminations. In such cases, the simplifying assumption that the components or elements of a pattern of stimulation and the information presented to the sensory channels

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find a one-to-one correspondence in the memories of these patterns has been modified, if not abandoned (see Wagner, 2003; see also Pearce, 1994, 2002). There is another class of phenomena that has represented an ongoing challenge to associative accounts of learning and represents the focus of interest in this thesis: perceptual learning.

1.3. Learning and perception

Perhaps the most significant challenge to the view that there is some simple correspondence between information in the external world and the representation of that information within the organism, is prompted by demonstrations of perceptual learning of the type first described by Gibson and Walk (1956). Gibson and Walk (1956) demonstrated that rats given simple exposure to stimuli acquired a reinforced discrimination between them more readily than rats who encountered the stimuli for the first time at the outset of discrimination training. This perceptual learning effect was observed in young rats given protracted exposure to geometric shapes in their home cages before learning to approach one stimulus rather than another to gain access to food. However, it transpired that none of these specific features of the experiment was critical to observing perceptual learning: The effect occurs in mature animals and a variety of species (for reviews, see Hall, 1991; Mitchell & Hall, 2014). Such demonstrations suggest that the way in which perceptual information is represented is, at least in part, shaped by previous experience. Furthermore, they beg the question, how does experience alter the way in which perceptual information is gathered, or processed, and subsequently shape the representations of stimuli?

1.3.1. An early associative perspective

William James (1890, pp. 508-515) devoted considerable space of his monograph, *The Principles of Psychology*, to evaluating how individuals might come to be experts in various

sensory domains, and how repetition, or practise, might change the way in which people perceive particular stimuli. Taking the fact that repeatedly sampling different varieties of wine allows people to better tell them apart, James presented an explanation that we now know as the *acquired distinctiveness of cues*. His description and the associative analysis that he proposed has foreshadowed both research and theoretical analysis:

"To illustrate, how does one learn to distinguish claret from burgundy? Probably they have been drunk on different occasions. When we first drank claret we heard it called by that name, we were eating such and such a dinner, etc. Next time we drink it, a dim reminder of all those things chimes through us as we get the taste of the wine. When we try burgundy our first impression is that it is a kind of claret; but something falls short of full identification, and presently we hear it called burgundy. During the next few experiences, the discrimination may still be uncertain -- "which," we ask ourselves, "of the two wines is this present specimen?" But at last the claret-flavor recalls pretty distinctly its own name, 'claret,' "that wine I drank at So-and-so's table," etc.; and the burgundy-flavor recalls the name burgundy and someone else's table. "

One class of observation has provided support for such an associative analysis (e.g., Honey & Hall, 1989; Hall, 1996) or variants of this analysis (e.g., Honey & Watt, 1998). Thus when two stimuli (A and B) have signalled different outcomes (e.g., food and no food, respectively; e.g., Honey & Hall, 1989) or accompanied different relationships (X➔food and Y➔no food, respectively; e.g., Honey & Watt, 1998) generalization between them is reduced relative the situation where both stimuli signal the same outcome or accompany the same relationship (for a review, see Honey, Close & Lin, 2014). However, Gibson and Walk's (1956) results represent a challenge to such an associative analysis. In their study,

simple exposure to two difficult to discriminate stimuli increased the ease with which they were discriminated, but under conditions in which it seems highly unlikely that the two stimuli would have become linked with different associates. Rather, given the nature of their study and the way in which exposure was carried out, stimuli would have been more likely to be associated with one another and subsequently less discriminable from one another. Indeed James (1890, p. 513) seems to have recognized this in describing the case where exposure to two compass points "practice refines our local discrimination on the skin".

The question these observations prompt is: How does simple exposure to two stimuli increase the ease with which a later discrimination is acquired between them? Two consistent findings seem to be especially relevant to answering this question. One involves the similarity of the to-be-discriminated stimuli and the second involves the schedule according to which the stimuli are exposed. In the selective review that follows, and the new research reported in Chapters 2 and 3, I focus on research from nonhuman animals because in such species one can be certain the various strategic influences that might come into play in people are unlikely to confound interpretation of the results (see Mitchell & Hall, 2014). However, where important parallels have been established they are reported.

1.3.2. Perceptual learning: Some consistent findings

Whether guided by intuition or detailed introspective analysis (James, 1890), one might have anticipated that any beneficial effect of preexposure to the to-be-discriminated stimuli should be most evident when those stimuli would otherwise have proven difficult to discriminate to start with. Not only is such an analysis borne out in the data (Mackintosh, Kaye & Bennett, 1991; Oswalt, 1972; see also Honey *et al*., 1994), but when the to-be-

discriminated stimuli are very easy to discriminate, prior exposure can even hinder later discrimination learning. This interaction between the nature of the exposed stimuli and later discrimination learning shows that perceptual learning does not simply reflect the fact that prior exposure means that representations of the critical stimuli are available at the outset of discrimination testing – otherwise prior exposure to the stimuli should always help later discrimination learning. The fact that preexposure can retard discrimination learning has been allied to the finding that exposure to a single stimulus most often retards the rate at which learning about that stimulus proceeds; an effect known as latent inhibition (Lubow & Moore, 1959; Honey & Hall, 1989). Somewhat paradoxically, it has been argued that this effect could also provide one basis for perceptual learning. For example, exposure to similar stimuli (to use the conventional notation, AX and BX), as represented in figure 1 below, will result in their shared or common elements (X) being encountered twice as frequently as the unique elements (A and B); and this might result in these common elements being learnt about less readily than the unique elements (see Honey & Hall, 1989; see also, McLaren, Kaye & Mackintosh, 1989). Thus differential latent inhibition to the common and unique elements might facilitate discrimination learning (or reduce generalization between them).

I will have cause to return to this simple explanation in the context of experiments reported in Chapters 2 and 3. However, the fact that this simple explanation of perceptual learning will not suffice is evident from the dramatic influence that the schedule of preexposure has on later discrimination learning.
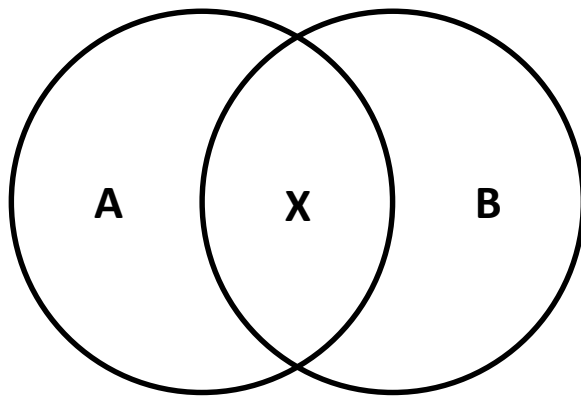
Figure 1. *A representation of the relationship between the sets of elements activated by two similar stimuli, with A and B denoting the elements uniquely activated by two stimuli and X their shared or common elements.*

This is evidenced by observations that alternating or intermixed exposure to two similar stimuli (i.e., AX, BX, AX, BX, AX, BX….) is a much more effective means of generating the perceptual learning effect than the equivalent amount of exposure to the stimuli, but in blocks (AX, AX, AX,….BX, BX, BX….). Clearly, these two schedules equate the amount of presentations of AX and BX. As a result, an explanation based upon differential latent inhibition to the common and unique elements is not well placed to explain the fact that the schedules have a markedly different influence on later discrimination learning (and, as we shall see, other assays of discriminability; but see, for further discussion McLaren, Forrest & McLaren, 2012). I will focus here on this latter finding, because it has generated the most theoretical heat.

In the first demonstration of the impact of the schedule of exposure on perceptual learning, chicks received two days of training (Honey *et al*., 1994). On the first day, they received two exposure sessions, and on the second they were given a heat-reinforced discrimination. During the exposure sessions, chicks received presentations of two geometric figures (e.g., a circle and a triangle that were both purple; AX and BX). For the intermixed group (see figure

2 for an illustration of the schedule of exposure), both sessions contained presentations of the two figures that occurred within seconds of one another in a pseudo-random sequence (AX, BX, BX, AX, BX, AX...); whereas in the blocked group all of the presentations of one

i. AX BX AX BX

ii. AX AX BX BX
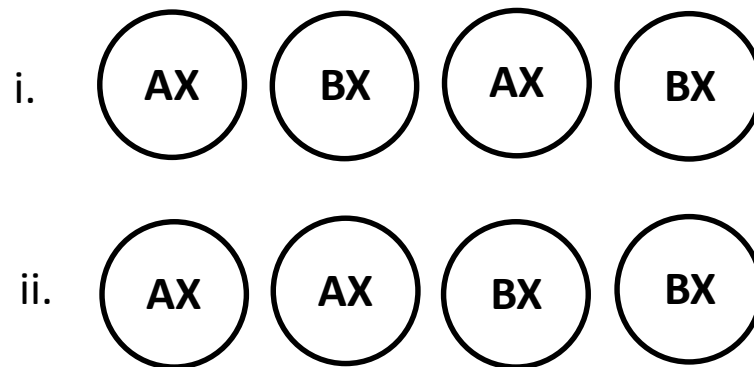
Figure 2. *Sequence i. shows an intermixed or alternating sequence of two similar stimuli and sequences ii a blocked sequence of the same stimuli.*

figure occurred in one session (i.e., AX, AX, AX,...) and all those of the other occurred in the other session (i.e., BX, BX, BX,...). Chicks that had received intermixed exposure to these similar stimuli acquired the reinforced discrimination more rapidly than those in the blocked condition.

Instances of this scheduling effect have been found in flavour-aversion procedures in rats using compounds constructed from various flavours (e.g., Symonds & Hall, 1995; see also, Balleine, Espinet & González, 2005, Blair & Hall, 2003), and with auditory stimuli in an appetitive-conditioning procedure (Mondragón & Murphy, 2010). Also, analogous effects have also been observed using a variety of stimuli and procedures with humans. For example, in humans the influence of schedule of preexposure has been demonstrated in flavor- and odor-aversion procedures (Dwyer, Hodder & Honey, 2004; Mundy, Dwyer & Honey, 2006); when the stimuli are more or less arbitrary familiar patterns and the participants' task at test was to identify whether successively presented images are the same or different (Dwyer, Mundy & Honey, 2011; Mitchell, Nash, & Hall, 2008; Mundy,

Downing, Dwyer, Honey, & Graham, 2013; Mundy, Honey, Downing, Wise, Graham, &

Dwyer, 2009); and when participants were required to learn to categorize familiar faces of

virtual twins as 'married' or 'unmarried' (Mundy, Honey & Dwyer, 2007, 2009). These

scheduling effects can be modulated by the ease with which the stimuli are discriminated:

as the stimuli become easier to discriminate so the advantage of having being given

intermixed exposure becomes less evident (Honey *et al*., 1994; see also, Mundy *et al*., 2007;

but see, Symonds & Hall, 1995).
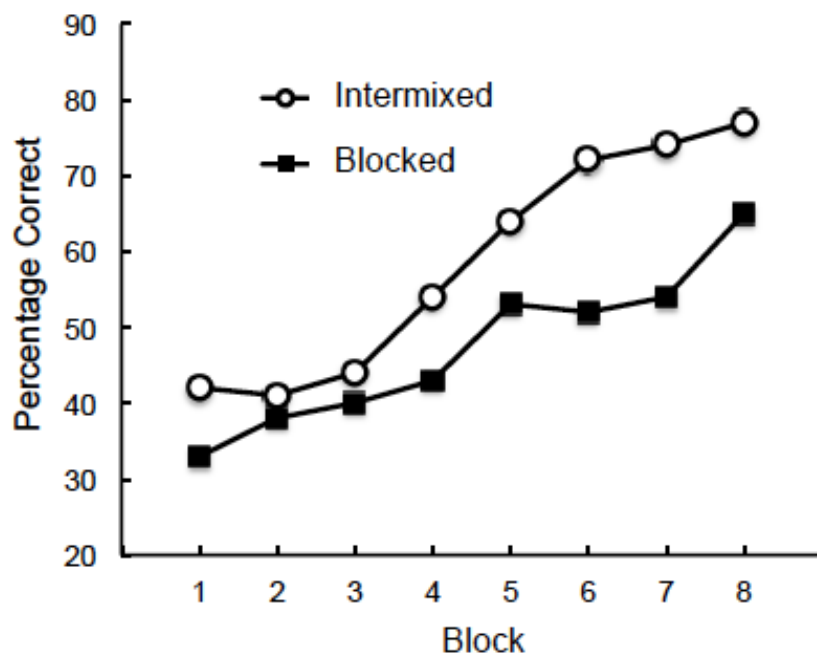
Figure 3. *A perceptual learning effect in an imprinting procedure. Mean percentage correct during a heat-reinforced simultaneous discrimination. During imprinting training, chicks either received presentations of two imprinting stimuli that were inter intermixed (AX, BX, BX, AX, BX, AX…) within two sessions, or presentations of one stimulus in one session and of the other stimulus in the second session (i.e., blocked: AX, AX, AX, …BX, BX, BX…). All chicks then received a simultaneous discrimination in which approaching one stimulus was reinforced by the delivery of a stream of warm air and approaching the other was not. [Adapted from: Montuori, L.M., & Honey, R.C. (2015). Representation in development: From a model system to some general processes.* Neuroscience and Biobehavioral Reviews, 50, *143-149.]*

1.3.3. Theoretical analyses of perceptual learning in animals

In James's (1890) initial description of perceptual learning, improvements in discriminative behaviour were attributed to association processes. According to James, exposure to a stimulus results in that stimulus becoming associated with stimuli encountered in its presence. During discriminative tasks, each stimulus is made distinct by virtue of its unique network of associations. James's account however was developed in order to explain how associative processes might, through training, enhance discrimination. In contrast, Gibson (1969) put forward an account of perceptual learning that was based on changes in attentional processes that occur as a result of passive exposure to stimuli. According to Gibson, preexposure to stimuli results in a process referred to as differentiation, whereby exposure results in an organism differentiating between invariant and variant features of a stimulus, and subsequently responding to stimulus features that did not previously hold the ability to direct responding. While this view of perceptual learning is able to explain effects such as those reported by Gibson and Walk (1956), there is little theoretical development of the precise mechanisms recruited during preexposure.

In contrast to Gibson's differentiation theory, McLaren, Kaye and Mackintosh (1989), put forward an account of perceptual learning that relies on associative processes that occur during exposure. In this case, three distinct mechanisms are identified that contribute to improved discrimination following preexposure. McLaren et al. take the view that stimuli can be characterised as consisting of populations of elements (some of which are unique to a particular stimulus, and some of which are shared, or common to similar stimuli), and that perceptual learning results from variations in the way in which these elements are able to elicit activity upon presentation. This view of perceptual learning takes from the observation

by Lubow (1959), that preexposure to a stimulus reduces its conditionability (latent inhibition). Adapting this to their theory of perceptual learning, McLaren et al. suggest that preexposure to two stimuli results in comparatively more latent inhibition to the common elements than to the unique elements. Accordingly, during discrimination training (or generalisation tests; Mackintosh, Kaye, & Bennett, 1989), the unique elements are more able to support conditioning than the common elements. In addition to latent inhibition, McLaren et al. suggest that preexposure encourages the formation of associations between the common and unique elements (x, and a or b) that make up each stimulus; and in particular among the sets of (unique) elements that always co-occur (unitisation). As a result of this process, responses established to a unique element that happens to be sampled on a given trial (a1) will also be evident when another unique element (a2) is sampled on a different trial. Finally, McLaren et al. suggest that the unique elements of one stimulus will enter into inhibitory associations with the unique elements of the other stimulus. This will occur to the extent that the a-x association formed on an A trial, for example, will enable a to be activated on a B trial by dint of the presence of x. This mechanism in particular helps in explaining how it is the aforementioned scheduling effects come to enhance perceptual learning, which I will come to shortly.

A further explanation for perceptual learning is provided by Hall (2003). Hall suggests that exposure to a stimulus will produce a decline in its effective salience. He also suggests that when an element is associatively activated but not present in the world it will undergo and increase in effective salience. This will occur, for example, because the a-x association formed on an A trial will enable x to activate a on a B trial. Like McLaren et al.'s account, this

analysis also predicts an effect of scheduling that is over and above the effects of differential exposure to the unique and common elements.

