Tactile and Multisensory Perception of Low-Level Spatial Features

Investigating the Effects of Crossmodal Interaction and Temporal Context

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Statement of Originality

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Abstract

Low-level surface features, such as orientation and spatial frequency, are critical for both somatosensory and visual perception. These features are extracted early in cortical processing and serve as the foundation for higher-order processing in both modalities. While traditional sensory research often focuses on unisensory perception and isolated trials, accumulating evidence highlights the important roles of multisensory and temporal context, challenging the validity of such approaches. This thesis investigates how crossmodal influences and perceptual history affect tactile perception of low-level spatial features. In Chapter 3, the characteristics of orientation perception in the somatosensory domain are examined, establishing a tactile oblique effect independent of exploration method (active vs passive) and demonstrating a parallel serial dependence effect. Chapter 4 explores the crossmodal transfer of orientation adaptation using a modified tilt aftereffect paradigm, revealing an asymmetrical crossmodal adaptation effect (tactile adaptation elicits a visual tilt aftereffect) and asymmetrical intramodal serial dependence effect. Chapter 5 investigates crossmodal integration of spatial frequency between vision and touch in virtual reality and shows a statistical optimal integration that is unaffected by spatial proximity between stimuli in different modalities. Together, these findings reveal a complex crossmodal interplay between vision and somatosensation in the perception of low-level spatial features and highlight the intertwined effects of temporal context (as revealed by serial dependence and adpataion effect). Collectively, these findings underscore the need for an integrative and holistic approach in perception research.

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CHAPTER 1

Introduction

1.1 Research Background

The perception of the external world has been a fundamental focus of psychological research. Understanding how physical stimuli from the environment are processed and brought into consciousness is a crucial step in understanding the functions of the human brain and its underlying neural mechanisms.

Historically, unisensory information was thought to be processed independently within dedicated pathways, progressing from primary sensory cortices to higher-order cortical areas. Multisensory integration was assumed to occur only in specialised higher-order multisensory regions (Beauchamp, 2005). However, recent studies provide growing evidence of direct connections between primary sensory cortices and reveal that multisensory influences and integrations can occur at surprisingly early stages of sensory processing (Henschke et al., 2014; Massé et al., 2016).

Similarly, traditional laboratory investigations of sensory perception often focused primarily on isolated trials, treating perception as a static process. Yet, recent research highlights the significant impact of perceptual history on current perception, demonstrated through phenomena such as sensory adaptation (Gibson, 1937) and serial dependence (Fischer & Whitney, 2014). These findings emphasise the dynamic and interconnected nature of sensory processing.

Vision, as the sensory modality with the largest proportion of the cerebral cortex dedicated to its processing (Sereno et al., 1995), has been shown to employ numerous intricate mechanisms, including those mentioned above, that facilitate the capture and interpretation of the dynamic and complex external world. This raises the question of whether other sensory modalities might leverage the existing neural infrastructure of the visual system through cross-modal connections spanning different levels of the cortical hierarchy, thereby enhancing the overall efficiency of sensory processing.

The perception of surface spatial features, such as orientation and spatial frequency, is fundamental to both somatosensory and visual perception. With a growing number of recent literature points to a close connection between the visual and tactile modalities (Merabet et al., 2004; Merabet et al., 2008; Prather et al., 2004; Sadato et al., 1996, 2004; Sathian & Zangaladze, 2002; Zangaladze et al., 1999; Zhang et al., 2004, 2005), and the similarities in the information these modalities capture. It is natural for one to wonder whether the two modalities share a common processing mechanism and whether the aforementioned phenomena, such as adaptation and serial dependence, can be replicated in touch or transferred crossmodally.

Hence, this thesis investigates whether the somatosensory perception of surface spatial features is influenced crossmodally by visual input and explores whether temporal effects, such as adaptation and serial dependence, are also present in tactile perception. By conducting a series of psychophysical experiments, this work aims to uncover the underlying mechanisms of multisensory perception and contribute to a more comprehensive understanding of how the brain integrates and processes sensory information.

1.2 Research Objectives and Aims

Within the context outlined above, this thesis aims to bridge critical gaps in our understanding of sensory processing by exploring somatosensory perception of surface spatial features from a dynamic and multisensory perspective. While prior research has extensively investigated visual perception, much less is known about how similar mechanisms operate in tactile perception or how the two modalities interact and influence each other dynamically through sensory processing. By adapting and extending well-established paradigms from visual research to the tactile domain, this thesis not only examines whether comparable phenomena can be observed in touch but also seeks to uncover the principles underlying tactile and multisensory perception of spatial features. In doing so, this thesis hopes to contribute novel insights into how sensory information is processed and integrated by the brain, and ultimately advance our understanding of how these fundamental processes of sensory information forms the foundation of human cognition.

1.3 Thesis Outline

This thesis is organised into seven chapters. The introduction (Chapter 1) provides the background and context from which the idea for this research emerged. It also explains the objectives of the thesis and outlines its structure. The literature review (Chapter 2) examines prior behavioural, neuroimaging, and computational studies on tactile and visuo-tactile perception of surface spatial features (e.g., orientation and spatial frequency). This includes discussions on well-established paradigms (e.g., orientation adaptation, serial dependence), anatomical findings, and theoretical or computational models of the underlying mechanisms.

Chapters 3, 4, and 5 present the three empirical studies conducted as part of this research. Chapter 3 investigates tactile orientation perception in both passive and active settings. This study aims to determine whether the somatosensory system exhibits characteristics similar to those of visual orientation perception, such as the oblique effect and serial dependence effect. By doing so, it seeks to further our understanding of how orientation information is processed and to explore whether similar orientation-processing mechanisms are shared between the visual and somatosensory modalities. Additionally, it examines the mechanisms underlying serial dependence and the stages of processing at which this phenomenon occurs, and helps to understand the critical influence of perceptual history on current perception.

Chapter 4 extends the exploration to another temporal influence, adaptation, by utilising the classic visual tilt aftereffect (TAE). This chapter investigates whether the adaptation effect can be observed in tactile perception and whether it can transfer between modalities (e.g., vision-to-touch and touch-to-vision). By examining these crossmodal effects, the chapter explores the possibility of a shared orientation-processing mechanism between vision and touch. Additionally, it uncovers evidence of potential non-reciprocal connections between the two modalities, providing further insights into the underlying processing mechanisms.

Chapter 5 investigates the integration of tactile and visual perception of surface spatial frequency using virtual reality (VR) technology. This chapter aims to validate the Bayesian model of multisensory integration in a more realistic and naturalistic environment.

Finally, the General Discussion (Chapter 6) integrates the findings from the three empirical chapters to provide a comprehensive and in-depth analysis of their implications for tactile and multisensory information processing mechanisms. This chapter examines how the results contribute to our understanding of sensory integration and processing, highlighting their relevance to existing theories and models. It also addresses the limitations of the empirical studies conducted in this thesis, such as methodological constraints or areas requiring further exploration. Additionally, the chapter outlines potential future research directions to build on these findings and deepen our understanding of tactile and multisensory perception.

CHAPTER 2

Literature Review

2.1 Overview

This chapter reviews tactile and multisensory perception of low-level spatial features in three parts: Section 2.2 examines key features, neural mechanisms, and behavioural paradigms in tactile and multisensory perception, with a focus on perception of two of the most basic low-level spatial features: orientation and spatial frequency. Section 2.3 discusses how multisensory processes influence tactile perception through different mechanisms, including multisensory integration and crossmodal cortical activation. Finally, Section 2.4 digs into two types of influence of perceptual history in tactile and multisensory perception: adaptation and serial dependence. The aim of this chapter is to review the current understanding of tactile perception of low-level spatial features from a multisensory and temporally dynamic perspective, and to identify gaps in the existing research that motivate the experimental work presented in Chapter 3, 4 and 5.

2.2 Tactile and Multisensory Perception of Low-level Spatial Features

Sensory perception has traditionally tended to be studied within the confines of individual modalities. This tendency comes from the belief that unisensory information is processed independently along distinct neural pathways, with integration occurring only at higher-level brain regions such as the superior colliculus (Alais et al., 2017). However, this view has been increasingly challenged by accumulating evidence over the past decades. Neurophysiological studies have revealed direct and early interactions between primary sensory cortices (Schroeder & Foxe, 2005), while neuroimaging research has demonstrated cross-modal cortical activation even during purely unisensory tasks (Sathian et al., 1997). These findings suggest that the interactions between sensory modalities are closer and more complex than previously assumed, highlighting the need for perception research to adopt a multisensory perspective.

When looking at somatosensory perception and the multisensory influence on it, low-level spatial features such as orientation and spatial frequency offer a valuable window into crossmodal interactions at the early stages of sensory processing. These features are not only among the earliest to be encoded in both the visual and somatosensory systems (Hsiao et al., 1993, 2002; Hubel & Wiesel, 2004; Shapley & Lennie, 1985), but also form the building blocks of sensory perception for more complex structures and functions such as shape and texture (Lieber et al., 2017; Yau et al., 2016). More importantly, multiple streams of evidence point to similarities between the two systems. Similarities have been shown in the neuronal processing of orientation and spatial frequency information in both touch and vision (Hsiao et al., 2002); there is also evidence of crossmodal cortical involvement during unisensory tasks (Sathian & Zangaladze, 2002; Sathian et al., 1997; Zangaladze et al., 1999; Zhang et al., 2005); and similar behavioural phenomena, such as the oblique effect, have been demonstrated in both modalities (Appelle, 1972; Lechelt, 1988). Together, this evidence points to a canonical mechanism for processing low-level spatial features between touch and vision and suggests a close connection between the two systems. Thus, making the low-level spatial features a great entry point into investigating the multisensory influences on tactile perception and understanding the complex relationship between the two systems.

To provide an overview of the current understanding of the two major low-level spatial features investigated in this thesis: orientation and spatial frequency perception, the following section will review existing knowledge on the neural mechanisms and behavioural phenomena related to the processing of these features in both somatosensory and multisensory perception.

2.2.1 Tactile and Multisensory Orientation Perception

2.2.1.1 Neuronal Mechanism of Tactile and Visual Orientation Perception

To understand orientation perception in the somatosensory system, it is essential to first consider its visual counterpart, where many foundational concepts and methodologies originate. Orientation is among the most extensively studied and well-characterised features in vision and is extracted early in the visual processing hierarchy. Neurons in the primary visual cortex (V1) have receptive fields that are selectively tuned to specific orientations at particular spatial scales. Stimuli near a neuron's preferred orientation elicit strong responses, with response strength decreasing systematically as the stimulus deviates from this preferred orientation (Hubel & Wiesel, 2004). Through the population activity of these orientation-selective neurons, the visual system encodes contours and edges across a range of orientations and spatial scales, forming a critical foundation for visual perception (De Valois & De Valois, 1988).

That said, the fundamental nature and importance of orientation perception are not exclusive to vision. Similar functions and mechanisms have also been identified in the somatosensory system. Functionally, similar to vision, orientation perception in touch is considered foundational for a range of essential tactile tasks, including object manipulation (Pruszynski & Johansson, 2014), shape perception (Hsiao, 2008), and the reading of embossed patterns such as Braille (Boven et al., 2000). The neural mechanism of orientation in the somatosensory system also exhibits parallels to that of vision. In the somatosensory system, orientation selectivity has also been observed as early as the first-order peripheral tactile neurons (mechanoreceptors) innervating the skin (Pruszynski & Johansson, 2014). In the central nervous system, orientation tuning to edge stimuli has been well-demonstrated through the population responses of neurons in both the primary (S1) and secondary (S2) somatosensory cortices (Hsiao et al., 2002).

Given the similarities in both the functional role and processing mechanisms of orientation in vision and touch, it is natural to ask whether a shared neural mechanism supports orientation processing across sensory modalities. Indeed, several lines of evidence support this view. Firstly, behavioural studies have revealed shared phenomena in orientation perception between the two modalities—most notably the oblique effect, which will be discussed in detail in the following parts of this section. Secondly, neuroimaging studies suggest that visual cortical areas may play a critical role in tactile orientation perception, a topic that will be explored further in Section 2.3.

2.2.1.2 Oblique Effect in Touch and Vision

One important feature that helps understand the underlying properties of the orientation-tuned neuron and is shown in both modalities is the oblique effect. The oblique effect in vision refers to the phenomenon where a reduced sensitivity in vision at the oblique (diagonal) orientations compared to cardinal directions (vertical and horizontal) (Appelle, 1972). This anisotropy was thought to be the result of the distribution and tuning bandwidth of orientation-selective neurons in the primary visual cortex: there seem to be more neurons tuned to the cardinal directions, with tighter tuning bandwidth when compared to the oblique direction (Li et al., 2003; Mansfield, 1974).

In somatosensory perception, similar anisotropies have also been investigated and demonstrated across various paradigms (Essock et al., 1997, 1992; Gentaz & Streri, 2004; Gibson & Craig, 2005a; Lechelt, 1988, 1992). However, unlike the relatively converging opinions in vision, there have been rather different findings and opinions on this matter. For example, studies examining tactile perception on the fingerpad have reported superior orientation acuity near the Cartesian directions (proximal-distal and medial-lateral) compared to the oblique orientations (Lechelt, 1988, 1992), similar to the oblique effect observed in vision. Other reports have indicated that proximal-distal orientation shows better acuity (Essock et al., 1997, 1992; Gentaz & Streri, 2004; Gibson & Craig, 2005b), while some studies found no evidence of an oblique effect (Craig, 1999). The mixed behavioural results from different paradigms suggest that various factors may influence tactile orientation acuity in touch. Indeed, neurophysiological studies have shown that slow-adapting type 1 (SA1) mechanoreceptors are mildly biased towards proximal-distal orientations (Khalsa et al., 1998), providing the neural basis for superior orientation acuity in that direction. However, other studies suggest that orientation perception in touch is not only guided by the intensity structure of the cutaneous mechanoreceptors, but also by the temporal structure of their responses (Pruszynski & Johansson, 2014), which seems to suggest that the exploration method, whether the stimulus is explored statically or actively, might also play a critical role. Thus, the oblique effect, as a behavioural paradigm, could serve as a valuable tool for investigating the underlying neural mechanisms in tactile orientation perception.

One interesting question raised by this seemingly canonical anisotropy across visual and tactile perception concerns the functional benefits it provides. Multiple studies have shown that the anisotropy in the distribution and tuning of orientation-selective neurons closely resembles the orientation statistics of natural scenes (Girshick et al., 2011; Harrison et al., 2023). This alignment may suggest a shared underlying mechanism: by matching the internal model of orientation distributions to the statistics of the external environment, the brain can achieve optimal statistical inference when noisy sensory inputs are combined with an internal prior. In other words, variation in the preferred orientations and tuning widths of orientation-selective neurons may constitute a way in which the brain embeds the natural statistics of orientation information as a Bayesian prior, thereby enhancing the efficiency of sensory processing at very early stages and enabling more effective interpretation of sensory inputs based on prior experience (Girshick et al., 2011; Harrison et al., 2023).

In somatosensory research, although little has been done on the distribution of orientation information from natural exposure, it is natural to consider the possibility that the same principle drives the anisotropy in tactile orientation perception.

2.2.2 Tactile and Multisensory Spatial Frequency Perception

2.2.2.1 Neural Mechanism of Tactile and Visual Spatial Frequency Perception

Another important low-level spatial feature in sensory perception is spatial frequency, which refers to the rate at which stimulus intensity or amplitude changes across space. In vision, it is well-established that visual scenes contain information across different spatial frequencies, and during perception, features are extracted through distinct spatial frequency channels (Kauffmann et al., 2014). To achieve this function, as mentioned in the previous section, neurons in the primary visual cortex (V1) have receptive fields that can be modelled as Gabor filters (Pollen & Ronner, 1983), with stimuli of specific orientations and spatial frequencies eliciting maximal responses. This property is known as orientation and spatial frequency selectivity (De Valois et al., 1982). Importantly, spatial frequency selectivity is not exclusive to V1; it is observed throughout the visual hierarchy, from retinal ganglion cells (Kelly, 1975) to higher-order cortical neurons (Foster et al., 1985).

In somatosensory perception, spatial frequency processing plays a similarly critical and fundamental role. Functionally, it is shown to be a critical component of fundamental functions such as roughness and texture perception (Bourgeon et al., 2016). From a neural processing perspective, receptive field properties of primary somatosensory neurons exhibit Gabor-like filtering of spatial variations in cutaneous afferent signals (Hsiao et al., 1993), and a substantial proportion of somatosensory neurons demonstrate spatial frequency selectivity (Bourgeon et al., 2016).

Hence, as a low-level spatial feature that plays a critical role in both visual and tactile modalities, with striking similarities in their underlying neural mechanisms, it is both natural and important to examine how spatial frequency information is processed and integrated across these modalities. This question will be explored experimentally and discussed in detail in Chapter 5.

2.2.2.2 Differential Crossmodal Processing of Microspatial and Macrospatial Features

In the preceding text, we demonstrated that orientation and spatial frequency, two fundamental low-level spatial features in both somatosensory and visual perception, are intertwined properties of sensory neurons' receptive fields and exhibit analogous functions and processing mechanisms across modalities. Hence, it is reasonable to expect that a common processing mechanism or cortical areas might be engaged by both modalities when processing these two features.

While evidence supports the crossmodal interaction of orientation (Lunghi et al., 2010; van der Groen et al., 2013) and spatial frequency processing (Roberts et al., 2024), there appear to be critical differences in how these features are processed: the involvement of visual cortex is found during tactile orientation discrimination tasks, but not for spatial frequency discrimination tasks (Sathian et al., 1997). This finding provides solid evidence for a systematic difference in the information pathways of the two types of spatial features, despite the previously mentioned similarities.

One distinction between the two types of low-level spatial features that may underlie this differential activation is their spatial scale. In somatosensory perception, features can be categorised into two types based on scale: macrospatial and microspatial features. Macrospatial features are larger in size, such as form or orientation, while microspatial features include finer details like texture or roughness (Stoesz et al., 2003). Numerous studies have demonstrated that the two types of stimuli differentially activate the brain, with tactile tasks involving macrospatial features appearing to engage the visual cortex, whereas microspatial tasks do not (Roland et al., 1998; Sathian et al., 1997; Stoesz et al., 2003). This evidence suggests that the two types of spatial features are processed separately. While Sathian et al. (1997) proposed that the involvement of the visual cortex may be mediated by mental imagery, this hypothesis has yet to receive concrete empirical support. Hence, in Chapter 4 and Chapter 5, the adaptation and integration paradigms were employed to investigate the tactile and multisensory processing of orientation and spatial frequency, in order to provide additional insights into the distinct cortical processes involved.

2.2.3 Active and Passive Exploration in Tactile Perception and Multisensory Perception

One distinctive feature of somatosensory perception that sets it apart from other sensory modalities is its inherently active nature. Tactile perception almost always involves voluntary movement of the limb, regardless of the objective or goal of the action. The cortical processing of somatosensory stimuli during active versus passive exploration has proven to be more complex than previously assumed. Behavioural studies have yielded mixed findings regarding whether active exploration enhances tactile acuity in the perception of surface spatial features. While some paradigms report little to no difference in performance between active and passive exploration (Olczak et al., 2018; Schwartz et al., 1975; Vega-Bermudez et al., 1991), others show superior performance during active perception (Heller, 1984; Smith et al., 2009), and still other studies have even shown that active movement can, in certain scenarios, suppress discrimination performance (Vitello et al., 2006). These inconsistent results suggest that the neural mechanisms underlying active and passive tactile processing are potentially more intricate than previously hypothesised, warranting further investigation.

Indeed, active exploration of surface features such as roughness has been shown to elicit different activation patterns in the somatosensory cortex compared to passive perception (Simões-Franklin et al., 2010). Moreover, the involvement of motor movement during tactile perception engages additional processes that may influence behavioural outcomes. For example, temporal cues generated by movement appear to be critical for the perception of tactile spatial frequency (Gamzu & Ahissar, 2001) and roughness (Cascio & Sathian, 2001). At the same time, evidence also supports the phenomenon of "tactile gating", whereby cutaneous input can be attenuated during voluntary motor actions (Casado-Palacios et al., 2023; Chapman, 1994; Colino et al., 2014; Schmidt et al., 1990), similar to the well-established movement-related suppression in vision, in which visual sensitivity decreases during saccadic eye movements (Matin, 1974). These different pathways through which active movement can influence tactile perception, along with the mixed psychophysical findings regarding tactile acuity in active versus passive perception, suggest that the underlying mechanisms are not yet fully understood. This issue is explored experimentally and discussed in more detail in Chapter 3.

2.3 Multisensory Influence on Tactile Perception

Sensory perception is rarely an isolated event; rather, it is often dynamically shaped by concurrent inputs from multiple sensory modalities. While earlier models posited independent processing channels, accumulating evidence from behavioural and neuroimaging studies confirms that cross-modal influence is a fundamental feature of the perceptual system (Alais et al., 2010; Schroeder & Foxe, 2005). Consequently, in the study of somatosensory perception, it is important to adopt a holistic view of the perceptual system and consider the influence of other sensory modalities, where the relevant previous studies will be reviewed in this section.

2.3.1 Multisensory Integration

The human perceptual system was shaped through evolution, with different sensory modalities specialised for detecting distinct types of energy and environmental changes. This system maximises the amount of information captured from the external world across diverse environments, particularly when the information available to a single sense is limited. However, this also means that in many scenarios, external stimuli would convey information simultaneously through multiple modalities: for example, moving objects often produce sounds, surface textures are typically perceived both visually and through touch, and speech is accompanied by both sound and mouth movements. When the same event is registered through different modalities, it is important for the brain to accurately identify the common source of these multisensory signals and to utilise their combined information to enhance the salience, accuracy, and efficiency of the sensory processing.