These accounts of perceptual learning all provide varying explanations for the demonstration that previous exposure to a stimulus enhances its ability to be discriminated. As I have already noted, the fact that the likelihood of observing perceptual learning is modulated by stimulus similarity suggests that the effect does not simply reflect the availability of representations of the to-be-discriminated stimuli at the outset of testing; and the sensitivity of the effect to the schedule of exposure shows that mere frequency of encounter with two similar stimuli is not a sufficient explanation. So, why should intermixed exposure to two similar stimuli help? A number of possible candidates for this process have emerged that share the general idea that the unique features or elements (call them a and b) of two similar stimuli (AX and BX) will be more likely to be (exclusively) activated by their corresponding stimuli after intermixed than after blocked exposure. There are a variety of candidate mechanisms that could affect this state of affairs. For example, intermixed exposure to AX and BX might result in the development of inhibitory associations between their unique features (a and b) that will counteract any tendency for a to be associatively evoked when BX is presented and b to be so activated on AX trials (see McLaren & Mackintosh, 2000): this inhibition develops because the formation of a-x and b-x associations will mean that x will activate b when its corresponding stimulus (B) is absent (on AX trials), and x will activate a when it is absent (on BX trials). Alternatively, the development of a-x and b-x associations will mean that a and b are repeatedly associatively activated (by x) when they are not present (on BX and AX trials, respectively) and it has been

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argued that this might maintain their processing (relative to *x*; see Blair & Hall, 2003; but see, Dwyer & Honey, 2007; Mundy *et al*., 2007).

These theoretical alternatives will be discussed in the contexts of the results presented in Chapters 2 and 3, and a variety of theoretical elaborations will be considered. However, for now it is sufficient to note that each is assumed to have general applicability and yet the critical observations upon which they are based in mammals (specifically rats) are dominated by the study of exposure to artificially constructed flavor compounds on the generalization of conditioned flavor aversions. One of the aims of this thesis is to examine perceptual learning effects in a quite different preparation: the discrimination of textures in rats.

1.4. Perceptual learning with textures

In their evocative accounts of perceptual learning, Gibson (1969) and James (1890) both drew on everyday examples where experience was assumed to have affected the sense of touch: While Gibson pointed to the feats of skilled wool graders, James described the facility with which professional traders "recognize, by feeling the flour in a barrel, whether the wheat was grown in Iowa or Tennessee" (p. 509). Demonstrations of perceptual learning involving tactile discriminations now abound in humans (e.g., Sathian & Zangaladze, 1997), but this is not true in nonhuman animals where studies have tended to use visual stimuli or flavors. Thus, early research was based on the finding that rats were better able to learn a reinforced discrimination involving previously exposed visual stimuli than novel stimuli (e.g., Gibson & Walk, 1956; Hall, 1980, 1991); whereas more recent investigations have been based on the observation that generalization of an aversion from one flavour to another in rats is less marked when both flavours have been exposed than when both are novel (e.g.,

Honey & Hall, 1989; Mackintosh *et al*., 1991; Symonds & Hall, 1995). While there are

notable examples where the key observations from such studies of perceptual learning in

rats have established counterparts in birds and people (e.g., Mitchell & Hall, 2014; Montuori

& Honey, 2015), one cannot simply assume that all sensory domains will be shaped in the

same way by experience. By the same token, theoretical analyses that have been

developed in the context of some classes of stimuli (e.g., flavour "cocktails" and geometric

forms; see above) might not be applicable to others. This constraint on the applicability of

associative analyses to instances of perceptual learning observed in other sensory domains

would be of interest in its own right and might expose a limitation in the analyses and

indicate a special property of the sensory system in question.

Thus far there has been little investigation into the behavioural neuroscience of perceptual

learning (at least with rodents), which may partly be attributable to the difficulty in studying

and manipulating the neurobiological bases of taste perception within the typical perceptual

learning paradigms. However, there exists a vast field of research dedicated to

understanding the neurobiological bases of tactile perception within the rodent, which has

provided a detailed understanding of signal (information) transmission from texture to

whisker to brain. This research provides a potentially fertile ground for the marrying of
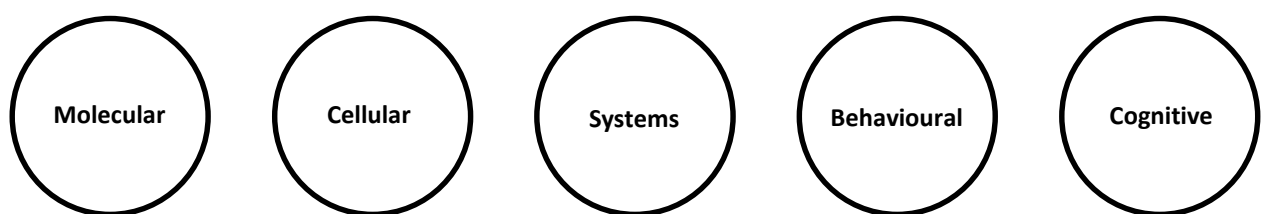
Figure 4. *Different levels of analysis used in the study of psychology and neuroscience. The extent to which the relationships between these levels can be determined and the appropriate terminology translated from one domain to the other determines how well understood a given phenomenon might be.*

associative (and psychological) explanations with the biological underpinnings. If it is the case that the perceptual learning phenomena that have been discussed thus far are replicable within the tactile domain, then it would be possible to study more directly and at a more functional level, the biological nature of perceptual changes. These considerations lead me to embark a programme of research directed towards understanding perceptual learning with tactile stimuli in rats. The research I present in this thesis is predominantly concerned with the behavioural and cognitive levels of analysis illustrated in Figure 4.

1.4.1. Extant studies of perceptual learning involving textures in rats

Investigation into the systems that underlie the sense of touch in rodents, specifically those that involve their whisker system, has provided detailed information about both the requisite neural circuits (Carvell & Simons, 1990; Brecht, 2007; Diamond, von Heimendahl, Knutsen, Kleinfeld, & Ahissar, 2008) and plasticity in the associated (barrel) cortex (Fox, 2002, 2008; see also, Oswald, Yee, Bannerman, Rawlins, Good & Honey, 2001; Ramos, 2013). Indeed, while there has been little effort to study perceptual learning with tactile stimuli in rodents from a psychological perspective (e.g., from the perspective provided by animal learning theory), there is a great deal of knowledge regarding the nature of tactile perception from a neuroscientific perspective. Perhaps not surprisingly, the tactile acuity of rodents rivals that of humans (Carvell & Simons, 1990), and this sensory ability is reflected in the organisation of the neural mechanisms which translate information from the whiskers to the sensory cortex. For instance, the cortical area responsible for processing whisker-generated information consists of clusters, or 'barrels', of neurons that represent each whisker (Woolsey & Van Der Loos, 1970); although there is some degree of overlap between proximal receptive fields (Harris, Petersen, & Diamond, 1999). The way in which texture

information is subsequently represented at a neural level appears to relate to the firing rate of these populations of neurons in the early regions of the sensory cortex, with higher firing rates corresponding to the perception, and correct identification, of rougher stimuli (Heimendahl, Itskov, Arabzadeh, & Diamond 2007). This characterisation of texture information processing is somewhat different to stimulus features mentioned earlier (e.g., motion, orientation), whose cortical representation allow for a clear distinction between 'common' and 'unique' elements (or populations of neurons for example). It is this distinction that allows associative explanations a ready account of perceptual learning. Thus, the populations of processing units are able to interact in way that is largely consistent with associative mechanisms, for example through mutual inhibition, or through grouping. Texture information however, as mentioned above, is initially coded through frequency, or rate, of firing (and indeed of whisker motion). In this case, it is not clear exactly how the associative mechanisms described here, and earlier, may apply, and it is not clear if there exist further layers of information processing that are equivalent to those described for motion or orientation. In the absence of these further processing layers, it may be that any perceptual learning effects involving textures would instead be related to changes in the firing rates in the barrel cortex. As a result, the use of texture in the investigation of perceptual learning effects provides an interesting testbed in which to assess the generality at a phenomenological and theoretical level.

Investigations into the tactile perception of rodents have not been limited to these cortical arrangements, but also include the behaviours utilised during exploration and discrimination. Depending on the task, and the degree of resolution required to discriminate between stimuli, the populations of whiskers used by the animal will vary (macro and micro

vibrissae; Harvey, Bermejo, & Zeigler, 2007; Morita et al 2011). Furthermore, individual performance in discrimination tasks can be predicted by: the animal's propensity to use higher resolution populations of whiskers, the duration of exploration (or whisker palpation) of the discriminanda, the movement patterns employed, and the extent to which whiskers are able to be bent during exposure (Carvell & Simons, 1995).

Interestingly, the disjoint between the extent to which these perceptual mechanisms have been studied (from a neuroscientific perspective) and the little that is understood about the nature of what is being represented, has been recognised by those who study these mechanisms. Thus Diamond, von Heimendahl, Magne Knutsen, Kleinfeld, and Ahissar (2008, p1.) state:

"While considerable knowledge exists about the representation of the physical properties of stimuli — like texture, shape and position — we know little about how the brain represents their meaning."

Given the aforementioned interest in the study of the sensory underpinnings of tactile perception, it is perhaps surprising that behavioural analysis of perceptual learning with tactile stimuli in rats has been very limited. Those studies that have employed tactile stimuli were not intended to demonstrate that exposure to such stimuli results in perceptual learning effects of the sort described by Gibson (1969) and James (1890). However, they do represent illustrative examples both of the effect of interest and one simple theoretical analysis of perceptual learning.

Experiments involving maze learning in rats have demonstrated that exposure to different floors coverings (red sandpaper and black rubber) in the arms of a radial maze, can facilitate the acquisition of a discrimination where food is available at the end of the arm with one floor covering but not at the end of the arm with the other floor covering (Chamizo & Mackintosh, 1989). This perceptual learning effect was interpreted as reflecting a redistribution of processing between the unique and common elements of the exposed arms. To take the concrete example provided by Chamizo and Mackintosh (1989): If the different floor types are considered the unique elements (denoted A and B) of the arms and the shared visual characteristics their common elements (denoted X), then exposure to AX and BX will result in a (greater) reduction in the processing of X than of A and B (greater latent inhibition; Lubow, 1973) because X is exposed on twice as many occasions as either A or B. Under these conditions, in the group given exposure to AX and BX the unique elements (A and B) will be better placed to enter into association with the presence or absence of food during discrimination learning than will the irrelevant, common elements (see Honey & Hall, 1989; McLaren *et al*., 1989).

Although the specific analysis outlined above seems to be inconsistent with the observation that rats in the control group were exposed to X alone (a maze arm with a green plastic floor; see p. 24, Chamizo & Mackintosh, 1989) subsequent experiments lent support to it. For example, in one experiment the walls of the arm containing a red sandpaper floor were painted black, while those of the arm with the black rubber floor were painted white. Under these conditions, exposure to the arms retarded later discrimination learning relative to a group that was simply placed in the radial maze, presumably because in this case exposure could only reduce the processing of the unique textures and visual stimuli that together

defined the to-be-discriminated arms (see Chamizo & Mackintosh, 1989; Trobalon, Sansa, Chamizo & Mackintosh, 1991). Perhaps more telling is the fact that a discrimination in which the floor coverings (A and B) were relevant and the extramaze cues were irrelevant to whether food would be available at the end of two arms, was facilitated by exposure to the extramaze cues (X) alone (see Experiment 1B, Trobalon, Chamizo & Mackintosh, 1992). Leaving aside the fact that differences between the tactile stimuli (rough and smooth) were correlated with differences in their visual characteristics (red and black), the latter results do not require the assumptions that exposure to textures resulted in any change in their discriminability.

1.5. A synopsis and rationale

The behavioural results outlined above confirm that rats can learn discriminations involving floor types (see Lawrence, 1949; see also Oswald *et al.*, 2001; Ramos, 2013), and this observation, coupled with the plasticity of the requisite cortical mechanisms, is consistent with the idea that perceptual learning effects might be observed in rats given exposure to floor-dwelling tactile stimuli. The theoretical analyses that have been developed for perceptual learning, largely on the basis of studies of flavour-aversion learning and discrimination (i.e., those outlined above and considered in more detail in Chapters 2-4), assume that the same general principles should apply to any sensory domain that an animal is sensitive. The point of departure for the experiments reported in Chapter 2 was to examine the effect of exposure to two such tactile stimuli, different grades of sandpaper (henceforth textures) presented on the floor of a standard operant chamber, on the acquisition of an appetitive discrimination involving those textures. Having demonstrated a perceptual learning effect in Experiment 1, the remaining Experiments in Chapters 2 and 3

examined the origin of this effect. The experiments all make use of the fact that a texture

dimension can be conveniently generated using different grades of sandpaper. The basis of

perceptual learning effects using such dimensional stimuli has not been examined in

rodents, and yet theoretical analyses have been developed that have assumed that the

same principles will apply to stimulus dimensions and the types of stimuli that have

routinely been used in studies of perceptual learning in rats (McLaren & Mackintosh, 2000).

Chapter 2: An analysis of perceptual learning effects with textures

2. Summary

Four experiments with rats investigated perceptual learning with a tactile dimension (where A = rough, E = smooth, and B, C and D = intermediate values). In Experiment 1, rats given exposure to A and E learnt an A/E discrimination (e.g., A→food/E→no food) more rapidly than those that were not; and in Experiment 2 rats given exposure to B and D acquired an A/E (but not a B/D) discrimination more readily than those exposed to A and E. In Experiment 3 rats exposed to C (the "midpoint") acquired an A/E discrimination more readily than rats given exposure to either a metal or paper floor; and in Experiment 4 exposure to a texture (e.g., A) that was adjacent on the texture dimension to the to-be-discriminated textures (e.g., B and D) improved discrimination relative to midpoint (C) exposure. Finally, in Experiment 5, exposure to a stimulus closer to the to-be-discriminated stimuli (e.g. B, C/ D) was found to have no effect on the rate at which the discrimination was acquired (compared to preexposure to A). These novel perceptual learning effects are interpreted as reflecting a re-distribution of processing between the notional components of the texture dimension.

2.0. Introduction

The aim of Chapter 2 was to demonstrate a perceptual learning effect using textures as the stimuli, and then to examine the origin of this effect by manipulating the nature of the preexposure stage. There were two principal questions that I needed to address. First, how the stimuli should be delivered to the animals to ensure that they were exposed to them. Following the studies described in Chapter 1 (i.e., Chamizo & Mackintosh, 1989; Trobalon et al., 1991, 1992), I chose to present the textures on the floor. This ensured that the rats

interacted with them, but it did not allow the way in which they interact with them (e.g., with their whiskers or feet) to be precisely controlled.   Second, once the delivery system was chosen the remaining issue concerned how the to-be-discriminated textures should be presented. The standard perceptual learning procedure (following Gibson & Walk, 1956) is to expose both of the stimuli; although perceptual learning effects can be observed after preexposure to one of the two-be-discriminated stimuli (e.g., Franken and Bray, 1973, Honey & Hall, 1989; Mackintosh, Kaye and Bennett, 1991; Mundy, Honey and Dwyer, 2007). Another feature of Gibson and Walk's procedure is that the stimuli were presented side by side, thereby allowing both to be inspected close together in time, and were difficult to discriminate (based upon how rapidly they acquired the later discrimination).

My point of departure in Experiment 1 was to examine the effect of exposure to two tactile stimuli (different grades of sandpaper, henceforth textures) presented on the floor of a standard operant chamber, on the acquisition of an appetitive discrimination involving those textures. The textures were similar and were presented relatively close together in time. Having demonstrated a perceptual learning effect in Experiment 1, Experiments 2-4 examined the origin of this effect by making use of the fact that a texture dimension can be conveniently generated using different grades of sandpaper.

The specific grade (average grit size) of each texture stimulus in each experiment was chosen on the basis of convenience, as it was not possible to generate these stimuli independently. Care was taken to select textures that sampled from regular points along the texture continuum, and each experiment was limited to some extent by the number of 'points' along the continuum that were required. For example, Experiment 1, requiring only three textures, allowed for greater flexibility with regards to the choice of stimuli.

Experiments that required four or more textures were more limited in the stimuli available. While the availability of textures allowed for some regularity in the intervals between each stimulus, textures were not able to be spaced equally apart. One particularly important caveat to note is that this variation in the use of textures makes it difficult to compare directly across the following experiments. In some cases, the evidence for perceptual learning was weaker. Furthermore, the evidence of discrimination following training was not as pronounced in some cases where stimuli are spaced more closely together on the continuum (i.e., where stimuli are more similar). In experiments where more similar stimuli were used, and there is little evidence for discrimination, it was not possible to determine whether the lack of an effect was due to the difficulty of the stimulus discrimination or to the absence of perceptual learning. Nevertheless, the discrimination stimuli were closely matched in terms of the differences in their grit sizes, and any differences between them were well below those deemed to be perceivable in studies that have mapped the limits of rat texture perception (Morita et al., 2011). In order to maintain similarity in the differences between the grit sizes of the stimuli, it was necessary to limit the 'width' of the continuum, resulting in some cases where stimulus discriminability came into question. While the textures used varied between experiments, Table 1 (below) represents those used in each experiment as ranging from A to E, with each letter designation in between representing a texture that lies within the two extremes.