2.3.1.1 Neuronal Mechanisms of Multisensory Integration

Subcortically, at the level of a single neuron, multisensory integration has been defined as the enhancement or suppression of the neuronal response to one sensory input by the presence of stimuli from another sensory modality. One important distinction is that the neural response to a multisensory stimulus cannot be simply deconstructed as the linear summation of its unisensory components, Instead, the presence of the additional cue altered the processing of the original cue, and vice versa, leading to changes in neuron's responses and, and ultimately, in perception, cognition, and behaviour (Meredith & Stein, 1986; Meredith & Stein, 1983). This principle is referred to as "superadditivity" (see Figure 2.1).

In addition to the superadditivity principle, multisensory integration is also governed by temporal and spatial rules. The temporal rule states that optimal integration of stimuli from different sensory modalities is achieved when the multisensory stimuli overlap in time

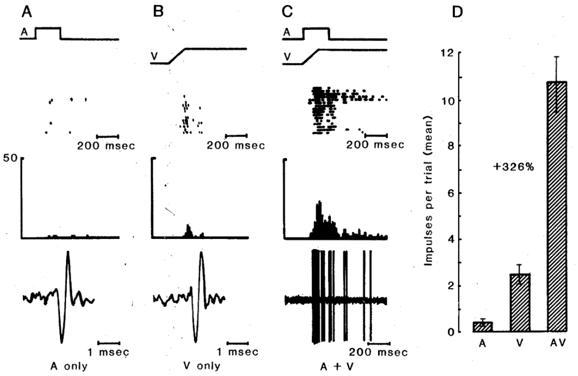

FIGURE 2.1: Example of multisensory enhancement in a neuron from the cat superior colliculus. When presented individually, neither the auditory (A) nor the visual (B) stimulus elicits a strong neuronal response, as shown by the raster plots and histograms of the responses. However, when the auditory and visual stimuli are presented in close temporal proximity (C), there is a marked increase in neuronal firing. Panel D shows a significant difference (326% increase) in the number of impulses in the multisensory (AV) condition compared to the strongest unisensory condition. This supralinear increase indicates that the multisensory response cannot be explained by a simple linear summation of the individual unisensory responses. Figure adapted from (Meredith & Stein, 1983).

(Meredith et al., 1987). Similarly, the spatial rule states that stimuli from different modalities will integrate only if their sources fall within the receptive field of the same multisensory neuron (Kadunce et al., 2001; Stein & Stanford, 2008). This principle is supported by both neurophysiological (Kadunce et al., 2001; Stein & Stanford, 2008; Stein et al., 1989) and behavioural evidence (Sambo & Forster, 2009; Stein et al., 1989), particularly in the context of visuotactile integration (Gepshtein et al., 2005).

Despite well-established research and literature supporting the temporal and spatial rules as fundamental principles of multisensory integration from the neurophysiological perspective, there is also substantial evidence from behavioural tasks that challenge these rules. Specifically, various studies have demonstrated that the validity of the spatial rule is task-dependent: facilitation based on spatial coincidence is not observed in nonspatial tasks or in tasks that do not require the orienting of spatial attention (for a review, see Spence (2013)). While neurophysiological evidence highlights that the receptive field properties of multisensory neurons adhere to the spatial principle, mixed findings from psychophysical studies indicate that integration can occur even in the absence of spatial colocalisation, depending on task demands and feature types. This suggests that interactions between sensory modalities may not be confined to the superior colliculus, a much-studied subcortical multisensory area in the mid-brain; and that, other mechanisms (e.g., in cortical areas) may support integration that does not conform to the spatial rule.

Indeed, in the cerebral cortex, studies in cats (Wallace et al., 1992), primates (Kaas & Collins, 2004), and humans (Beauchamp, 2005) have demonstrated that the convergence of multisensory information extends beyond simple orienting behaviours to more complex forms and feature-based processing (Stein & Stanford, 2008). While the receptive field properties and integrative principles of cortical multisensory neurons resemble those of subcortical neurons (Stein et al., 1995), but with larger excitatory regions and reduced surround inhibition, the rigidity of the spatial rule is relaxed, suggesting that higher-order multisensory integration may be less spatially constrained (Stein & Wallace, 1996).

Besides, numerous neurological and behavioural studies have provided evidence suggesting that the sensory systems are not functionally isolated. These findings will be discussed in detail in Section 2.3.2.In Chapter 5, the validity of the spatial principle in visuotactile integration of spatial frequency is investigated experimentally, and the implications for the mechanisms of multisensory integration are discussed in detail.

2.3.1.2 Maximum Likelihood Estimation (MLE) Model

One prominent framework for modelling multisensory integration is the Maximum Likelihood Estimation (MLE) model.The MLE model proposes that the brain combines information from different sensory modalities in a statistically optimal manner. Because sensory signals are inherently noisy and associated with uncertainty, the goal of multisensory integration is to combine cues from a common source to improve perceptual accuracy (Alais & Burr, 2019). Hence, the combined perception ($\hat{S}_{multisenory}$) could be seen as the weighted linear sum of the unisensory stimuli ($\hat{S}_i$):

$$\hat{S}_{multisenory} = \sum_{i} w_i \hat{S}_i \tag{2.1}$$

where the weight (w_i) of each modality is inversely proportional to its variance (σ_i^2), or uncertainty:

$$w_i = \frac{1/\sigma_i^2}{1/\sum_j \sigma_j^2} \tag{2.2}$$

Hence, the MLE framework predicts that the variance of the combined cue will be lower than that of any individual unisensory cue. In other words, by combining information from different modalities, the reliability of the percept is improved (Ernst & Bülthoff, 2004). The model also predicts that when estimates from different sensory modalities differ (e.g., different spatial frequency estimates), the combined estimate will lie between them, with a bias towards the more reliable modality. In doing so, biases present in unisensory perception can be reduced through the inclusion of a second cue, despite the redundancy of the information it carries. Both predictions made by the MLE model align with the fundamental principles of multisensory perception, that is, to enhance the accuracy and precision of perceptual representations of the noisy external world.

The MLE model has been extensively tested and validated in multisensory research across a wide range of behavioural studies, including visual–auditory (Alais & Burr, 2004) and visual-vestibular integration (Fetsch et al., 2010), etc. Specifically, between somatosensory perception and vision, optimal or near-optimal integration has been demonstrated across various features, including height (Ernst & Banks, 2002) and shape (Helbig & Ernst, 2007a; Helbig et al., 2012), etc.

It is important to note that, despite abundant behavioural evidence showing that the MLE model provides good predictions of experimental data, it does not account for all interactions between information from different modalities. First, the ability to integrate unisensory inputs is not always present and develops over time during childhood (Burr & Gori, 2012). Secondly, even when integration is clearly present, there are cases in which it is suboptimal (Arnold et al., 2019) or even superoptimal (Nikbakht et al., 2018), suggesting that the MLE framework may not fully capture the mechanisms underlying these tasks. In addition, there are also cases where the weighting of each sensory modality does not align with the predictions of the MLE model (Meijer et al., 2019). These pieces of evidence point to more complex interactions between multisensory signals than those accounted for by the MLE model. Some of the evidence for alternative mechanisms of multisensory interaction will be discussed in Section 2.3.2. In Chapter 5, visuotactile integration of spatial frequency information was tested against the predictions of the MLE model to extend its application to a new perceptual domain. Additionally, in Chapter 4, crossmodal adaptation paradigm was used to further explore the intrinsic interactions between sensory modalities.

2.3.2 Crossmodal Cortical Activation During Tactile Perception

As demonstrated in the previous sections, evidence from different lines of research has shown that the processing of multisensory information involves multiple mechanisms and pathways. In this section, the current understanding and opinions of other ways multisensory influences occur, including cross-modal plasticity, early connections, and top-down multisensory influences, will be explored.

2.3.2.1 Cortico-Crotical Crossmodal Connections

Earlier studies in sensory perception largely focused on single modalities, stemming from the notion that primary sensory cortices process information independently. The integration of information from different modalities was believed to occur in multisensory areas located higher up in the sensory hierarchy than unisensory areas (Alais et al., 2010). This framework is largely based on the historical lack of anatomical evidence supporting direct cortico-cortical connections between primary sensory cortices (Jones & Powell, 1970). However, recent advances in neurophysiology and neuroanatomical tracing techniques have demonstrated that this notion is no longer valid, revealing that such cross-connections are present and primary sensory cortices are capable of direct and functionally relevant cross-modal interactions (Cappe et al., 2009; Cappe & Barone, 2005). Behavioural studies have also reported crossmodal activation of the primary visual cortex (V1) from tactile stimuli (Merabet et al., 2007), as well as functional correlations between the primary visual cortex and the primary somatosensory cortex (S1) during tasks involving purely tactile stimulation (Vasconcelos et al., 2011). These findings provide behavioural evidence for the crossmodal engagement of primary sensory cortices, further complementing neurophysiological and anatomical evidence for direct early cortico-cortical connections between these areas.

2.3.2.2 Corssmodal Neuroplasiticy

Another important line of evidence supporting early crossmodal connections is crossmodal neuroplasticity. It has been widely demonstrated that sensory history, such as deprivation of a particular modality—can lead to plastic, adaptive changes in the structure and function of primary sensory cortices, where the deprived cortex is recruited by other modalities (Lee & Whitt, 2015). For example, abundant evidence in early visually deprived populations showed repurposing of the visual cortex for processing stimuli from other modalities, such as touch (Cohen et al., 1997; Sathian & Stilla, 2010).

This flexibility points to two important implications. First, the ability to adapt to changes in sensory experience and process information from other modalities suggests that the neural circuits underlying each sensory system can support the processing of information from different sensory inputs. This provides a biological basis for cross-modal processing of sensory communication (Ghazanfar & Schroeder, 2006). Moreover, the development of this cross-modal processing mechanism is only plausible when there are pre-existing connections between the primary sensory areas (Bavelier & Neville, 2002; Ewall et al., 2021). Together, these pieces of evidence demonstrate the biological basis for multisensory processing in the early sensory cortices, prompting a reconsideration of traditional models of sensory information processing.

2.3.2.3 Top-Down Multisensory Influence

Direct connections between primary sensory cortices may not be the only mechanism underlying crossmodal cortical recruitment; top-down pathways are also highly plausible: in a series of neuroimaging studies, tactile grating orientation tasks were shown to activate the extrastriate visual cortex (Sathian & Zangaladze, 2002; Sathian et al., 1997; Zhang et al., 2005). More importantly, the involvement of the visual cortex appears to be task-dependent, as a tactile spatial frequency discrimination task using the same physical stimulus does not evoke the same response (Sathian & Zangaladze, 2002). Additionally, transcranial magnetic stimulation (TMS) applied over this cortical area severely interfered with participants' ability to resolve orientation tactually (Sathian & Zangaladze, 2002). While providing concrete evidence for cross-modal involvement during tactile orientation perception, these findings also raise an important question: what are the information pathways between vision and touch? The early connections proposed in the previous sections do not explain why cross-modal cortical recruitment would depend on the task, in other words, the perceptual goal. The more plausible hypothesis here is that, in this scenario, the recruitment of the visual cortex during tactile perception is governed by top-down influences. Sathian et al. (1997) proposed that this top-down recruitment of the visual cortex might occur through the reconstruction of orientation information via mental imagery. Hence, in Chapter 4, a crossmodal orientation adaptation paradigm will be used to investigate the stages and mechanisms of multisensory processing and crossmodal cortical recruitment during tactile and visual processing of orientation information.

2.4 Impact of Temporal Context on the Current Perception

While traditional laboratory studies often assume that each perceptual judgment is made independently, the influence of perceptual history has been demonstrated across a wide range of psychological paradigms. Two key processes that highlight the role of perceptual history are neuronal adaptation and serial dependence. Although these mechanisms and their associated effects have been extensively studied and are relatively well-understood in the visual domain, much less attention has been given to their roles in other sensory modalities, such as touch, or to how they interact with multisensory processing. Hence, this section will review the current understanding of perceptual history effects and their implications for tactile and multisensory processing of orientation and spatial frequency.

2.4.1 Adaptation

2.4.1.1 Mechanism and Function of Neuronal Adaptation

Neuronal adaptation is a canonical mechanism observed across many types of neurons; at the single-neuron level, it refers to the reduction in neuronal responses following exposure to a stimulus (Benda, 2021). In perception, sensory neurons are typically tuned to specific features of a stimulus (e.g., orientation, spatial frequency), meaning their responses are strongest when the stimulus matches their preferred feature. A neuron's tuning curve describes its response across a range of stimulus values, with the peak indicating the neuron's preferred feature (Kohn, 2007). When neurons are repeatedly or continuously exposed to their preferred stimulus (the 'adaptor'), the properties of their tuning curves can shift—often resulting in reduced responsiveness and changes in sensitivity. This, in turn, alters the neural response to subsequent stimuli, typically producing a reduction in response (Butts & Goldman, 2006). When examining the population response of adapted neurons, those with tuning curves peaking near the adaptor typically show the strongest reduction in activity. As a result, the overall population response becomes asymmetric, leading to a shift in the population coding of the stimulus away from the adaptor. This neural shift is thought to underlie the repulsive perceptual biases observed following adaptation (Solomon & Kohn, 2014). This explanation of neuronal adaptation is known as the fatigue model.

At first glance, adaptation may appear detrimental to information processing, as the reduced firing rate can make it more difficult for individual neurons to differentiate between similar stimuli (Cortes et al., 2011). However, when considering population coding and the statistical regularities of natural scenes, adaptation emerges as a key mechanism for enabling efficient sensory coding. It facilitates the encoding of a constantly changing environment by dynamically adjusting the mapping between stimulus intensity and neuronal response. This allows the limited dynamic range of neuronal firing rates to be optimally allocated across the range of external stimuli based on the recent perceptual history, which improves accuracy and efficiency in the encoding (Wark et al., 2007).

Although the traditional fatigue model of adaptation accounts for many neurophysiological and behavioural phenomena, accumulating evidence has challenged the validity of the stimulus-specific fatigue framework (Solomon & Kohn, 2014). For example, several studies have reported attractive shifts following adaptation (Patterson et al., 2013; Wissig & Kohn, 2012), which does not fit into the fatigue model. Divisive normalisation, a potential canonical computation observed across various areas of neural processing, has been proposed as a plausible alternative framework that can account for these behaviours (Carandini & Heeger, 2011; Solomon & Kohn, 2014). The divisive normalisation model proposes that the response of a single neuron is scaled by the overall activity of a population of nearby or functionally similar neurons (normalisation pool) (Carandini & Heeger, 2011). The direction of the observed perceptual shift (attractive vs. repulsive) from the adaptor can be explained by whether the adaptation has a stronger effect on the classical receptive field of the target neuron or on the normalisation pool. In the former case, adaptation suppresses the response of the target neuron, leading to a repulsive shift. In the latter case, suppression of the normalisation pool reduces inhibition, thereby enhancing the target neuron's response and resulting in an attractive shift (Solomon & Kohn, 2014). In Chapter 4, divisive normalisation is discussed in detail within the context of crossmodal adaptation, aiming to further evaluate the validity of this framework as a canonical neural computation and to better understand the nature of asymmetrical crossmodal adaptation effects.

2.4.1.2 Orientation Adaptation and Tilt Aftereffect

The tilt aftereffect (TAE) is a classic and well-known phenomenon that serves as a valuable tool for investigating adaptation effects in orientation-selective neurons (Gibson, 1937). The tilt aftereffect (TAE) occurs when a tilted stimulus is presented for a prolonged duration. According to the fatigue model of adaptation, neurons tuned to orientations near the adaptor exhibit reduced responsivity, with the strongest suppression occurring in neurons whose preferred orientation matches the adaptor. As a result, the population representation of a subsequent stimulus is biased away from the adaptor orientation, causing the stimulus to be perceived as 'tilted' in the opposite direction (Solomon & Kohn, 2014).

In somatosensory perception, given the similarity in the mechanism of orientation encoding, it is natural to expect that a similar orientation adaptation effect should be present. Indeed, analogous tactile tilt aftereffects (TAEs) have been demonstrated in previous studies (Hidaka et al., 2022; Silver, 1969), suggesting that the population representations of orientation in vision and touch closely resemble each other. Together with evidence from crossmodal cortical activation during tactile orientation processing and other related findings, these results support the notion of shared or overlapping neural mechanisms underlying orientation processing across sensory modalities.

2.4.1.3 Crossmodal Transfer of Adaptation Effect

With robust behavioural shifts and a well-established theoretical framework, adaptation and aftereffects have become powerful tools for investigating the transfer of information between sensory modalities. In multisensory research, numerous studies have employed adaptation effects to probe the underlying mechanisms of crossmodal processing (Domenici et al., 2022; Ehrenstein & Reinhardt-Rutland, 1996; Konkle et al., 2009; Tonelli et al., 2017; Xiao et al., 2021). Specifically, between touch and vision, the crossmodal transfer of motion aftereffects has provided concrete evidence for shared motion representations (Konkle et al., 2009). Visual adaptation to a tilted grating has been shown to bias the perception of subsequent tactile two-point orientation stimuli on the forehead (Krystallidou & Thompson, 2016). These transfers of the aftereffects provide behavioural evidence for a common population of neurons involved in processing shared features across sensory modalities. In Chapter 4, a systematic experimental investigation of tactile and crossmodal visuotactile tilt aftereffects (TAE) is presented, alongside a discussion of the interaction between adaptation and another key perceptual history effect, serial dependence. This aims to further clarify the orientation processing pathways between the somatosensory and visual systems, while also probing the stages and mechanisms at which these two distinct perceptual history effects arise.

2.4.2 Serial Dependence

2.4.2.1 Serial Dependence in Vision and Other Modalities

In recent years, another form of temporal influence on the current perception has been widely reported in vision, where the current perception is systematically biased towards the recent past. This attractive bias is termed the serial dependence (SD) effect (for review, see Manassi et al. (2023), Pascucci et al. (2023) and Cicchini et al. (2024)). This attractive bias to the recent past was first observed in orientation perception by Fischer and Whitney (2014), in which they found the perception of the orientation of a Gabor patch was systematically biased toward the previous orientation, and this attractive shift peaked when the relative orientation difference was at around $27.78°$ (see Figure 2.2).

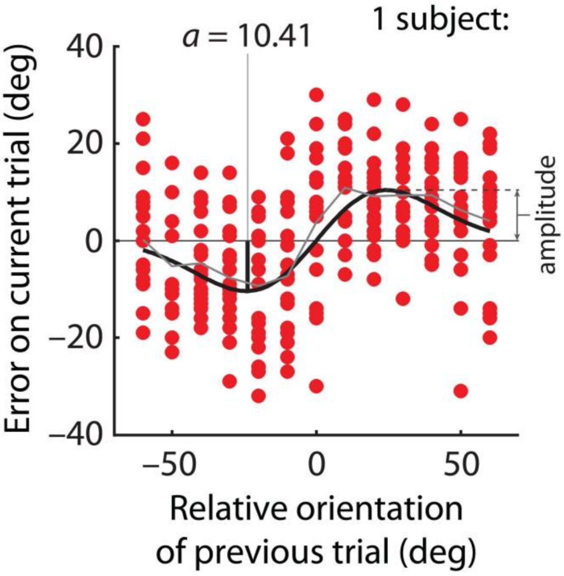

FIGURE 2.2: Attractive serial dependence effect observed in an orientation estimation task. Figure adapted from Fischer and Whitney (2014).

Since Fischer and Whitney (2014)'s finding, researchers have been adapting this paradigm and have since demonstrated serial dependence effect in a variety of different visual tasks, ranging from low-level visual features such as numerosity (Cicchini et al., 2014; Fornaciai & Park, 2020), colour (Barbosa & Compte, 2020), to higher-level features such as face identity (Liberman et al., 2014), face attractiveness (Xia et al., 2016), food preferences (Alais et al., 2024) and aesthetic judgements (Kim et al., 2019).

This broad range of serial dependence observed in vision suggests the potential presence of an underlying canonical processing mechanism in our perceptual system. Indeed, the serial dependence effect has also been investigated and demonstrated across various other modalities and tasks. In auditory perception, for example, it has been observed in features such as rate perception (Motala et al., 2020), emotion (Van der Burg et al., 2024), as well as in temporal order and magnitude judgments (Roseboom, 2019). Besides, the serial dependence effect has also been shown for olfaction (Van der Burg et al., 2021). These findings also support the notion that the serial dependence effect, instead of being an isolated phenomenon in vision, is a fundamental temporal processing mechanism that is universal across the perceptual systems.

2.4.2.2 Debates and Controversies in the Stage of Processing and Direction

As interest in serial dependence has grown, research in this field has expanded significantly over the past decade. With increasing efforts dedicated to this topic, controversies and debates have also emerged. The first hypothesis that has been challenged is the state of processing where the effect originates: Upon its discovery by Fischer and Whitney (2014), serial dependence was initially thought to originate from early perceptual processing and directly alter perception due to its spatial tuning. This view has been supported by a series of studies. Firstly, it was demonstrated that the attractive bias to the previous stimulus still occurs without a previous decision (Manassi & Whitney, 2022; Murai & Whitney, 2021), previous response (Cicchini et al., 2017; Manassi et al., 2018), or even an explicit task (Fornaciai & Park, 2018). A neuroimaging study using fMRI also demonstrated that orientation signals in primary visual cortex also shows a serial dependence effect(St. John-Saaltink et al., 2016).

However, while evidence continues to accumulate in support of this hypothesis, another set of findings has emerged in recent years that point to an alternative theory. Bliss et al. (2017) suggest that the serial dependence effect is absent at the time of perception and emerges as working memory is engaged and increases in magnitude with retention time. Fornaciai and Park (2018) found that the serial dependence effect was absent when no explicit task was given, suggesting that the effect likely originates from post-perceptual processing. Kim et al. (2020) used a binocular rivalry paradigm to reveal that serial dependence requires conscious awareness of the stimuli, providing strong evidence for the post-perceptual origin hypothesis. These findings suggest that the attractive bias observed with the behavioural paradigms might manifest during post-perceptual processing and working memory, rather than at the low-level perceptual stages. With no conclusive findings, further research is needed to clarify this issue. One possibility is that serial dependence originates post-perceptually but then manifests at a perceptual level through feedback.