2.1. Experiment 1: The basic effect

The design of Experiment 1 is summarized in Table 1 and involved two stages (preexposure and discrimination) in which rats were placed in operant chambers that were standard with the exception of modifications that enabled the floor to be covered with

sandpaper. There were two groups that differed in the treatments during the preexposure stage. For one group, the flat aluminium floor was covered, on different trials, with one of two types of sandpapers (A and E). These textures were presented in a way that involved two transitions on each day (A, E, E, A). These procedures equate the overall frequency with which the common and unique elements of the unique features of A and E were presented (see Honey, Bateson & Horn, 1994; see also, Dwyer, Hodder & Honey, 2004; Honey & Bateson, 1996; Mundy, Dwyer & Honey, 2006; Rodríguez & Alonso, 2014; Symonds & Hall, 1995). For Group Control, there was no sandpaper on the floor during the exposure stage, and the rats in this group were simply placed in the operant chambers with a flat aluminium floor. Thus, both groups received equivalent exposure to features of the operant chambers other than the floor, and any perceptual learning effect is therefore unlikely to be a consequence of differential exposure to these features (cf. Chamizo & Mackintosh, 1989). During the discrimination stage, all rats were placed in the chambers where the presence of one floor type (e.g., A) was paired with the delivery of food, whereas the presence of the remaining floor type (e.g. E) was not. The identities of the reinforced and the nonreinforced floor types was counterbalanced such that each was equally likely to be the reinforced or nonreinforced stimulus. Discrimination learning was monitored by recording food-well activity during the food-free periods at the start of each trial.

2.1.1. Method

Subjects. 16 male naïve Lister hooded rats (*Rattus norvegicus*; supplied by Harlan Olac Ltd, UK) served in Experiment 1. They were approximately 3 months old at the start of the experiment and were maintained at between 85% and 80% of their free-feeding weights by being given a restricted amount of food at the end of each day. Each experimental group contained 8 rats. For this, and all subsequent experiments, rats were housed and

maintained in accordance with UK Home Office regulations as set out in the Animals

(Scientific Procedures) Act, 1986. They were housed in pairs in a climate-controlled room

with a 12-hour light/dark cycle and given free access to water. All experimental procedures

were conducted during the light part of the cycle. 8 rats served in each experimental group.

Apparatus. Four operant chambers (Campden Instruments Ltd, Loughborough,

England: Test Chamber CI-410), arranged in a 2 × 2 grid, were used. Each was contained

within a sound-attenuating shell, the door to which remained open for the duration of the

experiment. Each chamber (24.5 cm × 23 cm × 21 cm; W × D × H) had 3 aluminium walls, an

aluminium ceiling and an aluminium floor that could be covered with sandpaper. The front

wall of the chamber was made from transparent Perspex. This wall served as the door and

allowed ambient illumination from the experimental room to enter the chamber. There was

a food well in the left-hand wall (5 cm × 4 cm × 6 cm: W × D × H) into which 45-mg TestDiet

food pellets (supplied by MLab, Richmond, IN) could be delivered. A top-hinged transparent

plastic flap guarded access to this food well. When this flap was moved by approximately 2

mm a food well entry response was recorded. Two grades of sandpaper (Wickes, UK) were

used, with the average grit size specified by ISO designations p40 and p100 (grit sizes 425μm

and 162μm, respectively). Two of the edges to the sandpaper protruded beyond the back

wall and door making them inaccessible to the rats. The edges that remained within the

chambers were protected with PVC A4 slide binders, and the front edge of the sandpaper

that extended beyond the door was secured to the aluminium floor with a bulldog clip. The

way in which the sandpaper was prepared, and how it is placed into the experimental

chamber, can be seen in Figure 5.

Table 1
Design of Experiments 1-4

Group	Exposure	Discrimination
Experiment 1: The basic effect		
Preexposure	A, E, E, A…A, E, E, A	A→food, E→no food
Control	Context alone	A→food, E→no food
Experiment 2a: The similarity of the exposed and tested textures (hard-to-easy)		
AE/AE	A, E,…A, E,…	A→food, E→no food
BD/AE	B, D,…B, D,…	A→food, E→no food
Experiment 2b: The similarity of the exposed and tested textures (easy-to-hard)		
BD/BD	A, E,…A, E,…	B→food, D→no food
AE/BD	B, D,…B, D,…	B→food, D→no food
Experiment 3: A midpoint exposure effect		
Midpoint	C, C,…C, C,…	A→food, E→no food
Control	Context alone	A→food, E→no food
Experiment 4: An adjacent exposure effect		
Midpoint	B, B,…B, B,…	A→food, C→no food
Adjacent	B, B,…B, B,…	C→food, E→no food
Experiment 5: A near preexposure effect		
Near	B, B,…B, B,…	C→food, E→no food
Far	A, A,…A, A,…	C→food, E→no food

Note: A, B, C, D and E denote textures along a dimension that ranged from rough (e.g., A) to smooth (e.g., E).

Procedure. There were two principal stages: preexposure and discrimination

training. On each of the 4 preexposure days, rats were placed in the operant chambers for 4

separate 3-min periods that were separated by an interval of, approximately, 1 min when

they were removed from the chamber and placed in a holding cage. For Group Control, the

floor of the chamber was aluminium, and for Group Preexposure this floor was covered with

the designated grade of sandpaper (A or E). For Group Preexposure the sequence in which

Figure 5. *The sandpaper stimulus, along with protective binders and bulldog clip*

the sandpapers were presented was: A, E, E, A for half of the rats while the remainder

received E, A, A, E on all sessions. For half of the rats in each group, A was the rough

stimulus (i.e., p40) and E was smooth (i.e., p100) and for the rest this arrangement was

reversed.

Rats were trained to retrieve food pellets from the food well in a 20-min session on

each of 2 days. On both days, food pellets were delivered on a variable time 60-s schedule.

On day 1, the flap in front of the food well was fixed in a deflected position, rendering the

food well accessible, and on day 2 the guard was returned to its vertical position and rats needed to displace it in order to gain access to the food pellets. On each of the following 8 days of discrimination training there were 4 × 5-min sessions (2 reinforced and 2 nonreinforced) that were separated by, approximately, 60 s. During reinforced sessions, 2 food pellets were delivered on a fixed-time 30-s schedule, and during nonreinforced trials no food was presented. The sequence according to which the reinforced and nonreinforced trials were delivered was counterbalanced across rats within a day: food, no food, no food, food for half of the rats, and no food, food, food, no food, for the remainder. These sequences alternated across days. The frequency of well entries was recorded during the first 30 s of each session when no food was delivered in either type of session.

2.1.2. Results and Discussion

During the initial stages of training performance appeared to be below chance. This was attributed to the order of presentation during training (CS+, CS-, CS-, CS+; CS-, CS+, CS+, CS-), with performance on each trial being influenced by the previous trial. As a result, during nonreinforced trials rats were biased to respond more (due to it being more likely to have experienced reinforcement on the previous trial), and during reinforced trials rats were biased to respond less (due to it being more likely to have experienced nonreinforcement on the previous trial). As the order of preexposure was counterbalanced over each 2-day period, it was deemed most appropriate to conduct analysis on blocks consisting of 2 days. Furthermore, in order to reduce the amount of variation that was seen over the training period, analysis was conducted using discrimination ratios (for this, and all subsequent experiments). These ratios were calculated by determining how much rats responded during reinforced trials, as a proportion of the total amount of responding during

reinforced and nonreinforced trials. Accordingly, a ratio of 0.5 demonstrated equal

responding in reinforced and nonreinforced trials. A ratio higher than 0.5 demonstrated that

rats were more likely to respond during reinforced trials, and a ratio lower than 0.5

demonstrated that rats were more likely to respond during nonreinforced trials. The results

from Experiment 1 are presented in Figure 6, which shows that, despite an initial bias to

respond incorrectly, as training proceeded performance improved in both groups. However,

this improvement was more marked in the group that had been exposed to the floor

textures, Groups Pre-exposure, than in Group Control, who experienced the floor textures

for the first time during discrimination training. ANOVA with group and block as factors

revealed no significant effect of group, $F(1, 14) = 1.85$, $p > 0.05$, $\eta_p^2 = 0.12$, a significant effect

of block, $F(3, 42) = 22.66$, $p = 0.00$, $\eta_p^2 = 0.62$, and an interaction between these factors, $F(3,$

$42) = 6.57$, $p = .001$, $\eta_p^2 = 0.32$. The overall levels of magazine entries did not differ between

groups, with means of 22.80 rpm for Group Control, and 20.49 rpm for Group Preexposure

($F<1$; $\eta_p^2 = 0.33$). The fact that the overall rates of responding did not differ between the

groups suggests that the introduction of novel floor coverings in Group Control did not

result in a general disruption of performance; and the pattern of results are instead

consistent with the view that the perceptual learning effect observed in Experiment 1 has a

different basis. T tests conducted on the final block of training revealed that both groups

responded above chance (control group, $t(7) = 2.44$, $p = 0.045$; preexposure group, $t(7) =$

3.59, $p = 0.01$).
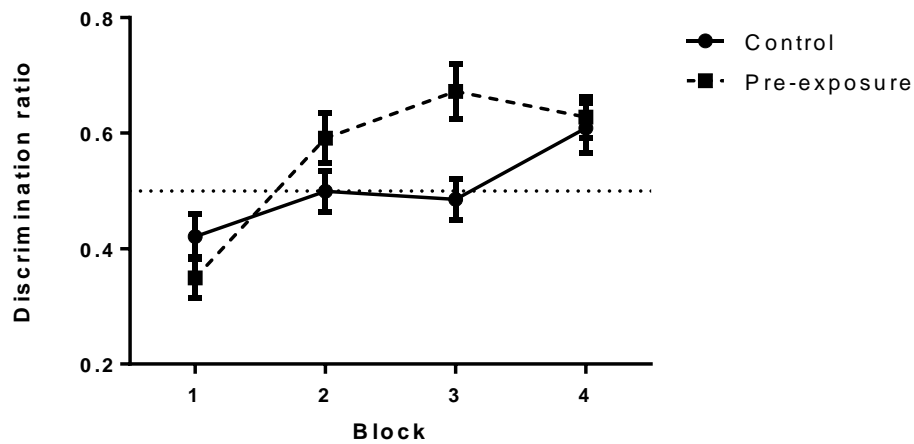
Figure 6. *Experiment 1: Mean discrimination ratios (±SEM) in Groups Preexposure (i.e., A, E, E, A), and Control.*

2.2. Experiments 2a and 2b: The similarity of the exposed and tested textures

One simple interpretation for the results of Experiment 1 follows from the observation that exposure to two similar stimuli will mean that the elements that they have in common will have been exposed more frequently than their unique elements. In the case of the textures, we can denote the more frequently presented common elements as X and the less frequently presented unique elements as A and E, and assume that all of the stimuli between A and E will also activate X. If this form of intermixed exposure to A and E results in an equivalent reduction in the processing of X relative to A and E then it should facilitate discrimination learning relative to a group for which A, E and X are more equally processed. This analysis immediately suggests conditions that should result in a more marked perceptual learning effect than does exposure to A and E themselves. Thus if one gave rats exposure to B and D this should affect a reduction in the processing of the common element X, but it should be less likely to result in a reduction in processing of the unique elements of A and E than would exposure to A and E. On these grounds, exposure to B and D should result in a more marked perceptual learning effect than exposure to A and E

when the tested discrimination involves A and E. This prediction was assessed in

Experiment 2a in Groups AE/AE versus BD/AE (see Table 1).

In Experiment 2b, I contrasted the effect of these two forms of exposure (to A and E

and to B and D) on the acquisition of a discrimination between B and D. Application of the

same form of analysis to this comparison would, without further assumptions, yield the

complementary prediction. The discrimination between B and D would proceed more

readily after exposure to A and E than after exposure to B and D, because both would affect

a reduction in the processing of X, but exposure to B and D would also result in a reduction

in the processing of the (unique) elements that are relevant to the tested discrimination.

However, a moment's reflection reveals that this prediction ignores the obvious possibility

that stimuli that are closer together on the texture dimension should share a greater

proportion of common elements, and be more difficult to discriminate. While exposure to A

and E might be less likely to impact on the elements that are uniquely activated by B and D

than would exposure to B and D, exposure to B and D might result in a more complete

reduction in the processing of their common elements than would exposure to A and E. In

this case then the effect of the different types of exposure (A and E or B and D) will be

determined by the relative contribution of these two effects. The value of such additional

considerations will be evident should the discrimination involving B and D proceed less

readily than that involving A and E, as would be expected if the way that I have

characterized our stimulus set (as an ordered dimension from A through B, C, and D to E)

reflects how the rats process the different floor types. It is worth noting, at this juncture,

that an analogous comparison was reported by Scahill and Mackintosh (2004) using a

flavour-aversion procedure in rats (see also Suret & McLaren, 2003). They found no

evidence that exposure to two easily distinguishable flavours (AX and BX or A and B) was

any more effective than exposure to two hard to discriminate flavours (aX and bX; where the intensity of the unique elements was reduced) in allowing rats to learn a discrimination in which aX was paired with illness and bX was not (but see, Sanjuán, Nelson & Alonso, 2014).

2.2.1. Method

Subjects, apparatus and procedure. 32 naïve Lister hooded rats (*Rattus norvegicus*) served in Experiment 2. The rats were, approximately, 3 months old at the start of the experiment and were housed and maintained in the same way as Experiment 1. The apparatus and procedure were that same as in Experiment 1 with the exceptions that the 4 grades of sandpaper that served as A, B, D and E were: p60, p80, p150, p320 (grit sizes 269μm, 201μm, 100μm, 46.2μm, respectively; 3M UK. Each experimental group contained 8 rats. In order to reduce the likelihood that differences in the visual features of the sandpapers could contribute to rats' ability to discriminate between them, there was no local illumination within the chambers, and the lights in the experimental room were turned off. There was very limited illumination from the computer screen that was located within the experimental room, and from light in the corridor outside of the experimental room entering the room from around the door to the experimental room. On each of the 4 preexposure days, rats were placed in the operant chambers for 4 separate 3-min periods that were separated by an interval of, approximately, 1 min when they were removed from the chamber and placed in a holding cage. For half of the rats (easy preexposure), preexposure consisted of exposure to the context with the floor of the chamber covered by the designated grade of sandpaper (A, E… E, A). The remaining animals (difficult preexposure) the sandpapers presented were: B, D… D, B. For half of the rats in each group, the discrimination stimuli were the same as those presented during preexposure (A, E, A/ E;

B, D, B/ D), while for the remaining half, the discrimination stimuli were different than the pre-exposed stimuli (A, E, B/ D; B, D, A/ E). For half of the rats in each condition, the rougher stimulus was reinforced (A, B), while for the remaining half the opposite was true. The remainder of the experimental procedure (magazine and discrimination) was identical to Experiment 1.

2.2.2. Results and Discussion

Figure 7 depicts the results from Experiments 2a (upper panel) and 2b (lower panel). Comparison of the panels suggests that the discrimination between A and E (upper panel) was acquired more rapidly than that between B and D (lower panel). It is also apparent from the upper panel that the discrimination between A and E developed more readily after exposure to B and D (i.e., in Group BD/AE) than after exposure to A and E (i.e., in Group AE/AE). ANOVA conducted on the results from Experiment 2a confirmed that there was an effect of group, $F(1,14) = 5.01$, $p < 0.05$, $\eta p^2 = 0.27$, and block, $F(2, 28) = 13.39$, $p < 0.001$, $\eta p^2 = 0.49$, but no interaction between these factors, $F<1$. In contrast, acquisition of the discrimination between B and D was not affected by these two forms of exposure (i.e., in groups BD/BD and AE/BD; cf. Scahill & Mackintosh, 2004; Suret & McLaren, 2003; but see Sanjuán *et al.*, 2014). ANOVA revealed an effect of block, $F(2, 28) = 3.90$, $p < 0.05$, $\eta p^2 = 0.22$, but no effect of group and no interaction between these factors, Fs<1. A parallel analysis of the overall rates of magazine entries demonstrated no difference in the rates of between the pre-exposure conditions within each discrimination, with means of 11.27 rpm for Group AE/AE, 11.78 rpm for Group BD/AE, $F<1$, $p > 0.05$, $\eta p^2 = 0.01$, and 7.51 rpm for Group BD/BD and 7.48 rpm for Group AE/BD, $F<1$, $p > 0.05$, $\eta p^2 = 0.00$. T-tests conducted on the final block of training revealed varying degrees of success. For rats being trained on

the AE discrimination, those preexposed to BD were responding better than chance ($t(7)$ = 4.77, $p < 0.05$), as were those preexposed to AE ($t(7)$ = 3.38, $p < 0.05$). For rats trained on the BD discrimination, those preexposed to BD responded better than chance ($t(7)$ = 2.50, $p < 0.05$), however those preexposed to AE responded at a rate no different to chance ($t(7)$ = 1.03, $p > 0.05$).
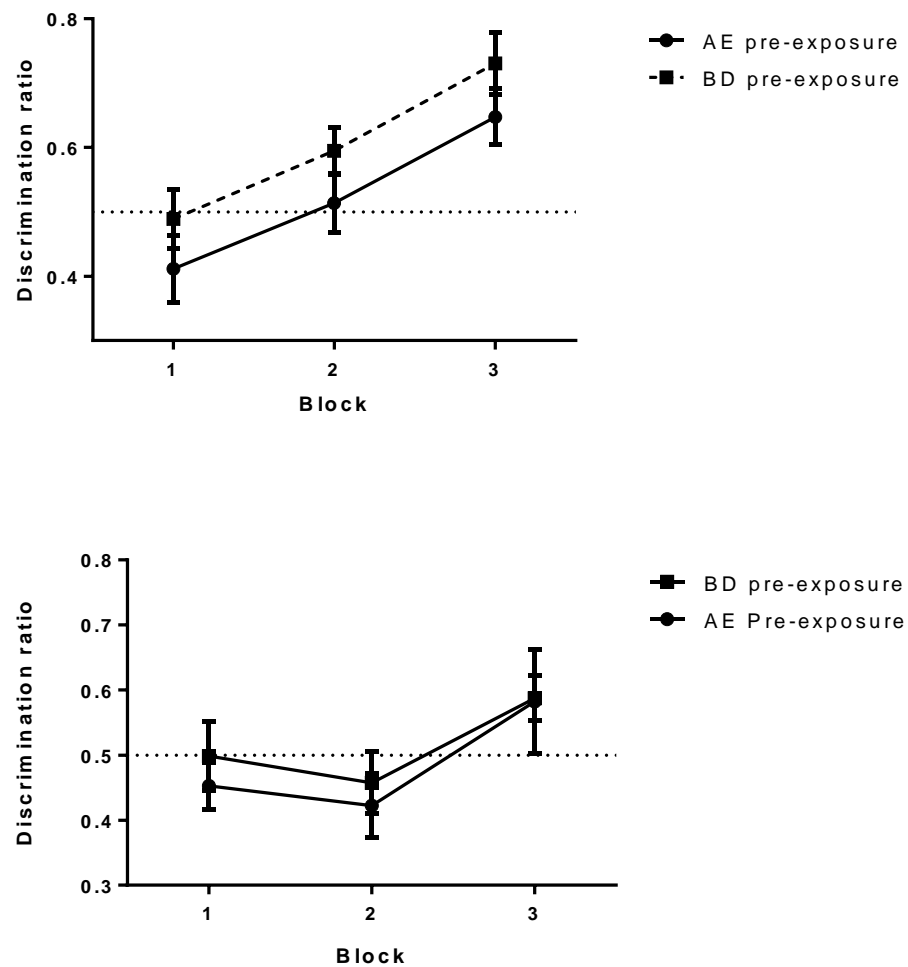
Figure 7. *Experiments 2a and 2b: Mean discrimination ratios (±SEM) in Groups AE/AE and BD/AE (Experiment 2a; upper panel), and Groups BD/BD and AE/BD (Experiment 2b; lower panel). The letters before the oblique (/) indicate the stimuli that were expose exposed and those after the oblique indicate the to-be-discriminated stimuli.*

The general observation that the discrimination between A and E proceeded more readily than that between B and D is consistent with our treatment of the stimuli as forming

a dimension where the proximity of the designated letters in the alphabet relates to their similarity to the rat. The fact that the discrimination involving A and E was acquired more rapidly after exposure to B and D than after exposure to A and E receives a ready explanation in terms of the redistribution of processing between the elements of A and E: Exposure to B and D will reduce the effective processing of the elements that are common to A and E (i.e., X), but will leave their unique elements (A and E) more effective than will exposure to A and E. As we have already noted, once it is allowed that B and D share elements that A and E do not, there is no good reason to anticipate that the two forms of exposure (to A and E or to B and D) will have different effects on the acquisition of a discrimination is between B and D.

2.3. Experiment 3: A midpoint exposure effect

The most direct prediction that follows from the analysis of the patterns of results observed in Experiments 1 and 2 is that exposure to a single texture (C) that lies between to be discriminated stimuli (B and D) should be sufficient to generate a perceptual learning effect (cf. Mundy, Honey & Dwyer, 2007). This prediction was tested in Experiment 3 in which one group was exposed to the midpoint (C) and the control group was simply exposed to the apparatus, and then both groups received a discrimination between B and D (see Table 1).

2.3.1. Method

Subjects, apparatus and procedure. 16 naïve male Lister hooded rats (*Rattus norvegicus*) served in Experiment 3. They were approximately 3 months old at the start of the experiment and were housed and maintained in the same way as Experiment 1. Each experimental group contained 8 rats. The apparatus and procedure were that same as in

Experiment 1 with the exceptions that one group, group midpoint, was pre-exposed to the context with the floor covered by a grade of sandpaper located between the to-be-discriminated stimuli (p80; 201mμ). Indeed, Experiment 3 was run concurrently with Experiment 1, and the results obtained from the control animals during Experiment 1 were used to conduct the analysis.

2.3.2. Results and Discussion

The results from Experiment 3 are presented in Figure 8, which shows that as training progressed discrimination performance improved, and that this improvement was more rapid in Group Midpoint than in Group Control. ANOVA confirmed that there was an effect of group, $F(1, 14) = 5.84$, $p <0.05$, $\eta_p^2 = 0.29$, and block, $F(3,42) = 10.61$, $p <0.001$, $\eta_p^2 = 0.43$, and no interaction between these factors, $F<1$, $\eta_p^2 = 0.32$. The overall levels of food-well entries, with means of 22.81 rpm for Group Control and 24.90 rpm for Group Midpoint did not differ significantly, $F<1$, $\eta_p^2 = 0.36$. This fact suggests that the introduction of a novel floor covering in Group Control did not simply disrupt performance generally. T tests conducted on the final block of training revealed that both groups responded above chance (control group, t(7) = 2.44, p = 0.045; midpoint group, t(7) = 6.33, p = 0.00).
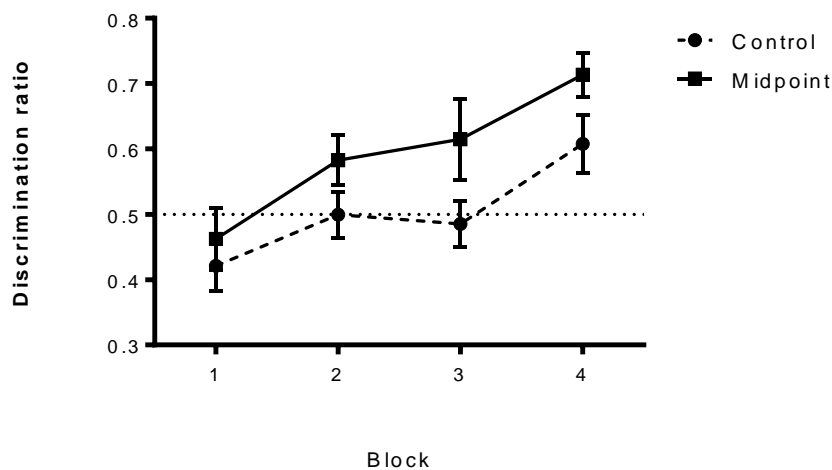
Figure 8. *Experiment 3: Mean discrimination ratios (+SEM) in Groups Midpoint and Control.*

The results of Experiment 3 serve to confirm that a perceptual learning effect can be observed by simply exposing rats to the midpoint between the to-be-discriminated textures. This observation is consistent with the analysis of the results of Experiment 2, where exposure to two textures (B and D) was more effective in improving later discrimination involving A and E than was preexposure to A and E. The results also provided a replication of an effect originally reported by Mundy *et al*. (2007) where exposure to the midpoint on a morph between two similar faces was sufficient to produce a perceptual learning effect in humans. Given that Experiment 3 was conducted as part of Experiment 1, this allows for some comparison of the preexposed group there, and the midpoint preexposure group here. In the former experiment rats were preexposed to the two discrimination stimuli, yet in the present experiment rats were only preexposed to the midpoint. While both preexposure groups performed better than their non preexposed comparisons, there is some indication that those in group midpoint were performing better on the discrimination task by the end of the discrimination period. Furthermore, a statistical comparison of the

midpoint preexposure and the preexposed group in Experiment 1 found no interaction ($F(3,42) = 1.85$, $p > 0.05$), or effect of type of preexposure ($F(1,14) = 0.90$, $p > 0.05$). In Experiment 4 I explore a novel prediction that can be derived from the analysis of the present set of results that has not been evaluated in previous studies of perceptual learning.

2.4. Experiment 4: An adjacent exposure effect

There has already been cause to argue that stimuli closer together on the texture dimension (e.g., B and D) are more similar to one another than stimuli that are further apart (e.g., A and E): The discrimination between B and D was less readily acquired than that between A and E (Experiment 2) and our theoretical analysis of the effects of exposure in that experiment required that B and D shared a greater proportion of common elements than did A and E. This theoretical analysis has a further implication in the context of exposure to the midpoint, C. Exposure to C will result in a reduction in the efficacy of the X elements that B shares with D, but C will also have some elements that it shares exclusively with B and others that it shares exclusively with D; these elements are subsets of those uniquely activated by B and D. Exposure to the midpoint will thus reduce the effectiveness of both the elements that are common to B and D, but it could also have some impact on their unique elements. Based on this observation, exposure to a stimulus (e.g., B) that is adjacent to the to-be-discriminated stimuli (C and E) might allow discrimination learning to proceed more readily than preexposure to the midpoint of C and E (i.e., D). Exposure to B will result in a reduction in the efficacy of elements that C shares with E (i.e., X) and to elements that B shares specifically C, whereas exposure to D will result in a reduction in the efficacy of X and elements that D shares with C and others that D shares with E. On this basis, the discrimination between C and E might be expected to proceed more readily after

exposure to B than after exposure to D; and similarly the discrimination between A and C should proceed more readily after exposure to D than after exposure to B. Experiment 4 tested this prediction in two groups: midpoint (exposure to B and then discriminate A and C or exposure to D and then discriminate C and E) and adjacent (exposure to B and then discriminate C and E or exposure to D and then discriminate A and C; see Table 1).

2.4.1. Method

Subjects, apparatus and procedure. 16 naïve male Lister hooded rats (*Rattus norvegicus*) served in Experiment 4. They were approximately 3 months old at the start of the experiment and were maintained in the same manner as in Experiment 1. The grades of sandpaper used in Experiment 4 were p60, p80, p100, p150, p320 (grit sizes 269μm, 201μm, 162μm, 100μm, 46.2μm accordingly; 3M UK). All rats were pre-exposed to the context with sandpaper covering the aluminium floor (B or D), with half of each preexposure group going on to receive A and C discriminations, and the remainder discriminating between C and E. Those rats pre-exposed to the stimulus in between the discriminanda (e.g. B, A/ C), were group midpoint, and the remainder making up group adjacent.

2.4.2. Results and Discussion

The results of Experiment 4 are presented in Figure 9. Inspection of this figure shows that discrimination performance improved over the course of the 4 blocks of 2 days of training, and that this improvement was more evident in Group Adjacent than in Group Midpoint. ANOVA with group and block as factors revealed significant effects of group, $F(1,14) = 6.15$, $p < 0.05$, $\eta_p^2 = 0.31$, and block, $F(3,42) = 7.49$, $p < 0.05$, $\eta_p^2 = 0.35$, and no interaction between these factors, $F<1$, $\eta_p^2 = 0.02$. The overall levels of magazine entries, with means of 17.81 rpm for Group Adjacent and 13.72 rpm for Group Midpoint, did not differ significantly, $F(1, 14) = 3.45$, $p > 0.5$, $\eta_p^2 = 0.20$. T tests conducted on the final block of

training revealed that the group preexposed to the adjacent stimulus responded above chance, $t(7) = 3.92$, $p = 0.01$. However, those preexposed to the midpoint responded no differently than chance, $t(7) = 0.98$, $p > 0.05$). The observation that the midpoint preexposure group were not responding above chance by the end of the training is somewhat at odds with the results described in Experiment 3. However, the grades of sandpaper used in this experiment were closer together on the texture 'continuum'. As a result, it may be the case that preexposure did have an effect, but due to the relative difficulty of the discrimination this effect was not observed.
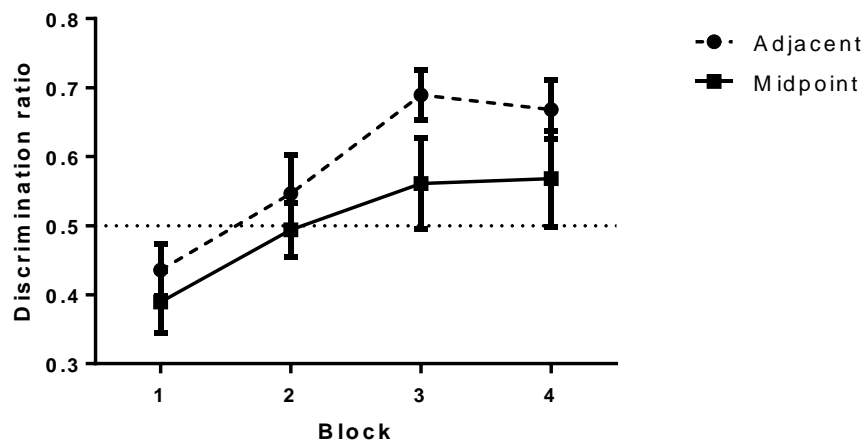
Figure 9. *Experiment 4: Mean discrimination ratios (±SEM) in Groups Adjacent and Midpoint.*

2.5. Experiment 5. The effect of near versus far preexposure

Experiment 4 demonstrated that preexposure to an 'adjacent' stimulus on the same dimension facilitates discrimination more than preexposure to a 'midpoint' stimulus located between the two discrimination stimuli on the continuum. The aim of Experiment 5 was to examine whether this effect is influenced by the distance of the adjacent stimulus from the to-be-discriminated stimuli. Thus, rats in Group Far either received exposure to A before discrimination training involving C and E or to E before discrimination training involving A

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and C. In contrast, rats in Group Near either received exposure to B before discrimination

training involving C and E or to D before discrimination training involving A and C.

2.5.1 Method

Subjects, apparatus and procedure. 32 male Hooded-Listar rats were used from the

same supplier, and housed and maintained in the same way as Experiments 1-4. The rats

were, approximately, 3-month old at the start of the experiment. The five grades of

sandpaper that were used as experimental stimuli were the same as those used in

Experiment 4. Preexposure was carried out in the same manner as previous experiments,

differing only in the stimuli presented. Each experimental group contained 8 rats. Rats in

Group Far received exposure to either A or E and those in Group Near received exposure to

B or D. After exposure to A or B rats received discrimination training involving C and E,

whereas after exposure to D or E rats received discrimination training involving A and C.

The identities of the stimuli (C or E, and A or C) that were reinforced or nonreinforced were

counterbalanced.

2.5.2 Results and Discussion

The discrimination training data from Experiment 5 are shown in Figure 10. A two-way

ANOVA revealed a that there was a significant effect of block $F(4,120) = 7.94$, $p < 0.0001$, η_p^2

$= 0.21$, indicating that over the course of the training animals came to respond more in the

reinforced than nonreinforced trials. However, there was no difference between

preexposure groups, $F < 1$, $\eta_p^2 = 0.01$, and no interaction, $F < 1$, $\eta_p^2 = 0.03$. These results

show that the adjacent effect observed in Experiment 4 is not affected by variation in the

similarity of the adjacent stimulus to the to-be-discriminated stimuli.   Of course, the fact

that the manipulation was without effect might only mean that the near and far stimuli

were not sufficiently different to impact on discrimination learning. T tests conducted on the final block of training revealed that only rats in the near preexposure group were responding above chance (near preexposure, t(15) = 2.43, p = 0.03; far preexposure, t(15) = 1.69, p >0.05). It is worth noting here that the near preexposure group can be considered identical in terms of their preexposure and training phases to the adjacent group reported in Experiment 4. Despite this, discriminative performance in the near group appears worse than that in the adjacent group.
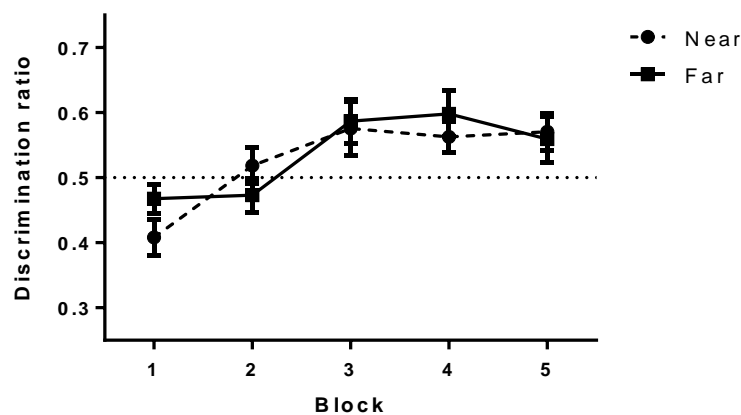
Figure 10. *Experiment 5: Mean discrimination ratios (±SEM) in Groups Near and Far preexposure*

2.6. General Discussion

Some studies of perceptual learning with animals have included textures as a part of the to-be-discriminated arrays (e.g., Chamizo & Mackintosh, 1989; Trobalon *et al*., 1991, 1993), but there has been no systematic investigation of perceptual learning with tactile stimuli *per se*. The lack of such evidence contrasts with the extensive use of the rodent whisker system as a model to examine neural plasticity (e.g., Diamond *et al*., 2008; see also, Oswald *et al*., 2002; Ramos, 2013). The set of experiments described here represents the start of a behavioural analysis of the impact of experience with tactile stimuli (or textures)

on their subsequent discrimination. Taken together, the results of Experiments 1-5 provide support for the view that the processing of our texture dimension changes in an orderly way as a consequence of simple exposure, and they provide converge on the nature of these changes. The results of each experiment suggest that the improvements seen in discrimination learning following stimulus exposure reflect a redistribution of processing among the elements of the dimension, and are consistent with a variety of theoretical analyses that have assumed that changes of this kind might underpin instances of perceptual learning in other preparations and sensory domains (e.g., Hall, 2003; Honey & Bateson, 1996; McLaren *et al*., 1989). They also provide support for the more general view that the same principles might be in operation across quite different preparations (see Mitchell & Hall, 2014; Montuori & Honey, 2015). Indeed some of the effects that I report have relatively direct counterparts in other preparations.