The debate over the state of origin is not the only controversy; with the growing number of studies in this area, another set of contradictory findings regarding the direction of this effect has emerged over the past years which further complicates the puzzle. As mentioned earlier, one major differentiation between the serial dependence effect and the classical sensory adaptation effect was its attractive nature. However, many studies have observed a repulsive serial effect or a mix of both attractive and repulsive effects (Alais et al., 2017; Sadil et al., 2023; Zhang & Alais, 2020; Zhou et al., 2024). These mixed findings, along with the inevitable involvement of repulsive neural adaptation, potential serial effects in decision-making and working memory, and the limitations of behavioural and neuroimaging paradigms in disentangling these processes, have made serial dependence a highly debated and unresolved topic. Studying serial dependence in the somatosensory domain will help to clarify this debate.

CHAPTER 3

Tactile Orientation Anisotropy and Serial Dependence

The work in this chapter has been submitted as a preprint at:

Wang, G., & Alais, D. (2025a, March 19). Characteristics of tactile orientation perception: Oblique effect, active vs passive exploration, and serial dependence [Pages: 2025.03.19.644099 Section: New Results]. https://doi.org/10.1101/2025.03.19.644099

3.1 Introduction

Orientation perception is one of the most fundamental aspects of the somatosensory system. Tasks such as object manipulation (Pruszynski & Johansson, 2014) and shape perception (Hsiao, 2008) heavily rely on the ability to resolve orientation through touch. Similar to visual orientation perception, orientation information is extracted very early in the somatosensory processing hierarchy, with selectivity to edge orientations being found in first-order peripheral tactile neurons innervating the glabrous skin (Pruszynski & Johansson, 2014), and orientation information is well represented in the population response of primary (S1) and secondary (S2) somatosensory cortex neurons (Hsiao et al., 2002). Considering the aforementioned similarities, it is not surprising to suggest that the two modalities might share the same orientation processing mechanism for efficiency. Indeed, over the years, evidence from both neuroimaging (Nikbakht et al., 2018; Sathian & Zangaladze, 2002; Sathian et al., 1997; Zangaladze et al., 1999; Zhang & Alais, 2020) and behavioural studies (Lunghi & Alais, 2013; van der Groen et al., 2013; Wang & Alais, 2024) has accumulated in support of this hypothesis. Therefore, it can be imagined that more visual phenomena could be replicated in the somatosensory modality if they indeed share common processing mechanisms. This could also provide further insight into orientation processing in somatosensation.

The oblique effect is a well-known anisotropy in visual perception, where performance in various tasks is superior along the cardinal directions compared to oblique orientations (Appelle, 1972; Essock, 1980; Heeley et al., 1997). In recent years, evidence has accumulated to reveal the mechanism of this visual orientation anisotropy: it appears that what led to the superior acuity at cardinal orientations is the greater amount of orientation-selective neurons tuned to these orientations and the tighter orientation tuning of these cardinally-tuned neurons (Li et al., 2003). Moreover, the similarity between the pattern of this orientation anisotropy and the orientation distribution in natural visual scenes seems to suggest that an environmental prior is embedded in cortical processing through this mechanism, which enables efficient encoding of orientation information at a very early perceptual stage (Girshick et al., 2011; Harrison et al., 2023).

Inspired by the anisotropy in visual processing and the similarity in orientation processing between vision and somatosensation, researchers began investigating whether there is evidence for an analogous "oblique effect" in touch. Not surprisingly, a similar anisotropy has been demonstrated in tactile orientation perception (Essock et al., 1997, 1992; Gentaz & Streri, 2004; Gibson & Craig, 2005a; Lechelt, 1988, 1992). Neurophysiological studies also showed that the slowly adapting type 1 (SA1) neurons, thought to be the main processing system of orientation information (Hsiao et al., 2002), is mildly biased towards stimuli in the proximal-distal orientation (Khalsa et al., 1998). However, unlike the rather consistent findings in vision, varied results have been reported regarding the somatosensory orientation anisotropy, with some reporting effects similar to the visual oblique effect where proximal-distal and medial-lateral are more accurate than oblique (Lechelt, 1988, 1992), while others report proximal-distal is superior to other orientations (Essock et al., 1997, 1992; Gentaz & Streri, 2004; Gibson & Craig, 2005a). Additionally, some studies reported no anisotropy in tactile orientation acuity (Craig, 1999). These mixed results raised an interesting question: Is this tactile oblique effect purely a result of the distribution of orientation-selection neurons, similar to the oblique effect in vision, or is it modulated by other factors that are unique to touch and which may vary between different tasks? For instance, the reference frame of visual orientation is almost always consistent due to gravity and the upright position, which supports the idea that anisotropy facilitates optimal inference based on the natural statistics of orientation distributions. In contrast, tactile perception, particularly at the fingertip, lacks such consistent reference frames during everyday interactions, which warrants further investigation into the tactile oblique effect to better understand these factors.

Another important difference between touch and vision that might mediate the observed anisotropy is the active nature of somatosensory perception. Researchers over the years have spent considerable effort investigating how active movement affects tactile perception, revealing multiple differences between passive and active tactile perception. It has been shown that cutaneous inputs can be attenuated during voluntary movement of body parts, a phenomenon known as 'tactile gating'. (Casado-Palacios et al., 2023; Chapman, 1994; Colino et al., 2014; Schmidt et al., 1990) By this principle active touch would be predicted to show inferior performance compared to passive exploration, however, most research comparing the two tasks showed little difference between the exploration methods (Olczak et al., 2018; Schwartz et al., 1975; Vega-Bermudez et al., 1991) or even active being superior to passive exploration (Heller, 1984; Smith et al., 2009). These contradictory results suggest that additional facilitatory mechanisms must be in play to counteract the effect of tactile gating. Complementing this, compared to passive touch, active exploration of a surface was found to produce different patterns of activation in the primary somatosensory cortex (S1) (Simões-Franklin et al., 2010), which shows that active exploration is not merely passive touch combined with additional motor movement. Instead, there appears to be a critical difference in cortical processes that differentiate these two modes of exploration, potentially engaging alternative sensory processing mechanisms and incorporating additional cues, which is likely to be developed as a result of our perceptual system adapting to the active nature of tactile exploration.

One possible origin of this difference is the additional cues involved during active touch due to the motor movement. Studies have found evidence that spatial (position) and intensity (force) cues are integrated during the active exploration of surface textures, combining in a manner consistent with maximum likelihood estimation (MLE) (Drewing & Ernst, 2006). The active movement of the finger introduces a changing temporal profile of receptor activation, which was found to improve performance on tactile spatial tasks (Cascio & Sathian, 2001; Gamzu & Ahissar, 2001).

Given the rather complex differences in processing mechanisms involved in active tactile perception, it is possible that the observed oblique effect could result from a combination of anisotropies originating at multiple levels of the tactile processing hierarchy. Hence, the different processes in active and passive tactile exploration might lead to different patterns of the oblique effect. Hence, in Experiment 1, we implemented a factorial design to examine the impact of active versus passive touch and its potential interaction with the oblique effect. We hypothesised that the oblique effect may differ between active and passive exploration, and active exploration might reduce the potential benefit of the proximal-distal direction with the involvement of potential tactile gating and additional temporal information.

Another feature of visual perception that has been widely investigated in recent years is the serial dependence effect, in which the current percept is systematically biased towards the previous percept (for review, see Pascucci et al. (2023), Cicchini et al. (2024) and Manassi et al. (2023)). This effect was first demonstrated on orientation perception (Fischer & Whitney, 2014), and was then observed on a variety of visual tasks, from low-level features like numerosity (Fornaciai & Park, 2018) and colour (Barbosa & Compte, 2020), to high-level features such as face (Liberman et al., 2014), facial attractiveness (Xia et al., 2016) and aesthetic judgement (Kim et al., 2019). This attraction to perceptual history is thought to be developed by the brain as a means to facilitate stable perception against the constantly changing visual input Cicchini et al., 2018.

However, despite extensive investigations, a debate continues regarding the origin of this effect. Evidence from various studies supports the low-level perceptual (rather than cognitive or decision) nature of this bias, as the attractive bias is observed without previous decision (Manassi & Whitney, 2022; Murai & Whitney, 2021) or response (Fornaciai & Park, 2018). However, there are also contradicting findings that suggest that serial dependence requires conscious awareness of the previous stimulus (Kim et al., 2020), and gains in strength in post-perceptual processing such as when maintained in working memory for a later decision (Bliss et al., 2017). As the exact mechanism of the serial dependence effect is still unclear, more investigation is needed to clarify this puzzle.

Although a few attempts have been made to examine serial dependence in other modalities (Fornaciai & Park, 2019b; Motala et al., 2020; Van der Burg et al., 2024), it has not been extensively investigated in touch. In our previous research, we were the first to demonstrate an attractive serial dependence effect in tactile orientation perception (Wang & Alais, 2024), as occurs in vision. However, as the paradigm was not optimised for serial dependence analysis, we undertook Experiments 2 and 3 to further clarify the serial dependence effect in touch. Given the similarity between vision and somatosensation in orientation perception, we proposed that a similar attractive serial dependence effect should be observed in tactile orientation perception. Consistent with this, Bae (2024) demonstrated that serial dependence in vision interacts with the oblique effect, which points to the two processes happening at a similar processing stage. Hence, we proposed to examine tactile serial dependence and whether it interacts with the oblique effect in Experiment 2. In Experiment 3, by separating the response from perception, we hope to investigate whether the observed serial dependence is indeed a low-level perceptual effect, or if it relies on the post-perceptual processing.

3.2 Method

3.2.1 Participants

A total of 36 naive participants were recruited for this study, 12 participants participated in each of the 3 experiments. All participants reported being right-hand dominant with no recent history of damage to the right index finger and no history of damage or diseases of the nervous system. This research was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048), and all methods were carried out in accordance with relevant guidelines and regulations. Participants were first and second-year psychology students from the University of Sydney, recruited through the Sydney University Psychology SONApsych research participation system, and were given course credit for their participation. Informed consent was obtained from all participants prior to the commencement of the experiment.

3.2.1.1 Apparatus and Stimuli

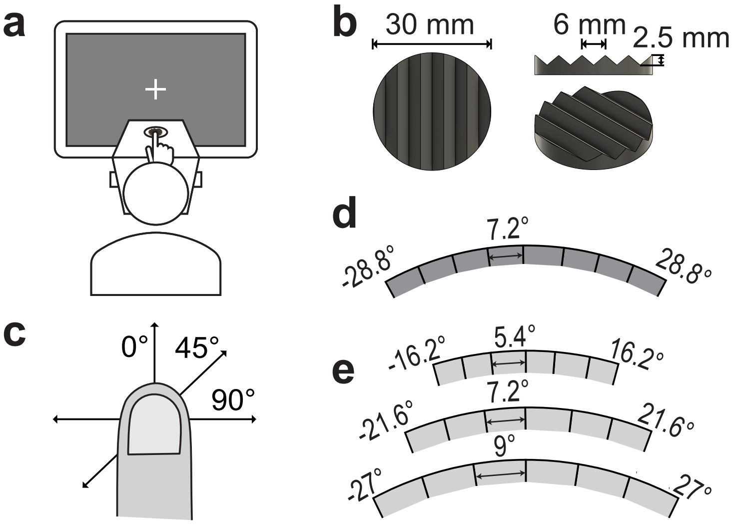

FIGURE 3.1: Experimental setup and the tactile stimulus used in the study. **a.** The participant was seated facing the tactile device, and a screen that displayed instructions, with their right index fingerpad positioned above the circular opening. The tactile grating disk was raised through the opening at a specified orientation and for a controlled duration. Participants were required to maintain an upright position and fixate on the fixation cross during the experiment to prevent body rotation. **b.** The tactile grating discs used in the experiment had a 30 mm diameter. They were 3D-printed with a triangular wave of 6 mm spatial period and 2.5mm peak-to-trough distance. **c.** Sets of stimulus orientations were centred around three orientations: proximal-distal: 0°, oblique: 45°and medial-lateral:90°. **d.** The nine stimulus orientations used in Experiment 1 ranged from -28.8°to 28.8°, with a 7.2°gap between each orientation level. These orientation levels are with respect to the centre orientation of each block. **e.** The three sets of stimulus orientations used in Experiments 2 and 3 were individually selected for each participant based on their performance in a preliminary test of orientation acuity. This approach aimed to address the significant variability in orientation acuity observed in Experiment 1, thereby ensuring better-fitting psychometric functions for serial dependence analysis.

The tactile stimuli used in all experiments were 3D-printed using an Ultimaker S5 3D printer. The circular stimulus disk had a diameter of 30 mm with the top surface being a triangular wave of 6 mm spatial period and a peak-to-trough amplitude of 2.5 mm, the disk was designed in FreeCAD and is shown in Figure 3.1b. The stimulus disk was attached to a motor assembly that consisted of a stepper motor and a servo motor. Each step of the stepper motor corresponded to an angular rotation of $1.8°$, and was used to control the orientation of the stimulus disk. The servo motor could elevate or lower the stimulus disk as commanded, which was used to control the presentation time of the stimulus. The motor assembly also contained a light sensor to calibrate the position of the stepper motor at the beginning of each test block. The motor assembly was controlled by MATLAB scripts via an Arduino UNO board and Adafruit Motor Shield V2.3. The aforementioned motor assembly was housed in a 3D-printed cuboid container, featuring a circular opening on the top surface with a diameter of 35 mm, through which the stimulus was raised for exploration by the participant. The entire box and motor device was fixed on a table in front of the participant. On the table beyond the box was a computer screen, which was used to deliver instructions to the participant during the experiment (see Figure 3.1a).

Prior to the commencement of each trial block, participants were instructed to sit in front of the screen with their heads resting on a chinrest. They were then asked to place their right hand in a pronated (palm-down) position on top of the container, which was located directly in front of their torso. The right index finger was positioned over the circular opening, pointing straight forward towards the screen (see Figure 3.1a). At the beginning of each block, the grating stimulus disk was positioned underneath the top surface, which prevented the participant from touching it. During the experiment, the stimulus disk was rotated on each trial to the designated orientation by the stepper motor and then raised to the top surface through the circular opening by the servo motor so it could be touched (passively or actively, depending on condition) by the participant. It was then lowered back down after a controlled stimulus duration after each presentation.

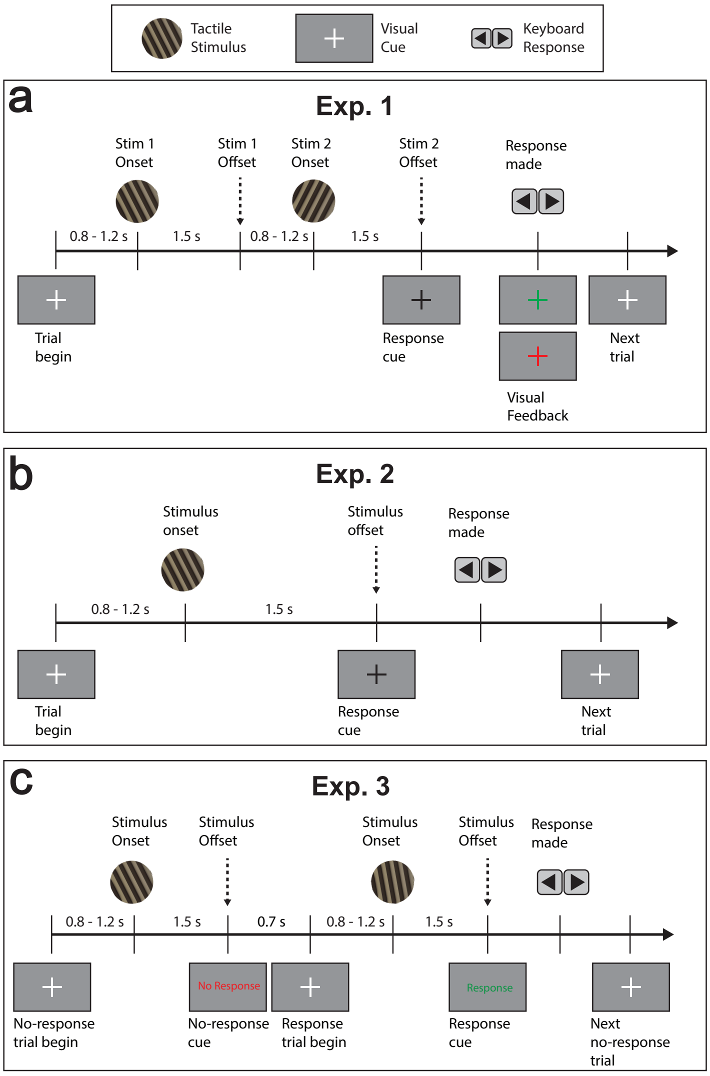

FIGURE 3.2: **a.** Experiment 1 procedures: Each trial in the 2IFC task included two tactile stimulus presentations, each lasting 1.5 seconds. Following the presentations, participants responded by indicating whether stimulus 2 was CCW or CW relative to stimulus 1. Responses were made using the arrow keys, and visual feedback was provided through a subsequent colour change in the fixation cross. **b.** Experiment 2 Procedures: Experiment 2 utilised a single-stimulus 2AFC task. After presenting a single stimulus, participants responded using the arrow key to indicate whether the stimulus was CCW or CW relative to a reference orientation. The reference orientations of the block (proximal-distal, oblique, or medial-lateral) were shown to participants prior to the commencement of each block. **c.** Experiment 3 Procedures: Experiment 3 employed the single-stimulus 2AFC task similar to Experiment 2; however, participants were cued to respond on only every second trial.

3.2.2 Design and Procedure

3.2.2.1 Experiment 1: Tactile Orientation Acuity

The 12 participants involved in Experiment 1 attended two sessions on different days. In each session, they were instructed to perform the same orientation discrimination task using different methods (passive vs active), with the order of sessions counterbalanced to mitigate potential learning effects. For the passive condition, participants were instructed to passively feel the orientation of the stimulus disk without moving their index finger. In the active touch condition, participants were instructed to freely explore the grating disk by stroking their index finger over the grating to feel its orientation.

Each session of the experiment comprised six blocks. One of the three reference orientations (proximal-distal: 0°, diagonal: 45°, and medial-lateral: 90°, see Figure 3.1c) was used for each block to assess the variations of orientation acuity at different axes. Each reference orientation was tested in two blocks. The sequences of the reference orientations were also counterbalanced between participants to minimise potential learning effects.

In both the active and passive conditions, participants were required to perform a simple two-interval-forced-choice (2IFC) orientation discrimination task. In each trial, the tactile grating disk will be presented to the participant twice, each lasting 1.5 seconds. This presentation duration was chosen based on pilot data and is consistent with prior work using comparable grating-orientation tasks (Craig, 1999). The two stimuli consisted of the reference orientation of the block and a test stimulus, which was drawn from the nine test stimuli around the reference orientation, ranging from -28.8°to 28.8°with respect to the reference orientation of the block (see Figure 3.1d). The order of the reference stimulus and test stimulus was pseudo-randomised to ensure an equal number of trials for both orders. The two presentations were separated by a randomised interval between 0.8 and 1.2 s while the stepper motor rotated the grating disk to the next orientation. The rotation included a randomised component so that the interstimulus interval and any motor-related noise were uncorrelated with the orientation change, preventing these cues from signalling the upcoming orientation.

After the two intervals of stimulus presentation, the fixation cross on the screen turned from white to black to cue the participant to respond using the left and right arrow keys, indicating whether the second presentation of the grating stimulus was rotated more counter-clockwise (left arrow key) or clockwise (right arrow key) in comparison to the first presentation. After their response, the fixation cross changed colour (correct response: green; incorrect response: red) to provide feedback and there was another 0.8 to 1.2 s random interval before the start of the next trial

Following the two presentations, the fixation cross on the screen changed from white to black, serving as a response cue. Participants indicated their response using the left and right arrow keys, signifying whether the second presentation of the grating stimulus was rotated more counter-clockwise (CCW: left arrow key) or clockwise (CW: right arrow key) compared to the first presentation. After the response, the fixation cross changed colour again (correct response: green, incorrect response: red) to provide visual feedback. After 300 ms, the fixation cross would turn white, indicating the start of the next trial.

3.2.2.2 Experiment 2: Tactile Orientation Serial Dependence

As the two-interval 2IFC paradigm in Experiment 1 was not optimal for serial dependence analysis, Experiment 2 used a single-interval 2AFC task. The same three centre orientations used in Experiment 1 were used to replicate the oblique effect observed earlier and demonstrate the validity of the new paradigm as a measure of orientation acuity. However, in contrast to Experiment 1, only the passive touch method was employed.

Unlike Experiment 1, the range of the orientation used in Experiment 2 was different for each participant. At the beginning of each session, a preliminary test of approximately five minutes was conducted, which was designed to address the considerable variability in tactile orientation acuity observed in Experiment 1. The preliminary test employed the most extreme stimulus orientation from the three orientation sets to establish a preliminary estimation of participants' relative tactile orientation acuity. One of the three stimulus ranges would be selected based on the participant's performance in the preliminary test, to ensure a better psychometric function fitting for bias estimation (see Figure 3.1e). Moreover, each set of orientations only comprised seven levels to reduce the number of trials needed.

Prior to the commencement of the block, one of the three centre orientations was presented to the participant on the screen, serving as the reference orientation for that block. During each trial, participants were presented with a stimulus orientation for 1.5 seconds. Following this, they were visually cued by the colour change of the fixation cross and responded using the arrow keys, indicating whether the stimulus was more CCW or CW compared to the reference orientation of the block. No feedback was given in this experiment.

3.2.2.3 Experiment 3: Alternating Response

To differentiate the serial effect between response and perception, we implemented an alternating response paradigm in Experiment 3. The procedure closely follows the design of Experiment 2, with only the proximal-distal reference orientation (0°) used in this experiment to further simplify the design. In this experiment, participants were cued to respond only on every second trial. In the trials where no response was required, participants were instructed to solely focus on feeling the orientation of the stimulus without the need to make a response. Following the stimulus presentation, a "No Response" prompt appeared on the screen for 0.7 s, to maintain a similar time gap between trials as those with responses.