For example, the finding from Experiment 3 that exposure to the midpoint along the texture dimension is clearly compatible with an equivalent effect reported by Mundy *et al*. (2007) in humans using face morphs, and with the finding that exposure to X alone is sufficient to facilitate a discrimination between the arms of a maze (AX and BX; Chamizo & Mackintosh, 1989) and between two flavour cocktails (Mackintosh *et al*., 1991). The observation in Experiment 2 that exposure to two stimuli that are close to one another on the texture dimension (i.e., B and D) was more effective improving discrimination of A and E than was exposure to A and E can be considered to be another instance of this midpoint effect. By contrast, these two forms of exposure (to B/D and to A/E) had no effect on the acquisition of a difficult discrimination (i.e., between B and D). This observation is consistent with results in humans (Suret & McLaren, 2003) and rats (Scahill & Mackintosh, 2004; but see Sanjuán et al., 2014).

The novel asymmetry demonstrated in Experiments 2a and 2b, between the effects of exposure to A/E and B/D on later learning involving either A/E or B/D, can be derived from the idea that exposure simply results in a redistribution of processing among the elements of the exposed stimuli. Thus, exposure to A and E will be more likely to impact on the unique elements of A and E than will exposure to B and E, with both forms of exposure having a similar effect on the elements that A and E share. On these grounds, exposure to B and D should result in a greater perceptual learning effect than should exposure to A and B. In contrast, exposure to A and E should be less likely to impact on both the common and unique elements of B and D than will exposure to B and D. Therefore, these two forms of exposure might not be expected to have different effects on the acquisition of a discrimination involving B and D. In Experiment 4, I showed that exposure to a stimulus (B) than was adjacent to the to-be-discriminated stimuli (C and E) was more effective in promoting their discrimination than was exposure to the midpoint (in this case D). In this case, I argued that exposure to B will be less likely to change the processing of those elements that C shares with E than will exposure to D (cf. Experiment 2), but that exposure to B will also have less impact on the unique elements of E than will exposure to D. The fact that adjacent exposure is more beneficial than midpoint exposure indicates that the beneficial effect of exposure to B (in leaving the processing of the unique elements of E high) outweighs the fact that this form of exposure will be less effective in reducing the processing the common elements of C and E. This analysis will clearly depend on the adjacent stimulus not being too distant from the to-be-discriminated stimuli. However, this interpretation was somewhat inconsistent with the final experiment, where there was no effect of varying the similarity of the adjacent pre-exposed stimulus.

The general idea that exposure to exemplars from a texture dimension results in some relatively long lasting change in the processing of texture dimension leaves many issues unanswered. Most pressing perhaps is how the dimension is represented. There is fairly good evidence that my description of the stimuli as an ordered list (A, B, C, D and E) maps onto how the rats treat the stimuli, with the most obvious being that a discrimination between exemplars that were further apart on the dimension (A and E) was acquired more readily than between exemplars that were closer together (B and D; Experiment 2). I have chosen to describe the similarity between the various exemplars in terms of the overlap between the notional elements that each is assumed to activate (Atkinson & Estes, 1963), but there are a variety of ways to implement this analysis. For example, McLaren and Mackintosh (2002; see also, Suret & McLaren, 2003) suppose that a dimension might be represented by an ordered set of units (call them 1-5), with a stimulus activating a pattern of activity across this set (e.g., stimulus C might activate units 2-4). They assume that each unit responds most strongly to one value on a dimension and less strongly to neighbouring values, and that increases in intensity are represented by a corresponding increase in the activation of the units and the recruitment of additional, adjacent units. Within this scheme, exposure to two stimuli (e.g., B and D) is assumed to result in a reduction in the salience of their corresponding units (1-3 and 3-5), with the result that the unit/s that are activated on each trial (in this case 3) will lose their capacity to become active at a point at which the less frequently presented (unique) elements (1, 2 and 4, 5) will have a non-zero activation value.[1] These changes in salience will mean that a discrimination between two

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[1] This reduction in salience is held to be determined by the difference between the activation arriving at a unit from other units with which the target unit has an association (e.g., those that define the context or other members of the set activated by the stimulus) and the activation generated by the presentation of the stimulus itself.

preexposed stimuli will occur more readily than between two novel stimuli, provided that the stimuli would tend to activate overlapping sets of units in the first instance. This particular view of perceptual learning does not quite account for the novel observation preexposure to the adjacent stimuli was more effective than preexposure to the midpoint stimuli, as it would suggest that adjacent preexposure would be less effective in reducing the salience of the common elements of the to be discriminated stimuli. However, one way of accounting for this may be to consider the effects of elements or features of the stimuli that aren't directly related to the continuum (or indeed those elements that are consistent across the continuum). For example, we might take the view that preexposure to any stimulus along the continuum would reduce the salience of elements such as the 'presence' of a textured floor (along with elements such as the protective plastic binders). Alternatively, this effect may be due to the changes in the makeup of a stimulus as we move along the continuum. In the case of adjacent preexposure, the stimuli closest on the continuum will be most affected by any changes in salience of the common elements. Midpoint preexposure on the other hand, will have the result of affecting each of the to be discriminated stimuli equally.

In the context of the present set of experiments, it is interesting to note that neurons in the barrel cortex respond preferentially to stimulation of one whisker and less to adjacent whiskers, and the adaptation in such responses following repeated stimulation can be highly whisker specific (see Katz, Heiss & Lampl, 2006). Whether or not these neuronal processes can be tied to computational analyses of perceptual learning, and to perceptual learning, remains an open issue.

The novel perceptual learning effects described in Chapter 2 are consistent with a theoretical analysis based upon a very simple assumption: exposure to a stimulus results in a reduction in its processing that generalizes to other similar stimuli. Analyses based upon this assumption clearly have broad explanatory power across different preparations and stimulus classes in animals (flavours, geometric patterns, spatial displays and now textures) and people (flavours, visual stimuli). It is a matter for future research to determine whether additional assumptions will be needed to provide a complete account of perceptual learning involving textures in rodents.

The experiments presented in Chapter 2 provide an appropriate foundation upon which to conduct further research on the nature of perceptual learning effects with textures. The basic effect, that preexposure has some impact on subsequent discriminations, is complemented by a variety of preexposure effects related to the theoretical accounts used to explain such effects. One such analysis of perceptual learning predicts that, in addition to preexposure alone, varying the schedule of preexposure varies the extent to which the effect is observed. Additionally, one consistent finding from the experiments presented in Chapter 2 was that in the initial stages of training rats responded more in the presence of nonreinforced stimuli, and responded less in the presence of reinforced stimuli. Throughout these experiments this tendency towards biased responding appeared to diminish over time and was attributable to the order of stimulus presentations, with prior reinforced trials biasing rats towards more responding on subsequent nonreinforced trials, and prior nonreinforced trials biasing rats towards responding less on reinforced trials. It is perhaps worth noting that a similar effect was demonstrated in the results reported by Honey etc (see figure 3. for a summary). A similar analysis of the results also applies to this study, in which the order of presentation during training was one on

which the previous trials unduly affected each subsequent trial. Although initial responding was affected by this procedural element in these experiments, based on the consistent demonstration of perceptual learning effects presented in Chapter 2, I sought to explore further the origin of this effect in Chapter 3 by using a different measure of perceptual learning.

Chapter 3: Exploration of schedule effects in perceptual learning with textures

3. Summary

Two experiments with rats examined whether or not the schedule according to which two textures (A and E) were presented affected later discrimination between them. In this case, after intermixed (A, E…A, E,…) or blocked exposure (A, A,…E, E,…) rats received conditioning trials with one texture (e.g., A-food) followed by a generalization test with the other (e.g., E). In two experiments, using different parameters, there was no evidence of either a scheduling effect or indeed any sign that exposure to A and E reduced generalization relative to control groups for whom A and E were novel at the outset of conditioning.

3.0. Introduction

Chapter 2 successfully demonstrated a variety of basic perceptual learning effects using a novel experimental paradigm: discrimination learning with textures following preexposure to textures. The aim of Chapter 3 was to examine whether other effects of interest might be observable using the same stimuli, but with a different test procedure. The experiments in Experiment 1 demonstrated that simply pre-exposing animals to textured stimuli (A and E) produced a perceptual learning effect. These effects can be explained by an account of perceptual learning in which there is a redistribution of processing amongst the constituent elements of the stimuli present at discrimination, resulting from the preexposure itself.

The account outlined immediately above, however, is not sufficient to explain another observation: that changes in the schedule on which preexposure stimuli are presented also results in a perceptual learning effect. Early work carried out by Honey, Bateson and Horn (1994) on imprinting with chicks demonstrated the critical role that schedule plays over and above mere exposure to a stimulus. In the experiment carried out by Honey et al., chicks

were pre-exposed to two shapes on either a schedule that maximized the potential for stimulus comparison (e.g. ABABABA), or one which controlled for the total amount of exposure while minimizing the potential for comparison (e.g. AAAABBBB). Animals pre-exposed with the alternating, or intermixed schedule, were better at a discrimination involving the stimuli than those pre-exposed with a 'blocked' schedule. While this was true for shape stimuli, it is worth pointing out that the same effect was not found when the stimuli differed in colour. In this case the reverse was true, with blocked preexposure being more beneficial to the discrimination. Honey et al. suggest that this may be due to the relative difficulty of the two different discriminations, and that intermixed preexposure to already distinct stimuli may produce conditions favourable to the development of excitatory associations between the stimuli. Such a scenario would subsequently result in more generalization from one stimulus to the other. This particular account of the results is consistent with previous findings which demonstrate that the effect of preexposure is affected by the difficulty of the discrimination (Oswalt, 1972).

The intermixed-blocked effect has proven to be remarkably consistent across behavioural measures, stimulus type and species. Based on Gibson's differentiation theory of perceptual learning (1969), perhaps it is not surprising that preexposure schedule has such a dramatic effect on discrimination. According to Gibson, one way in which perceptual learning comes about is through stimulus comparison. Comparing intermixed (A, B, A, B) to blocked (A, A, B, B) preexposure reveals that stimuli presented in an intermixed schedule are more able to be compared than those pre-exposed on a blocked schedule, despite being matched on overall preexposure. This effect is also accounted for by the theoretical view put forward by Mackintosh Kaye and Mackintosh (1989). According to this view, the beneficial effects of

intermixed preexposure can be attributed to the formation of inhibitory associations between the unique elements of two stimuli (a and b), due to the presence of one predicting the absence of the other, and thus reducing the amount of generalisation between the stimuli. An alternative explanation for the intermixed blocked effect comes from Hall (2003), who suggests that the formation of within-compound (a-x and b-x) associations during the intermixed preexposure schedule allows the unique elements to be activated during trials on which they are absent: the presentation of AX will result in the activation of the representation of the unique element B, and vice versa. This state of affairs is assumed to increase the effectiveness of A and B during intermixed exposure. Given the fact that exposure to two textures results in a perceptual learning effect, it seems appropriate to explore the generality of this effect and to examine its origin by examining the effect of schedule of exposure.

3.1. Experiment 6: Intermixed versus blocked preexposure

Experiment 6 sought to directly test whether the intermixed-blocked effect could be observed using textured stimuli (see Table 2). One group of animals, Group Control, were pre-exposed to the context with an aluminium floor. Group Intermixed and Group Blocked were both pre-exposed to the context with textures A and E serving as the flooring. For Group Intermixed preexposure took the following form on each of the four days of exposure: A, E, A, E; while for Group Blocked each of the first two days involved exposure to A on 4 separate occasions, and the next two days involved exposure to E on 4 occasions. Following preexposure, all groups received magazine training and were subsequently given conditioning trials with one of the 2 stimuli (e.g. A→food). After 4 days of conditioning, rats then received test trials with the remaining stimulus (i.e., E).

Table 2

Design of Experiments 6 and 7

Group	Exposure	Conditioning	Test
Experiments 6 & 7: Scheduling effects (intermixed vs blocked)			
Intermixed	A, E,... A, E,	A→food	E
Blocked	A, A,... E, E	A→food	E
Control	Context alone	A→food	E

3.1.1. Method

Subjects and apparatus. 24 male Lister hooded rats were used that were housed in the same way as in Experiments 1-5. The rats were, approximately, 3 months old and were maintained at between 85% and 80% of their free-feeding weight. The apparatus was that used in Experiments 1-5. Two grades of sandpaper were used as experimental stimuli, with the grit size being in accordance with the corresponding ISO designations: p80, p150 (grit sizes 201μm, 100μm, accordingly; 3M UK). These were also used in Experiments 2, 4 and 5. Each experimental group contained 8 rats.

Procedure. There were three principal stages: preexposure, conditioning and generalisation. On each of the 4 preexposure days, rats were placed in the operant chambers for 4 x 3-minute periods that were separated by intervals of approximately 1 minute, where they were removed from the chambers and placed in home cages. For Group Control, the floor of the chamber was aluminium. For Groups Intermixed and Blocked, the floor of the chamber was the textured stimuli, with the difference between the groups being the schedule on which the stimuli were pre-exposed. For Group Intermixed, half of

the animals received the preexposure schedule A, E, A, E; for the remaining half the schedule was E, A, E, A. For half of the animals in Group Blocked, the preexposure schedule was A, A, A, A for the first two days, and E, E, E, E for the remaining two days; for the remaining half this schedule was reversed. The identity of the sandpaper that served as A or E was fully counterbalanced and, regardless of exposure schedule, the textured floors were replaced on each exposure trial.

Rats were then trained to retrieve food pellets from the food well in the same way as in Experiments 1-5. Conditioning sessions occurred over the next 4 days of training. Each day consisted of 2 sessions that were each 5 minutes long, and during which food was delivered on a variable time (VT) 30-sec schedule. Half of the rats in each group were trained with texture A as the flooring, with the remaining half being trained with texture E as the flooring. The final generalisation tests were carried out the following day, with the untrained stimulus serving as the flooring. These were 3 minutes long, with behavioural responses measured in 10-second blocks.

3.1.2. Results and Discussion

Three of the control animals consistently failed to respond across the acquisition phase and were thus excluded from the following analysis. The results of the acquisition phase for the remainder of the animals are presented in Figure 11. Inspection of this figure suggest that there was little or no increase in responding over the 4 days of training. ANOVA with group and day as factors revealed no effect of group $F < 1$, 0.06 no effect of day $F < 1$, 0.02 and no interaction between these factors $F(2,18) = 1.03$, $p > 0.05$. 0.10 A supplementary analysis of the first two trials was conducted given the possibility that there was a ceiling effect generated through pooling responding over the first 4 trials of conditioning (i.e., Day 1). The

results from the first two trials of conditioning are presented in Figure 12. ANOVA with group and trial as factors confirmed that there was an effect of trial, $F(1,18) = 5.345$, $p < 0.05$, but no effect of group and no interaction between these factors, $Fs < 1$.
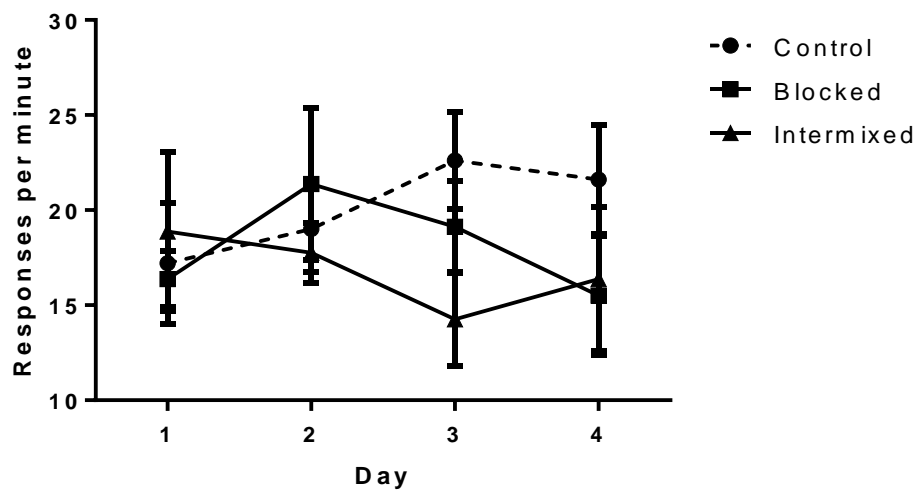
Figure 11. *Mean responses per minute (± SEM) during acquisition trials over 4 days*
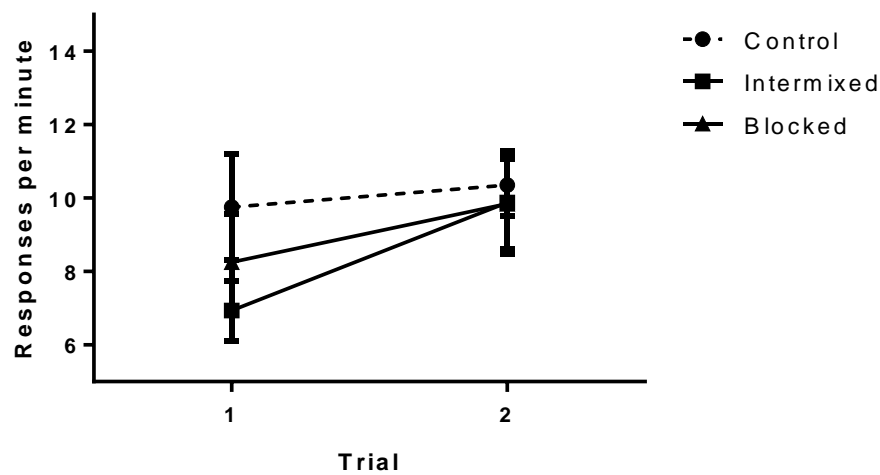
Figure 12. *Mean responses per minute (± SEM) during the first 2 acquisition trials on day 1*

The results of the generalisation test are presented in Figure 13. Responding appeared to extinguish over the course of the generalisation trial, and there was some indication that generalization was more persistent in Group Control than in Groups Intermixed and Blocked, which did not differ. However, an ANOVA with group and block as factors revealed that while there was an effect of block, $F(9,162) = 4.91$, $p <0.001$, 0.21 there was no effect of exposure condition, $F(2,18) = 2.37$, $p > 0.05$, 0.21 and no interaction between block and group, $F < 1$. 0.10
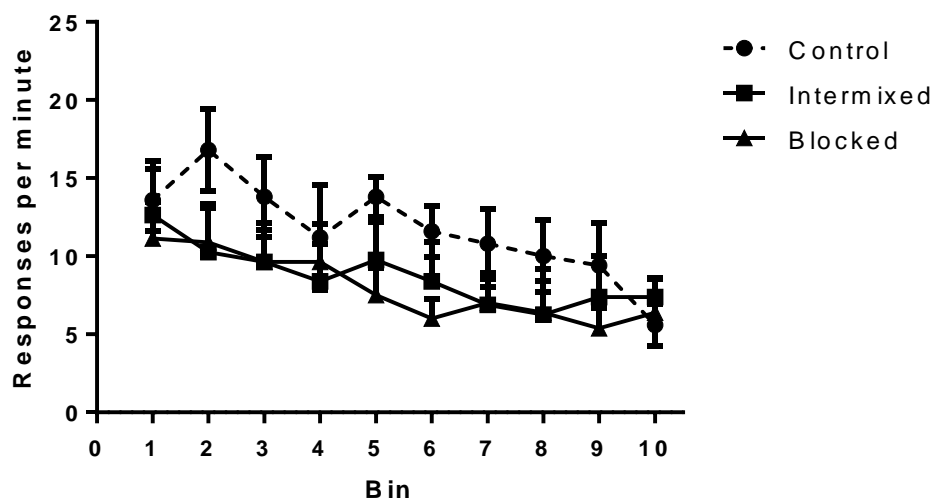
Figure 13. *Mean responses per minute (± SEM) over the 5 minute generalisation test, recorded in each 30-second bin.*

Thus, while the acquisition of conditioned responding appeared to proceed more slowly in rats in Groups Intermixed and Blocked and there being some sign that there was less generalization in the latter groups than the former group, there was no statistical evidence for either of these effects. This is surprising and makes it difficult to derive any firm conclusions from the results of Experiment 6.

3.2. Experiment 7: Extended intermixed versus blocked preexposure

The lack of any statistically significant effects of preexposure in Experiment 6 is surprising given the reliable effects of preexposure observed in Experiments 1-4 in Chapter 2 (although the stimuli used here appeared to be difficult to discriminate in Experiment 2b, as noted in the discussion below). There is no need for the sensitivity of a discrimination learning procedure (e.g., in Experiments 1-4) to be equivalent to a conditioning and test procedure in revealing the effects of stimulus preexposure. However, we do know that both latent inhibition and perceptual learning effects can be observed when a conditioning and test procedures is used (see Honey & Hall, 1989; but see, Honey, 1990). Therefore, I decided to conduct another experiment to examine whether preexposure schedule might have an effect on perceptual learning when the preexposure stage is more protracted.

3.2.1. Method

Subjects, apparatus and procedure. 24 male Lister hooded (Harlan) rats were used. Rats were housed in the same way as in Experiment 6 and maintained at between 85% and 80% of their free-feeding weight. The experimental procedure was identical to Experiment 2 with the exception that the rats received 8 as opposed to four preexposure sessions on each day. Each experimental group contained 8 rats.

3.2.2. Results and Discussion

As in Experiment 6 (and unlike in Experiments 1-5) 3 animals in the control group, 1 in the intermixed, and 1 in the blocked group, failed to respond reliably by the end of the acquisition sessions, and so were excluded from the subsequent analysis. The results presented in Figure 14 show the changes in responding over the course of the acquisition phase. As in the previous experiment, an ANOVA conducted on the levels of responding

over the 4 days did not yield any significant change, with no effect of day, $F(3, 48) = 2.76$, $p > 0.05$, $\eta_p^2 = 0.15$ no effect of group membership $F < 1$, $\eta_p^2 = 0.03$, and no interaction between these factors, $F(6,48) = 1.39$, $p > 0.05$, $\eta_p^2 = |\ 0.03$. Figure 15 shows responding in the first two trials of acquisition, and as in Experiment 6, an analysis that focused on the initial two acquisition trials revealed an effect of trial, $F(1,16) = 6.07$, $p < 0.05$, $\eta_p^2 = 0.33$, no effect of group $F < 1$, 0.03 and no interaction $F < 1$, $\eta_p^2 = 0.07$.
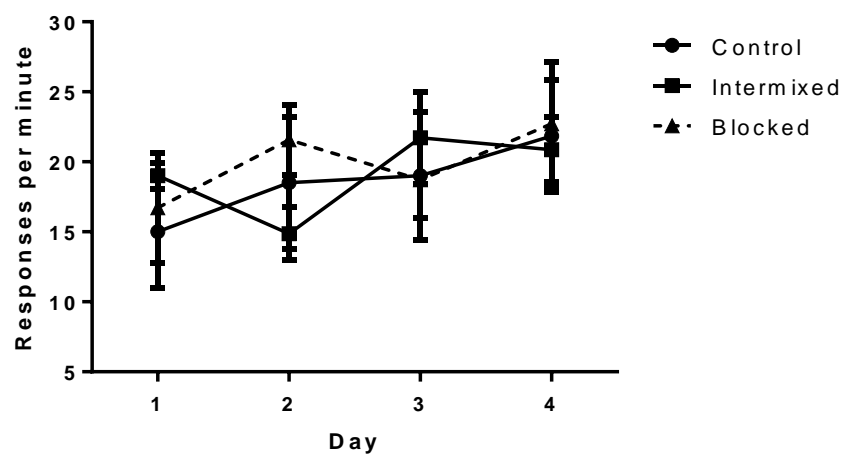
Figure 14. *Mean responses per minute (± SEM) during acquisition trials over 4 days*
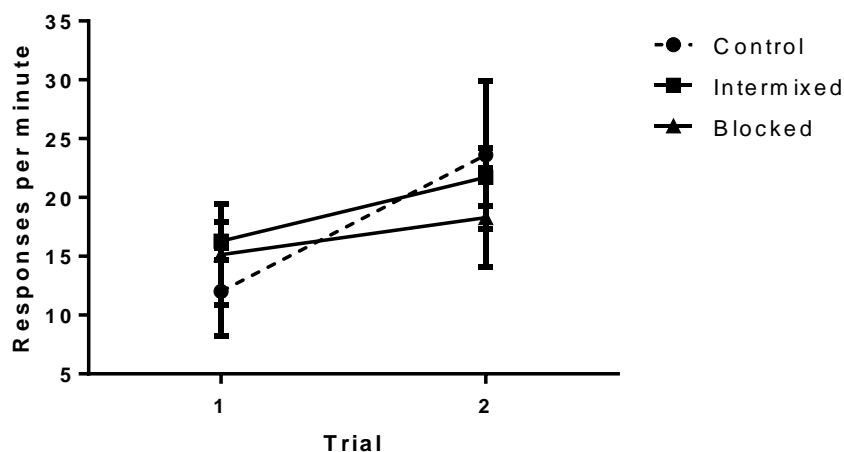
Figure 15. *Mean responses per minute (± SEM) during the first 2 acquisition trials on day 1*

The results of the generalisation test, collapsed into 30-second bins, show that while responding decreased over the course of the test trial, there was no difference in responding based on preexposure condition. This observation was borne out by an analysis using bin and preexposure condition as factors, with there being a significant effect of bin, $F(9, 144) = 4.73$, $p < 0.001$, $\eta_p^2 = 0.23$, no effect of exposure, $F < 1$, $\eta_p^2 = 0.02$ and no interaction between these factors, $F < 1$, $\eta_p^2 = 0.02$.
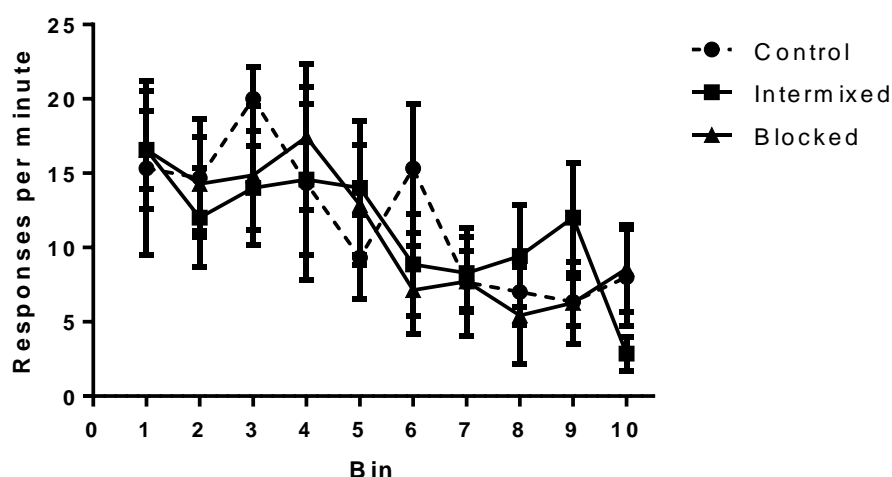
Figure 16. *Mean responses per minute (± SEM) over the 5 minute generalisation test, recorded in each 30 second bins*

3.3. General discussion

Experiments 6 and 7 sought to further examine the origin of the perceptual learning effects observed with textures in the experiments reported in Chapter 2. Unfortunately, in neither experiment was there any evidence that preexposure to two stimuli (A and E) had any effect on either conditioning (e.g., to A) or generalization (e.g., to E). These failures to observe either perceptual learning or latent inhibition are surprising given the reliable nature of

these effects elsewhere and the consistent findings reported in Chapter 2 that used the same stimuli and general procedures. However, barring theoretical reasons for the inability to observe an effect in these instances, it is possible that the observed results are due to the choice of stimuli. Experiments 6 and 7 both used sandpaper grades p80 and p150, as was the case in experiment 2b. Although Experiment 2b used discrimination training as a measure of perceptual learning, there was little improvement in the discrimination following the training procedure. As a result it is entirely possible that the inability to observe an effect in the experiments reported in this chapter was due to the difficulty of the stimulus discrimination used.

One immediately available explanation for the failure of Experiments 6 and 7 to demonstrate perceptual learning effects was the amount of training given to the animals during the acquisition phase of the experiments. In both experiments, rats received a great deal of exposure to one of the stimuli during the conditioning stage itself. Given the fact that exposure to a single stimulus can produce perceptual learning effects (e.g., Honey, 1990) extensive exposure during the conditioning stage might have reduced any contribution of preexposure to the stimuli. This possibility seems inconsistent with the observation that there was substantial generalization in all three conditions in both Experiment 6 and Experiment 7. In any case, unlike demonstrations of perceptual learning using flavour aversion where conditioning proceeds readily (e.g. Mackintosh, Kaye & Bennett, 1991), the procedure used in Experiments 6 and 7 used a greater number of conditioning trials.

There are many other differences between Experiments 6 and 7, on the one hand, and successful demonstrations of latent inhibition and perceptual learning, on the other.

However, perhaps the most disquieting feature of the results described in Chapters 2 and 3 is the contrast between Experiment 1, where a perceptual learning effect was evident, and Experiments 6 and 7, where there was little sign of such an effect. The obvious difference between the chapters is the assays of perceptual learning: discrimination learning or a generalization test. It is possible that the latter assay is simply more sensitive than the former. One obvious way to address this issue would be to conduct Experiments 6 and 7 but with the discrimination learning procedure from Chapter 2. This is certainly one possible for future research (see Chapter 5). However, in Chapter 4 I chose to investigate further one of the critical results from Chapter 2: the observation that exposure to the midpoint between the to-be-discriminated stimuli facilitates the ease with which they are subsequently discriminated.

Chapter 4: Analysis of the midpoint effect

4. Summary

Two experiments with rats examined the origin of the midpoint effect that was presented in Chapter 2. In Experiment 8, rats were pre-exposed to the rough side of the midpoint stimulus (C; Group midpoint), or to the non-textured side of the same sandpaper (Group Control). They then received discrimination training with stimulus B and D. As in Experiment 3, preexposure to the midpoint facilitated discrimination learning, with rats in Group Preexposure learning this discrimination faster than those in Group Control. Experiment 9 sought to determine whether this effect was specific to the context of preexposure. In one context (X) rats were presented with the midpoint stimulus (C), while in the remaining context (Y), rats were exposed to the non-textured side of the sandpaper. Rats then received discrimination training in which B was paired with food and D was not. For Group Same, discrimination training occurred in context X, and for Group Different training was in context Y. While the rate at which this discrimination proceeded did not differ between groups, there was a difference in the rate of overall responding during the discrimination phase, with animals in Group Different responding more than those in Group Same.

4.0 Introduction

In Chapter 3 I sought to examine whether preexposure schedule, which has previously been demonstrated to affect the perceptual learning effect, would be observed in a generalisation test with the novel textured stimuli. The lack of any effect of preexposure in this case prompted me to return to the other compelling demonstration of perceptual learning in Chapter 2: the midpoint effect seen in Experiment 3. Not only is this a compelling demonstration of perceptual learning, it is also critical to our understanding of perceptual

learning in both rats (e.g., Mackintosh, Kaye & Bennett, 1989), and people (Mundy, Honey & Dwyer, 2007).

Experiment 8 examined whether the effect could be observed when different textures served as B, C and D, and when the control condition was the reverse side of the sandpaper rather than the aluminium floor. Clearly, one needs a control floor that differs from the midpoint (C). However, the use of a floor that is smooth, but is otherwise similar to C would be a useful additional feature. The reverse side of the paper (R) seemed to be a reasonable compromise and useful additional control. Experiment 8 compared the effects of exposure to C and R on the acquisition of a discrimination between B and D. This control was also used in Experiment 9, which examined whether the effects of exposure to the C (or R) was specific to the context in which exposure occurred. This is a theoretically interesting question. It has been assumed that the effect of midpoint exposure reflects a redistribution of processing away from the common elements (e.g., B and D) and towards their unique elements. However, there is no direct evidence that this is the case. It has previously been shown that latent inhibition can be attenuated by a context change between preexposure and conditioning (e.g., Hall & Channell, 1986). If latent inhibition contributes to the observation of a midpoint effect then a change of context between preexposure and test should attenuate this midpoint effect. If the midpoint effect reflects latent inhibition to the common elements then this effect should be context specific.