3.2.3 Data Analysis

3.2.3.1 Psychometric Function Fitting:

Psychometric functions were individually fitted for each participant and each condition using the hierarchical Bayesian psychometric function fitting of the Palamedes Toolbox in MATLAB (Prins, 2023):

$$\Psi(x;\alpha,\beta,\gamma,\lambda) = \gamma + (1-\gamma-\lambda)F(x;\alpha,\beta) \tag{3.1}$$

where $F(x;\alpha,\beta)$ is a cumulative Gaussian function with threshold α and slope β. The point of subjective equality (PSE) is obtained as the threshold (α, 50% CW response) of the fitted psychometric function, where non-zero PSE denotes the participants' bias in orientation judgement. The slope (β) denotes the steepness of the psychometric function, which is used as a measure of orientation acuity. The parameters γ and λ represent the guess rate and the lapse rate, which denotes the difference between asymptotes of the psychometric function to 0% and 100%, respectively. The threshold (α) and slope (β) were set to vary freely across participants and conditions, while the guess rate (γ) was constrained to equal lapse rate (λ), and fixed across multiple conditions within a single participant. This was done to ensure that the guess rate and lapse rate can better capture the actual intentional lapse which should be roughly the same across different conditions as the conditions were broken into different blocks and counterbalanced within a session. This should help better capture the potential differences in orientation bias and acuity among conditions through the two free parameters α and β.

3.2.3.2 Serial dependence analysis:

The serial dependence effect was quantified as the difference between the point of subjective equality (PSE) between the different previous stimulus/response conditions, following the standard approach established by Fischer and Whitney (2014), calculated as the equation below:

$$\Delta PSE = PSE_{CCW} - PSE_{CW} \tag{3.2}$$

where a positive value indicates the current perception is attracted towards the previous stimulus/response and a negative value indicates the current perception is repulsed away from the previous stimulus/response.

3.2.3.3 N-back serial dependence effect:

As the Shapiro-Wilk test indicated that the PSE differences deviated from normality, we used non-parametric permutation tests to analyse the n-back stimulus/response serial dependence effect. For each n-back stimulus/response condition, 10,000 permutations were created by random swap PSE_{CCW} and PSE_{CW} for each participant. The p-value of the permutation test is calculated as the proportion of permuted t-statistics that were greater than the observed t-statistic obtained from the original ΔPSEs (see Figure 3.6c):

$$p_{perm} = \frac{count(|t_{permutation}| \geq |t_{obs}|)}{10,000} \tag{3.3}$$

The family-wise error rate was then controlled using the Holm-Bonferroni procedure:

$$p_{holm} = (C - i + 1)p_{perm} \tag{3.4}$$

Where C represents the number of tests conducted for each family (in this case, $C = 6$ as the analysis was conducted up to the 6-back effect), and i represents the rank of the particular p-value in ascending order.

3.3 Results

3.3.1 Experiment 1: Tactile Orientation Acuity

3.3.1.1 Effect of Touch Method and Reference Orientation on Orientation Acuity

A two-way repeated-measures ANOVA was conducted to examine the effect of the touch method (passive, active) and reference orientation (vertical, oblique, horizontal) on the tactile orientation acuity (Figure 3.3b). The tactile orientation acuity is quantified using the slope (β) of the fitted psychometric function, with a higher value (steeper slope) representing better orientation acuity. The sphericity assumption was checked for reference orientation ($\chi^2(2) = 1.316$, $p = .518$) and the interaction between touch method and reference ($\chi^2(2) = 2.791$, $p = .248$) using Mauchly's test but neither was significant.

The passive touch condition ($M = 0.064°$, $SD = 0.035$) showed significantly lower tactile orientation acuity than the active touch condition ($M = 0.082°$, $SD = 0.035$) ($F(1, 11) = 11.815$, $p = .006$, $n_p^2 = .518$). There was a significant main effect of reference orientation on tactile orientation acuity ($F(2, 22) = 10.459$, $p < .001$, $n_p^2 = .487$). There was no significant interaction effect between the touch method and central orientation ($F(2, 22) = 3.034$, $p = .069$, $n_p^2 = .216$). Post hoc tests on the main effect of centre orientation using Holm correction revealed that tactile orientation acuity was significantly higher for the stimulus around vertical orientation ($M = .092, SD = 0.027$) compared to the oblique orientation ($M = .068, SD = 0.039$, $t(11) = 3.255$, $p_{holm} = .007$, Cohen's d = 0.781) as well as horizontal orientation ($M = .059, SD = 0.033$, $t(11) = 4.410$, $p_{holm} < .001$, Cohen's d = 1.058). There was no significant difference between oblique and horizontal centre orientation ($t(11) = 1.155$, $p_{holm} = .260$, Cohen's d = 0.277).

3.3.1.2 Effect of Touch Method and Reference Orientation on Orientation Bias

Another two-way repeated-measures ANOVA was carried out on the PSEs to examine the biases in tactile orientation perception under each condition. The sphericity assumption was checked for reference orientation ($\chi^2(2) = 1.772$, $p = .412$) and the interaction between touch method and reference ($\chi^2(2) = 0.451$, $p = .798$), but neither was significant.

The PSEs were found to differ significantly around different reference orientations ($F(2, 22) = 4.090$, $p = .031$, $n_p^2 = 0.271$). No significant differences in PSEs were found between passive ($M = -4.940°$, $SD = 9.280°$) and active touch method ($M = -3.060$, $SD = 5.201$, $F(1, 11) = 1.626$, $p = .228$, $n_p^2 = 0.129$). No significant interactions were found ($F(2, 22) = 0.043$, $p = .958$, $n_p^2 = 0.004$).

Post hoc tests revealed that the orientation judgments near the horizontal orientation ($M = -6.926, SD = 8.661$) were significantly biased towards the CW direction compared to orientation judgments near the vertical orientation ($M = -1.438$, $SD = 4.628$, $t(23) = 2.841$, $p_{holm} = .028$, Cohen's $d = 0.744$). No significant differences in PSEs were found between oblique ($M = -3.637$, $SD = 7.915$) and vertical ($t(23) = 1.139$, $p_{holm} = .267$, Cohen's $d = 0.298$), or between oblique and horizontal ($t(23) = 1.703$, $p_{holm} = .205$, Cohen's $d = 0.446$).

3.3.1.3 Serial Dependence Effect in 2AFC Tactile Orientation Acuity Experiment

Although the 2AFC paradigm is not optimal for assessing the serial dependence effect, we attempted the serial dependence analysis by dividing the trials based on the average stimulus orientation of the previous 2IFC trial. The normality assumption was checked with the Shapiro-Wilk test, and no significant deviation from normality was found ($W = .950$, $p = .636$). A one-sample t-test on the ΔPSE revealed that trials with an average orientation of the previous trial CCW to the average of the current trial exhibited a significantly lower PSE compared to trials with an average orientation of the previous trial CW to the current trial ($M = -2.921°$, $SD = 3.388$, $t(11) = -2.987$, $p = .012$, Cohen's d = -0.862), which indicates a significant repulsive serial dependence effect.

3.3.2 Experiment 2: Tactile Orientation Serial Dependence

3.3.2.1 Oblique Effect in Single-Stimulus Tactile Orientation Acuity Experiment

To verify whether the oblique effect we observed in Experiment 1 was paradigm independent, two one-way repeated measures ANOVAs were performed to evaluate the effect of reference orientation on the PSEs (α) and slopes (β) with the single-stimulus test in Experiment 2. The sphericity assumption was checked for reference orientation for both analyses using Mauchly's test and the assumptions were both met (PSE: $\chi^2(2) = 2.795$, $p = .247$; Slope: $\chi^2(2) = 4.879$, $p = .087$).

For the PSE analysis (Figure 3.4a), unlike Experiment 1, no significant orientation bias was found at different reference orientations ($F(2, 22) = 0.161$, $p = .852$, $n_p^2 = 0.014$).

When looking at the slope (Figure 3.4b), orientation acuity differs significantly as a function of reference orientation ($F(2, 22) = 4.647$, $p = .021$, $n_p^2 = 0.297$). *Post hoc* analysis with Holm-Bonferroni family-wise correction found that orientation acuity at vertical orientation ($M = 0.099$, $SD = 0.039$) was significantly better than the oblique orientation ($M = 0.068$, $SD = 0.021$, $t(11) = 2.747$, $p_{holm} = .035$, Cohen's $d = 0.964$) as well as horizontal orientation ($M = 0.071$, $SD = 0.033$, $t(11) = 2.518$, $p_{holm} = .039$, Cohen's $d = 0.883$). No significant differences in orientation acuity were found between oblique orientation and horizontal orientation ($t(11) = -0.229$, $p_{holm} = .821$, Cohen's $d = -0.080$).

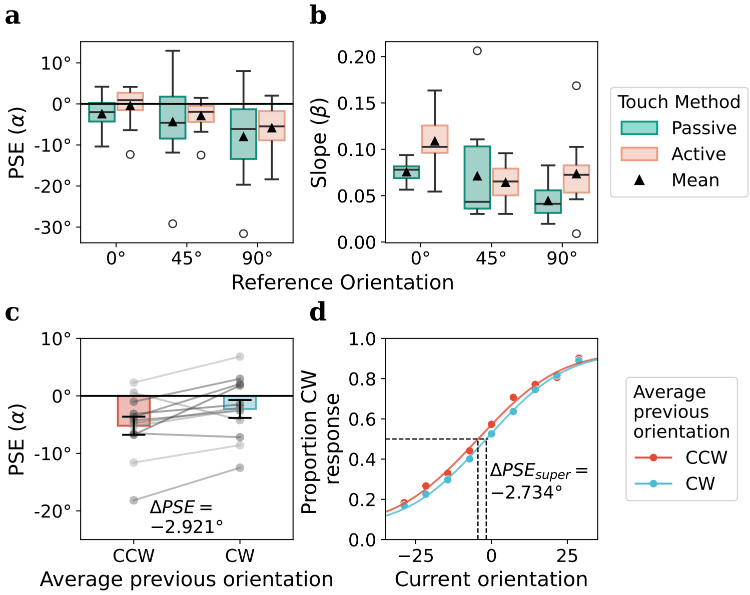

FIGURE 3.3: Experiment 1 results: **a.** The bias in orientation perception for all participants using the active vs passive touch method at the three different centre orientations (0°, 45°, and 90°) was quantified using the point of subjective equality (PSE) (threshold α from the fitted psychometric function, 50% CW response). A positive value represents a CCW bias, and a negative value represents a CW bias. No significant differences were found between active and passive touch ($p = .228$). Significant differences were found between different reference orientations ($p = .031$), with post hoc analysis showing the medial-lateral (0°) axis demonstrating CW biases compared to the proximal-distal axis (0°) ($p_{holm} = .028$) The central line represents the median, the box denotes the interquartile range (Q1–Q3), and whiskers extend to 1.5 times the IQR. Circles indicate outliers. And the triangle indicates the mean. **b.** The tactile orientation acuity for all participants under each condition was quantified using the slope of the fitted psychometric function (β), where a higher value represents a steeper psychometric function (better orientation acuity). Active exploration showed significantly higher orientation acuity than passive touch ($p = .006$). When looking at the orientation acuity (slope of the psychometric function, β), it is also significantly better near proximal-distal orientation (0°), compared to oblique (45°) ($p_{holm} = .007$) or medial-lateral (90°) ($p_{holm} < .001$). **c.** Serial dependence analysis: trials were divided based on the average orientation of the two stimuli in the previous trial, and the PSEs under the CCW and CW average previous stimulus orientations indicated a significant repulsive serial dependence effect ($p = .012$). Error bars represented standard errors. **d.** Psychometric functions for the supersubject data (all participants aggregated)reveal a shift in the PSE between the CCW and CW average previous stimulus orientation conditions. This shift indicates that the response in the current trial is repelled from the average orientation of the previous stimulus.