4.1. Experiment 8: The midpoint effect with a novel control condition

The design of Experiment 8 is summarized in Table 3 and is based on Experiment 3. After exposure to either C (Group Midpoint) or R (Group Control) all rats received a discrimination in which B was paired with food and D was not. Group control in this case (as

opposed to Experiment 3) received preexposure to the reverse (and grit free) side of the

textured stimulus. While the justification so far for using textured stimuli has been based on

the suggestion that textures as presented here exist on a continuum, so far there has been

no demonstration that there is no contribution to perceptual learning of potential 'off

dimension' elements. For instance, in the case of previous exposure conditions, the

interpretation of results has solely focused on the similarity of the designated grit sizes,

rather than any remaining features of the textured stimulus.

Table 3

Design of Experiments 8 and 9

Group	Exposure	Discrimination
Experiment 8: Replication of the midpoint effect		
Midpoint	C, C,…C, C,…	B→food, D→no food
Control	R, R,…R, R…	B→food, D→no food
Experiment 9: Context specificity of the midpoint effect		
Same	**X**: C, C… C, C	**X**: B→food, D→no food
	Y: R, R,…R, R…	
Different	**X**: C, C… C, C	**Y**: B→food, D→no food
	Y: R, R,…R, R…	

While the potential for visual cues to impact on results has been minimised by the

dimming of light within experimental rooms, there remains the possibility that olfactory

cues, or cues associated with the shape or presence of the stimuli themselves, may in some

way play a role in the effects observed in previous chapters. Experiment 8, by using the reverse side of the textured stimuli, reduces the likelihood that the presence of such cues contributed to any observed effect. I assumed that both sides of the sandpaper would generate more similar odours than would sandpaper and a metal floor.

4.2.1. Materials and Methods

Subjects. 16 male Lister hooded rats were used that were housed in the same way as in Experiments 1-7. The rats were, approximately, 3 months old and were maintained at between 85% and 80% of their free-feeding weight. The apparatus was that used in Experiments 1-5. Three grades of sandpaper were used as experimental stimuli, with the grit size being in accordance with the corresponding ISO designations: p80, p100, and p150 (grit sizes 201µm, 162µm, 100µm, accordingly; 3M UK). The procedure was the same as in Experiment 3 other than the fact that p100 served as C; the reverse side of C served as the floor for Group Control, and the discrimination was between p80 and p150 (i.e., B and D). Each experimental group contained 8 rats.

4.1.2. Results and discussion

The results from Experiment 8 are presented in Figure 17, which shows that as training progressed discrimination performance improved, and that this improvement was more rapid in Group Midpoint than in Group Back. ANOVA confirmed that there was an effect of group, $F(5, 14) = 5.34$, $p <0.05$, $\eta_p^2 = 0.28$, and block, $F(3,42) = 3.94$, $p <0.05$, $\eta_p^2 = 0.22$, and no interaction between these factors, $F<1$, $\eta_p^2 = 0.004$. The overall levels of food-well entries, with means of 22.81 rpm for Group Control and 24.90 rpm for Group Midpoint did not differ significantly, $F<1$, $\eta_p^2 = 0.36$. This fact suggests that the introduction of a novel floor covering in Group Control, in this case C rather than R, did not simply disrupt

performance generally. T tests carried out on the final block demonstrated that rats in the midpoint exposure group were performing above chance, however the rats preexposed to the reverse were not (midpoint exposure, $t(7) = 3.02$, $p = 0.02$; reverse preexposure, $t(7) = 0.33$, $p > 0.05$).
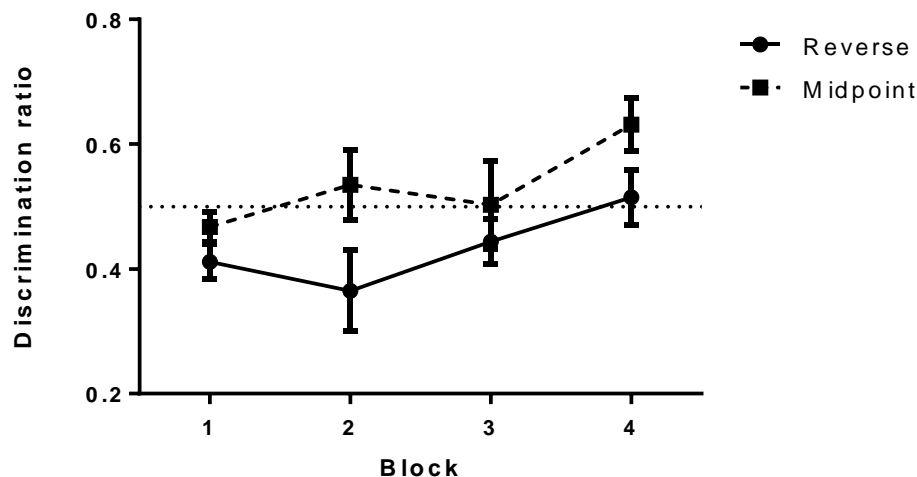
Figure 17. *Mean discrimination ratios (±SEM) in Groups Midpoint and Reverse preexposure*

The observation of a midpoint effect in Experiment 8 is consistent with the findings of Experiment 3, and more broadly consistent with the characterisation of the textured stimulus as being comprised of common and unique elements. Importantly, this experiment includes the only non-preexposed control group using the p80/p150 stimuli. The observation here that accurate discriminative performance on a p80/p150 discrimination requires exposure to the midpoint has consequences for the interpretation of previous results, where the same stimuli were used (Experiments 2b, 6, and 7). In these previous experiments, discrimination training and generalisation tests using these stimuli appeared to be particularly difficult. The observation that the preexposure group were able to discriminate between the stimuli indicates that at the very least these stimuli are discriminable with the appropriate preexposure procedures are carried out, and is

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consistent with previous observations that perceptual learning effects are dependent on the difficulty of the discrimination (Oswalt, 1972).

These results also lend support to the idea that perceptual learning is, at least part, attributable to latent inhibition to the elements that B and D share (i.e., their common elements). If the beneficial effect of preexposure to C reflects a standard latent inhibition effect then it should be abolished by a change of context. The aim of Experiment 9 was to investigate this prediction.

4.1. Experiment 9: Context change and the midpoint effect

The design used in Experiment 9 is depicted in Table 3. All rats received presentations of C in context X (e.g., a chamber decorated with spotted wallpaper) and presentations of R in context Y (e.g., a chamber decorated with checked wallpaper). After the preexposure stage, rats in Group Same received discrimination training with B and D in context X, while those in Group Different received training in context Y. If exposure to C enhances the acquisition of a discrimination between B and D because it results in a conventional latent inhibition effect to the elements shared by B and D, then a change in context (for Group Different) should impair the discrimination between B and D relative to when the discrimination like preexposure to C occurs in context X (for Group Same).

4.1.1 Method

Subjects. 16 naïve Lister hooded rats (*Rattus norvegicus*; supplied by Harlan Olac Ltd, UK) served in Experiment 9. They were approximately 3 months old at the start of the experiment and were maintained at between 80% and 85% of their free feeding weight by being given a restricted amount of food at the end of each day. They were housed and maintained in the same way as in Experiments 1-8. Both experimental groups contained 8

rats.

Apparatus. The same four operant chambers (Campden Instruments Ltd, Loughborough, England: Test Chamber CI-410), arranged in a 2 × 2 grid, were used. Three grades of sandpaper (Wickes, UK) were used, with the average grit size specified by ISO designations p80, p100, and p120 (grit sizes 200μm, 162μm, and 125 respectively). The contexts, X and Y, were created by decorating the upper pair of chambers with laminated spotted wallpaper and the lower pair with laminated checked wallpaper (for details, see Honey & Watt, 1999). The laminated sheets were fixed to the walls and ceiling, but not to the doors.

Procedure. There were two principal stages: preexposure and discrimination training. On each of the 4 preexposure days, rats were placed in the operant chambers for two pairs of 3-min sessions that were separated by an interval of, approximately, 1 minute, when they were removed from the chamber and placed in a holding cage. One pair of sessions was in the morning (between ≈ 1000 and 1200) and one pair was in the afternoon (between ≈ 1500 and 1700). All animals were preexposed to the midpoint stimulus (C) in one context (X), and were preexposed to the reverse of C (R) in the remaining context (e.g. Y). For both Groups Same and Different, the identity of the contexts that served as X and Y was counterbalanced, and the contexts in which C and R were presented was counterbalanced.

After the preexposure stage rats were trained to retrieve food pellets over the course of two days in the same way as in previous experiments, but in undecorated boxes with standard grid floors. On the next 8 days rats received discrimination training. Rats in Group Same received training in the same context as they had received preexposure to C

(i.e., context X), and those in Group Different receiving training in the context in which they had received preexposure to R (i.e., context Y). For both groups, presentations of B were paired with food and D was not. The identity of the stimulus that served as B and D was counterbalanced within each group. On each day of discrimination training there were 2 5-min B trials and 2 5-min D trials that were separated by, approximately, 60 s. During B trials 2 food pellets were delivered on a fixed-time 30-s schedule, and during nonreinforced trials no food was presented. The sequence according to which the reinforced and nonreinforced trials were delivered was counterbalanced across rats within a day: food, no food, no food, food for half of the rats, and no food, food, food, no food, for the remainder. These sequences alternated across days. The frequency of food well entries was recorded during the first 30 s of each session, when no food was delivered in either type of session.

4.1.2. Results and discussion

The results from Experiment 9 are presented in Figure 18, which shows that at the start of training the discrimination ratios were below .50, which as discussed in Chapter 2 likely reflects the sequencing of the reinforced and nonreinforced trials. Nevertheless, as training progressed performance improved. There was, however, no consistent difference between the groups in the rate at which discrimination progressed (from approximately 0.42 to 0.55). ANOVA confirmed that there was an effect of block, $F(3,42) = 5.84$, $p < 0.01$, $\eta_p^2 = 0.29$, but that there was no effect of group, $F<1$, and no interaction between these factors, $F<1$. T tests carried out on the final block showed that neither rats preexposed in the same or different contexts to the discrimination training were performing above chance (different, $t(7) = 1.56$, $p > 0.05$; same, $t(7) = 1.06$, $p > 0.05$). As a result, no conclusive statements can be made about the differential effects of preexposure in this instance.
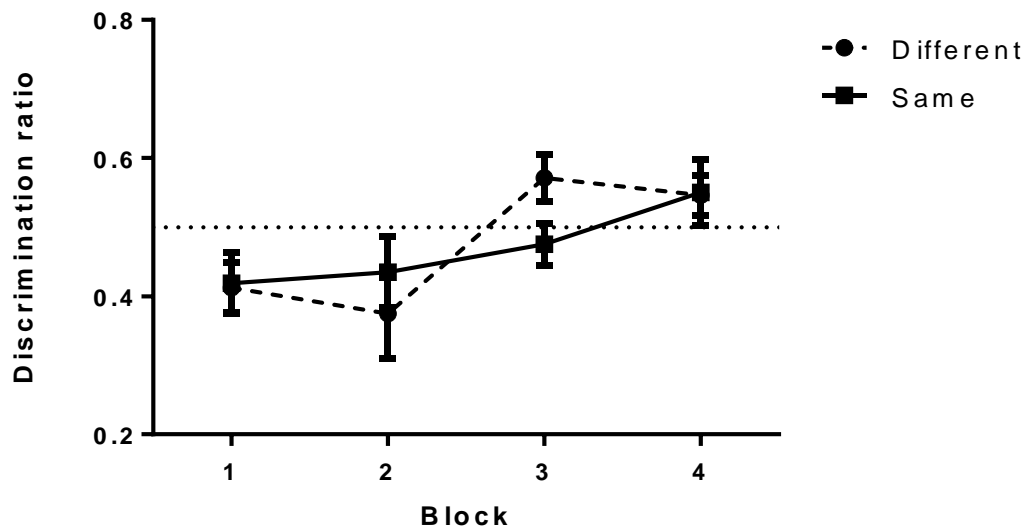
Figure 18. *Mean discrimination ratios (±SEM) in Groups Different and Same*

However, analysis of the overall rate of food well entries shown in Figure 19 revealed that these rates were higher in Group Different than in Group Same. ANOVA confirmed that there was an effect of group $F(1, 14) = 6.18$, $p <0.05$, $\eta_p^2 = 0.31$, and of block $F(3, 42) = 5.84$, $p <0.01$, $\eta_p^2 = 0.29$, but no interaction between these $F(3,42) = 2.4$, $p >0.05$, $\eta_p^2 = 0.15$. Thus while discrimination learning was unaffected by conducting training in a context that differed from where C was preexposed, the levels of responding were affected by the same manipulation. One interpretation of this finding is that the midpoint effect is left unaffected by a change in context that augments conditioned responding generally. However, previous demonstrations of the relationship between context change and latent inhibition have shown that context changes between preexposure and the conditioning phase are weak at best, and at worst have no effect on the demonstration of latent inhibition. Thus it is not clear from this experiment the extent to which latent inhibition contributes to the midpoint effect.
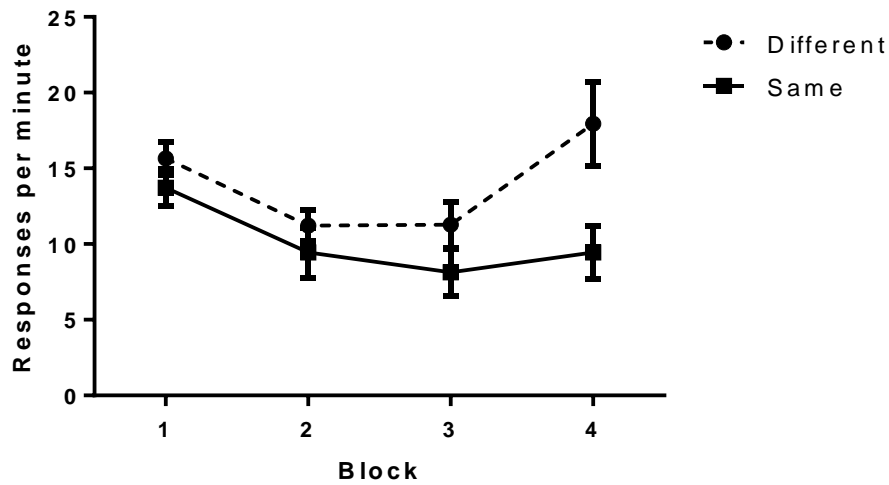
Figure 19. *Mean rates of responding across blocks (±SEM) in Groups Different and Same*

4.1.3. General discussion

Experiment 8 confirmed the reliability and generality of the midpoint effect

demonstrated in Experiment 3. Thus the effect is not restricted to a specific sandpaper or

the use of a metal floor as the control stimulus. Rather in Experiment 8 rats that had

received exposure to C acquired a discrimination between B and D more rapidly than those

that had received exposure to the reverse side of the same sandpaper (R). In Experiment 9 I

used the stimuli from Experiment 8 to assess whether or not the different effects of

exposure to C and R were context specific. Both groups of rats, Same and Different,

received exposure to C in context X and R in context Y, and then rats in Group Same

received discrimination training involving B and D in context X while those in Group

Different received discrimination training in context Y. There was no difference in the rate

at which rats in the two groups acquired the texture discrimination, and the results revealed

that neither group had learned the discrimination by the end of the training period. This

pattern of results might have reflected the fact that the rats did not encode the contexts in

which C and R were presented, or did not detect the change during training. However, the

supplementary finding that the overall rates of responding were higher in Group Different than in Group Same is inconsistent with this possibility. This dissociation suggests that learning about B and generalization to D was affected by the change of context, but that the effects of preexposure to C on the discriminability of B and D was not affected by this manipulation. It appears then that some other process, that is not context specific, must be responsible for the midpoint effect. This conclusion is based upon the assumption that exposure to C (and R) only resulted in a reduction in the processing of the common elements of B and D. If preexposure had also affected the unique elements of B and D (perhaps to a lesser extent) then the predictions concerning the impact of a change of context on latent inhibition become less clearcut (see p. 71, Trobalon, Chamizo, & Mackinotsh, 1992).

Additionally, there procedural considerations that impact on the possible explanation for the results of Experiment 9. Rats were preexposed on 4 separate days, but only received 2 sessions of preexposure in each context (as opposed to 4 sessions of preexposure in a single context as in the previous experiments). At the outset of the experiment it was not clear whether the appropriate methodology would be to equate the total amount of preexposure to the midpoint stimulus, or to equate the number of individual context exposures. In this case, the choice was made to equate the total amount of exposure to the midpoint stimulus, however this may have had the effect of reducing the likelihood of observing a perceptual learning effect. It is also worth noting that the discriminanda used in this experiment were highly similar to one another, using a stimulus continuum that was decidedly narrower than that used in previous experiments. This choice was made based on the observation that perceptual learning effects are more pronounced

when a discrimination is made more difficult (Oswalt, 1972). However, this choice clearly

rendered the discrimination in Experiment 9 particularly difficult, and when taken together

with the observation that latent inhibition is only partially responsible for perceptual

learning effects, may have contributed to the observed null effect.

Chapter 5

5.1. Overall Summary

The experiments presented in this thesis investigated perceptual learning using a novel experimental paradigm, including an analysis of the extent to which effects found in paradigms that use explicitly constructed stimuli (e.g. conditioned taste aversion) could be demonstrated using stimuli that exist along a stimulus continuum. Where perceptual learning effects were observed they were, to a first approximation, consistent with effects that have been observed in both rodent and human. Moreover, the analysis of the new demonstrations of perceptual learning were explicable in terms of a reduction in the effective processing of the elements that the to-be-discriminated stimuli share; or a redistribution of processing between the unique and common elements of these stimuli. This is not to say that there were no surprising observations from these experiments. The observation that preexposure to an adjacent stimulus was more effect at facilitating discrimination than was midpoint preexposure was novel (Experiment 4). So too was the demonstration that changing contexts between preexposure and training had no demonstrable effect on the rate of discrimination learning: an effect that would be expected given some theoretical explanations for perceptual learning. Perhaps the most unexpected result was the failure to generate an effect of preexposure schedule, or a basic perceptual learning effect, when using a generalisation test (Experiments 6 and 7). I will now provide a summary the results of this thesis, followed by a more detailed analysis of their implications.

5.2. Summary of results

5.2.1. An analysis of perceptual learning effects with textures

Chapter 1 featured a series of experiments in which a variety of perceptual learning effects were observed using textures created by the insertion of sandpapers on the floors of standard operant chambers. These effects were seen across a range of experimental designs, which varied the difficulty of the discriminations and the relationship between the preexposed and trained stimuli. Thus, these experiments provide compelling demonstrations that preexposure to textured stimuli facilitates subsequent discrimination learning. They also provided some theoretically important boundary conditions for the effect of interest.

In Experiment 1, rats learned a discrimination between textured stimuli more quickly if they had been preexposed to those stimuli prior to training. This experiment both validated a new discrimination learning procedure and showed that it was sensitive to the effects of preexposure. In Experiment 2, I examined whether discriminations along the presumed texture dimension (A, B, C, D and E), between A and E or between B and D, were affected by whether rats had been preexposed to A and E or B and D. The discrimination between A and E was more readily acquired after exposure to B and D than after exposure to A and E themselves. This effect has some theoretical significance that I will come to later on. The discrimination between B and D, that was acquired relatively slowly, and was not affected by whether rats had been preexposed to A and E or B and D. The observation that the discrimination between stimulus B and D proceeded more slowly than the discrimination between A and E is consistent with the idea that A-E form an effective continuum. The finding that exposure to B and D facilitated a discrimination between A and E provided the basis for Experiment 3. Experiment 3 provided the first demonstration that

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preexposure to a single midpoint stimulus (C) located between the discrimination stimuli (e.g. A and E) is sufficient to produce the perceptual learning that had thus far been seen only when preexposure had been to two stimuli (cf. Experiments 1 and 2). This demonstration further ties the perceptual learning effects seen with textures to empirical findings from other preparations in people (Mundy et al., 2007) and rats (Mackintosh, Kaye & Bennet, 1991) and the theoretical analyses and debate that these observations have generated.

One analysis of the midpoint effect reported in Experiment 3 is that preexposure to a stimulus along the texture continuum is sufficient to produce a perceptual learning effect. Experiment 4 provided a demonstration that this was not the case, with preexposure to a stimulus (B) adjacent to the to-be-discriminated stimuli (C and E) being more beneficial that preexposure to their midpoint (D). The results of Experiment 4 are somewhat more difficult to reconcile with an account of perceptual learning that assumes latent inhibition of the common elements as its primary mechanism: because preexposure to the stimulus with less common elements was more effective at facilitating discrimination learning than preexposure to the stimulus shared more common elements with the discrimination stimuli (cf. McLaren et al., 1989). As mentioned in Chapter 2, however, there are ways in which to explain this outcome without abandoning the idea that perceptual learning reflects a redistribution of processing between the unique and common elements: exposure to the midpoint might also reduce the processing of the unique elements of both C and E in a way that exposure to B will not. There is an alternative analysis of the adjacent effect in terms of the acquired equivalence and distinctiveness of cues (e.g., Miller & Dollard, 1941; see also Honey & Hall, 1989). Specifically, exposure to B might allow C (but not E) to "borrow" the unique elements of B and enable C to be better discriminated from E. The fact that

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exposure to A and E did not facilitate a discrimination between B and D is inconsistent with this analysis (Experiment 3).

Experiment 5 was conducted to investigate whether the adjacent exposure effect found in Experiment 4 was affected by the similarity between the preexposure stimuli and the discrimination stimuli. However, there was no effect of stimulus similarity in this case. It might be the case that the preexposed stimuli (A or B) were not sufficiently different from one another to produce such an effect on a discrimination between C and E.

The results reported in the set of experiments presented in Chapter 2 are broadly consistent with the theories of perceptual learning presented in Chapter 1. For example, the finding that preexposure to a midpoint on the stimulus dimension was effective at producing perceptual learning, is readily explained by the theory put forward by McLaren et al. (1989), if one considers that such a stimulus can be represented as sharing some of the elements of the later discriminated stimuli. If preexposure to these overlapping, or shared elements, results in the development of inhibition, then during discrimination training the unique elements of the discrimination stimuli are able to support learning more readily than those that were initially preexposed. This analysis is equally viable in the explanation of the midpoint effect (Experiment 3), and the explanation of the difficult-easy preexposure effect (Experiment 2a), where on a continuum of rough to smooth (A – E) preexposure to BD produced a perceptual learning effect when compared to AE preexposure. That is not to say that AE preexposure was ineffective at producing a perceptual learning effect, however in this case, due to the absence of a nonpreexposed control group there is no way of telling whether AE preexposure had any effect. There is reason to believe however that this would be the case. Despite the use of different grades of sandpaper, Experiment 1 showed that preeexposure to the discrimination stimuli improved discrimination relative to a

nonpreexposed control group. In both cases, one would expect such an effect based on the

mechanisms put forward by McLaren et al. that suggest that preexposure results in the

formation of associations between the sets of elements that make up each stimulus.

Furthermore, in Experiment 1 preexposure to two stimuli provides the necessary conditions

for the development of mutual inhibition between the unique elements of each stimulus.

The effect reported in Experiment 2a however provides a situation where each of these

mechanisms is likely to be involved to some degree. Preexposure to BD in this case allows

for the mutual inhibition of elements that, while not necessarily present during training,

bare some similarity to those unique to the discriminanda. As a result, BD preexposure

allows for some inhibition of common elements and potentially for mutual inhibition of

unique elements (those that are shared between preexposure and training stimuli, but not

between the training stimuli themselves).

The demonstration in Experiment 4 that preexposure to the adjacent stimulus

produced a perceptual learning effect relative to preexposure to the midpoint stimulus is

somewhat more difficult to immediately account for in these terms. One might expect,

based on the view that perceptual learning is at least in part due to latent inhibition of the

common elements, that preexposure to a stimulus sharing more elements in common with

the discriminanda would be more effective. This was clearly not the case, however it

remains possible that further processes worked towards producing this effect, and that

these results speak to the relative contributions of the mechanisms described by McLaren et

al. For example, while any inhibition to the elements that make up the adjacent stimulus

may have had little bearing on the training, preexposure to this stimulus may have allowed

for the process of unitisation (whereby the set of elements become associated with one

another) in a way that preexposure to the midpoint does not. If this is indeed the case, it

speaks to the possibility that unitisation contributes more to the perceptual learning effect than the inhibitory processes described. The aforementioned analysis of the results is largely consistent with the view that these stimuli can, to some degree, be characterised as existing on a continuum where proximity on that continuum refers to both te physical characteristics of the stimulus and the extent to which stimuli share elements or activation patterns. This is largely in keeping with the existing literature, and particularly those experiments that use explicitly created stimulus compounds. However, as I will note later, there are more basic reasons to question whether there may be a difference in the way in which theories of perceptual learning account for textured stimuli.

5.2.2. Exploration of schedule effects in perceptual learning with textures

In Chapter 2, I sought to further examine the origin of perceptual learning effects with textures. Unfortunately, in neither experiment was there any evidence that exposure to two stimuli (A and E) had any effect on either conditioning or generalization. Although there is widespread evidence of such effects elsewhere, neither Experiments 6 or 7 demonstrated either latent inhibition or perceptual learning. This was surprising given the results of Experiments 1-5 (see Chapter 2). One immediately available explanation for the failure to detect latent inhibition was that any increase in conditioned responding was rapid (across the first two trials) and thereafter was relatively modest. The fact that there was no perceptual learning effect in the generalization test is more difficult to explain, especially given the fact that there was an orderly decline in responding across the extinction test. Perhaps the fact that the conditioning stage involved substantial exposure to one of the textures was sufficient to outweigh any advantage of being exposed to the to-be-discriminated stimuli. Certainly, conditioning proceeds very rapidly in the most often used

procedure for studying perceptual learning in rodents (flavour-aversion learning; e.g., Mackintosh, Kaye & Bennett, 1991) and requires little additional exposure to the conditioned stimulus.

If I now just consider the fact that there was no difference between intermixed and blocked exposure, ignoring the control group, there are a range of other parametric issues that might be responsible. These include the amount of preexposure trials and the inter-trial intervals used. Experiment 7 sought to explore this by doubling the number of trials and reducing the time between preexposure sessions (cf. Gibson, 1969). However, these changes were not sufficient to produce an effect of preexposure schedule. It is perhaps worth mentioning that the suggestion that the beneficial effect of intermixed preexposure is due to the formation of inhibitory associations between the unique elements of the exposed stimuli predicts that reducing the inter-trial interval would not enhance perceptual learning. It is thus a moot point whether the changes made in Experiment 7 should have increased the likelihood of observing an intermixed/blocked effect.

The view that perceptual learning effects reflect the formation of inhibition between the unique elements of two similar stimuli (e.g., AX and BX) is linked to theoretical analyses that view stimuli as being composed of various unique (A and B) and common elements (X) that become linked (A-X and B-X) and provide the basis for representations of A and B to be activated when they are not there. It is perhaps worth noting that the stimuli used in the present experiments differ from such compound stimuli by occurring along a naturally occurring continuum. I have assumed that changes in the similarity of stimuli, and the distribution of notional elements that make up each stimulus, is related to variations in total grit size. An alternative characterisation of these changes may be as variations in the total

amount of particulate matter on each sheet rather than the size, as smaller grit size allows for more particles on each sheet of sandpaper (and vice versa). In either case, however, the analysis of the textures as existing on a single stimulus dimension remains plausible, and is supported by the finding in Experiment 2 that changing the stimuli directly impacted the difficulty of the discriminations. The nature of textured stimuli then may be considered an explanation for the absence of scheduling effects in Experiment 6 and Experiment 7. To suggest that stimuli that exist on a single continuum (rather than being made up of elements or features) cannot be characterised in terms of common and unique elements, would be premature (see Chapter 2). However, at least some accounts of the intermixed/blocked effect would seem to apply less readily to a continuum. For example, how could intermixed presentation of stimuli result in inhibition between the 'largeness' or 'smallness' of the particulate matter. It is not impossible, but it seems implausible. Of course, some accounts of inhibition (Konorski, 1968) are based on just such antagonism (e.g., between the memories of food and no food).

5.2.3. Analysis of the midpoint effect

Chapter 4 revisited the midpoint effect. Experiment 8 replicated the effect with new stimulus and new control. Experiment 9 made use of the new procedures to investigate whether the midpoint effect was context specific. There was no apparent effect of changing context between the preexposure and conditioning phases on discrimination learning. This observation is difficult to explain in terms of a theory of perceptual learning that relies on latent inhibition of the common elements. However, there was an effect on the total amount of responding, with animals trained in a different context to that in which they received texture preexposure responding more. The change in context was detected.

These findings may be taken to suggest that the loss in effectiveness of the common elements, if that is responsible for the midpoint effect, is not contextually mediated (cf. Wagner, 1981; see also, McLaren et al., 1989). The effect of adapting the common elements may be mediated by some other process that is long term, but is unrelated to latent inhibition. Alternatively, it may be that the relationship between latent inhibition and context is not as clear cut as has been described. In the experiment conducted by Hall and Channel (1986) for example, a change of context was shown to either have no effect on latent inhibition, or to weakly attenuate the effect. As a result it is necessary to conduct a more sensitive study of the midpoint effect, in order to determine whether it is due to latent inhibition. This may be possible through attempting to directly these stimuli following preexposure to the midpoint stimulus. Of course, there are many accounts of adaptation or habituation that do not rely on context-stimulus associations (for a review, see Hall, 1991), which would account for the current observations.

5.3. Future directions

One immediately apparent experiment that would be required in light of the present set of studies would be a further investigation of the intermixed/blocked effect using a test procedure that was more successful at producing a perceptual learning effect; namely, discrimination learning. The use of such a procedure would avoid some of the problems with the conditioning and generalization test that were identified above.

Experiment 9 demonstrated that changing contexts between preexposure and discrimination training affected the way in which animals behaved, not in terms of their ability to discriminate between the stimuli but in terms of their overall levels of responding. Clearly, the change in context was detected, but it would be interesting to examine, in other ways, the consequences of detecting the change. Previous work has shown that whisking

behaviour in rats is a reliable predictor of their performance on subsequent discriminations (Carvell and Simons, 1995). While the relationship between whisking behaviour and stimulus experience has yet to be demonstrated. Perceptual learning then provides an ideal case in which to examine changes in behaviour that result from experience, but it would also be of considerable interest to examine the consequences of experience in terms of the modulation of whisking behaviour.

Part of the rationale behind using textures as a novel stimulus was that they provided a novel way to study perceptual learning. That is, previous studies of perceptual learning have relied on manipulating stimulus compounds, rather than using stimuli that vary along a single continuum. These previous studies have been easily explained within the associative framework presented, and indeed have contributed to the characterisation of stimuli as consisting of unique and common elements. While attempts have been made here to discuss perceptual learning effects on a stimulus continuum within such a framework, it is possible to take the view that such an analysis breaks down when considering the very nature of perception. For example, the mutual inhibition mechanism proposed by McLaren et al. (1989) is more easily applied in the context of an experiment where specific stimuli are, or are not, present on consecutive trials. Applying this particular mechanism to a stimulus such as texture becomes difficult when taking into account the fact that texture information as used here has been shown to be coded on the basis of whisker frequency, or neuronal firing rates. To suggest that stimuli become more discriminable due to a high firing rate (or frequency) inhibiting a low firing rate (or frequency), is difficult to maintain. Put more simply, if a stimulus is represented on a single dimension, how can its extremes inhibit one another? Are the phenomenological qualities of 'roughness' and 'smoothness', able to affect each other's perception? One might make the case that the

very presence of 'roughness' suggests the absence of 'smoothness', without recourse

inhibitory mechanisms. This is perhaps the fundamental question left open by the present

set of experiments, perceptual learning effects notwithstanding.

5.4. General conclusions

There is a great deal of work that has been done studying the neural encoding of

texture information in rats' vibrissal system. This ranges from the behaviour of the animals,

the dynamics and physicality of the whiskers, to the way in which this is translated into

neuronal information, and the way in which this information is then represented at a

cortical and subcortical level. While these studies frequently use textures such as those used

in the present set of experiments in discriminations that occasionally involve food reward,

there are none so far that have attempted to describe how whisker related behaviour or

brain activity might change as a result of previous experience with textured stimuli. That

changes in stimulus processing at a cortical level might be important for the way in which

stimuli are subsequently perceived or processed, and this information then goes on to

influence behaviour is something worth investigating. The fact that the vibrissal system in

rats is so well described provides a unique opportunity to investigate behavioural,

associative questions where there is already a high degree of knowledge regarding how this

information is processed within the brain.

The set of experiments reported on here provide a first pass, and general overview,

of the extent to which the effect of experience may affect the discriminability of textures.

These experiments demonstrate that the phenomenon of perceptual learning can be

reliably reproduced using stimuli that are not constructed of discrete features. While I

identified some surprising novel findings, there were also a number of occasions where

commonplace observations were not replicated. This work provides a foundation upon

which future investigations into the relationship between experience and perception, and

the way in which textures are encoded physically and expressed behaviourally.

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