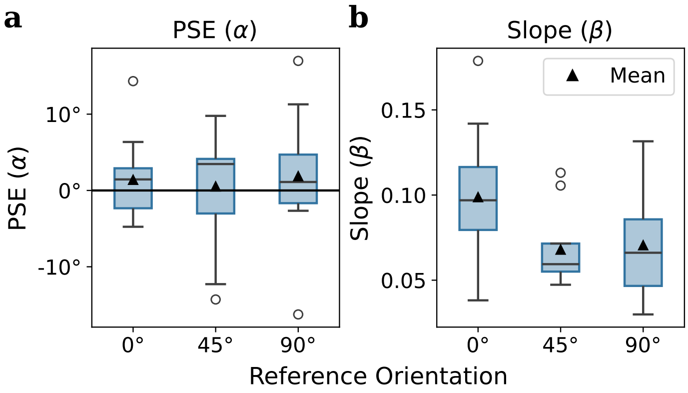

FIGURE 3.4: Experiment 2 results: **a.** PSEs (α) of the fitted psychometric functions at each reference orientation. Unlike Experiment 1, no significant differences were found between different reference orientations ($p = .852$). The central line represents the median, the box denotes the interquartile range (Q1–Q3), and the whiskers extend to 1.5 times the IQR. Circles indicate outliers. And the triangle indicates the mean. **b.** Slopes (β) of the fitted psychometric functions at each reference orientation were used to assess the anisotropy in orientation acuity. Significant differences were found between different reference orientations ($p = .021$), with post hoc analyses indicating the proximal-distal axis (0°) exhibiting superior orientation acuity compared to the oblique orientation ($p_{holm} = .035$) as well as horizontal orientation ($p_{holm} = .039$).

3.3.2.2 Stimulus-Driven Serial Dependence Effect

To evaluate the serial dependence effect, a two-way repeated measures ANOVA was conducted to examine the effect of the previous stimulus orientation (CCW vs. CW to the current stimulus) and reference orientation (vertical, oblique, horizontal) on the biases in tactile orientation perception (Figure 3.5a). The orientation bias was quantified using the PSE (α) of the fitted psychometric function, where a positive value represents a leftward (CCW) bias in orientation, and a negative value represents a rightward (CW) bias. The sphericity assumption was tested for centre orientation ($\chi^2(2) = 4.829$, $p = .089$) and the interaction between previous stimulus orientation and centre orientation ($\chi^2(2) = 1.199$, $p = .549$) using Mauchly's test, but neither was significant. Trials preceded by the CCW stimulus ($M = 3.193$, $SD = 7.224$) showed a significantly more leftward bias than the CW stimulus ($M = -1.173$, $SD = 6.178$) ($F(1, 11) = 15.528$, $p = .002$, $n_p^2 = .585$), which indicates an attractive serial dependence effect. There was no significant main effect of centre orientation on the tactile

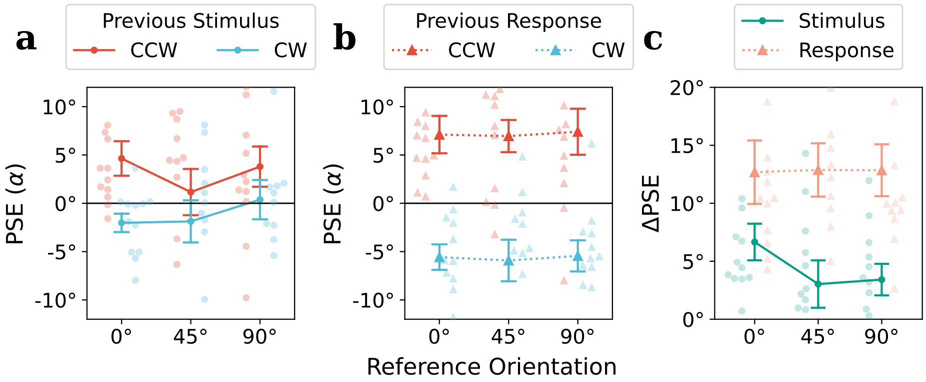

FIGURE 3.5: Experiment 2 serial dependence effect: **(a)** Significant attractive serial dependence effects were found with respect to the previous stimulus orientation ($p = .002$). No significant differences were found between different reference orientations, and no interaction was found between previous stimulus orientation and reference orientation. **(b)** Significant attractive serial dependence effects were found with respect to the previous response ($p < .001$). No significant differences were found between different reference orientations, and no interaction was found between previous stimulus orientation and reference orientation. **(c)** When comparing the stimulus-driven and response-driven serial dependence effect, the response-driven effect was significantly stronger ($p < .001$). No significant differences were found between reference orientations, and no significant interactions were found. Error bars represent standard errors.

orientation bias ($F(2, 22) = .669$, $p = .522$, $n_p^2 = .057$) or interaction effect between the previous stimulus orientation and centre orientation ($F(2, 22) = 1.652$, $p = .215$, $n_p^2 = .131$).

3.3.2.3 Response-Driven Serial Dependence Effect

A similar two-way repeated-measures ANOVA was conducted to examine the effect of the previous response and centre orientation on the biases in tactile orientation perception (Figure 3.5b). The sphericity assumption was tested for centre orientation ($\chi^2(2) = 2.246$, $p = .325$) and the interaction between previous response and ($\chi^2(2) = 1.055$, $p = .590$) using Mauchly's test, but neither was significant.

Trials preceded by the CCW response ($M = 7.155$, $SD = 6.780$) showed a significantly more leftward bias than the CW response ($M = -5.645$, $SD = 5.814$) ($F(1, 11) = 45.398$, $p < .001$, $n_p^2 = .805$), which also indicates an attractive serial dependence effect. There is no significant main effect of centre orientation on the tactile orientation bias ($F(2, 22) = .033$, $p = .968$, $n_p^2 = .0503$) or interaction effect between the previous response and centre orientation ($F(2, 22) = .003, p = .997, n_p^2 < .001$).

To investigate the difference in attractive serial dependence effect between the previous stimulus and previous response (Figure 3.5c), a two-way repeated-measures ANOVA was performed on the PSE differences (ΔPSE, see Equation 3.2) of different types of previous influence (stimulus vs response) and centre orientations. The sphericity assumption was tested for centre orientation ($\chi^2(2) = 0.261$, $p = .877$) and the interaction between centre orientation and type of previous influence ($\chi^2(2) = .873$, $p = .646$) using Mauchly's test, neither was significant.

The previous response ($M = 12.800$, $SD = 8.189$) showed a significantly more attractive serial effect compared to the previous stimulus ($M = 4.371$, $SD = 5.903$) ($F(1, 11) = 56.295$, $p < .001$, $n_p^2 = .837$). No significant differences were found for centre orientation ($F(2, 22) = .352$, $p = .707$, $n_p^2 = .031$). No significant interaction were observed ($F(2, 22) = 2.798, p = .083, n_p^2 = .203$).

3.3.3 Experiment 3: Tactile Orientation Serial Dependence With Alternating Responses

3.3.3.1 N-back Stimulus/Responses Serial Dependence Effect in Experiments 2 and 3

Shapiro-Wilk tests were carried out to assess the normality assumption and found the distribution of n-back ΔPSEs significantly deviated from normality for Experiment 2 ($W = .779$, .722, .724, .824, .778, .871, $p = .005$, .001, .001, .018, .005, .067). We therefore carried out multiple non-parametric permutation tests with family-wise Holm-Bonferroni correction to test the serial dependence effect with respect to n-back stimulus/responses for both Experiments 2 and 3.

To compare the results between Experiments 2 and 3, the analysis was only carried out on the blocks with a vertical reference orientation from Experiment 2. The attractive serial

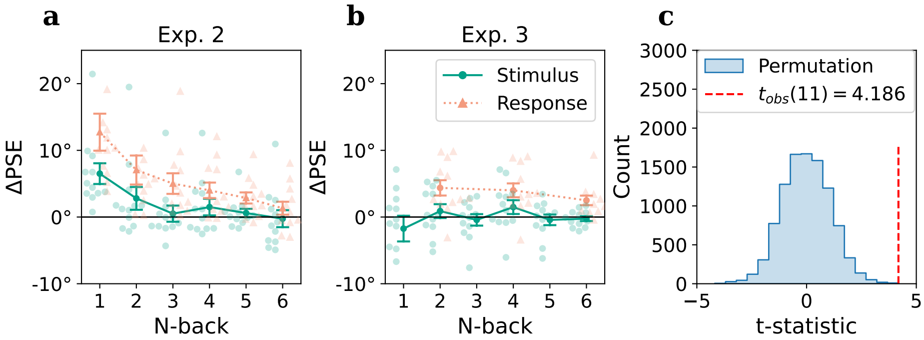

FIGURE 3.6: N-back serial dependence effect in experiments 2 and 3: **a.** The mean ΔPSE between the trials with CCW stimulus and CW stimulus in the n-back trials (green line) and between CCW response and CW response in the n-back trials (orange line) in Experiment 2. Significant attractive serial dependence effects were observed for 1-back stimulus and 1-back to 5-back responses (see Table 3.1 and Table 3.2 for statistics). Error bars represent SEM. **b.** No significant serial dependence effects were observed with respect to the n-back stimulus. Significant attractive serial dependence effects were observed for 2-back, 4-back, and 6-back responses (see Table 3.3 and Table 3.4 for statistics). Error bars represent standard errors. **c.** An example of the non-parametric permutation test that was used to assess the n-back serial dependence effect. The example is for the 1-back stimulus in Experiment 2. The blue histogram shows the t-statistic distribution from the 10,000 permutations, the observed t-statistic is shown by the red dashed line. The p-value was calculated as the percentage of permuted t-statistics that exceed the observed statistics and were corrected using the Holm-Bonferroni procedure, $p_{Holm;perm} = .0048$.

dependence effect with respect to the previous stimulus was only significant for the 1-back stimulus (see green line in Figure 3.6a and Table 3.1). With respect to the previous response, the attractive serial dependence effects were significant up to the 5-back response (see orange line in Figure 3.6a and Table 3.2).

In Experiment 3, no significant serial dependence effect was found with respect to the previous stimulus (see green line in Figure 3.6b and Table 3.3). Since the responses were only requested on every second trial, the attractive serial dependence effects can only be calculated for the 2, 4 and 6-back responses, and were found to be significant for all three (see orange line in Figure 3.6b and Table 3.4).

Table 3.1: Experiment 2 N-Back Statistics With Respect to the Previous Stimulus

N-back	M	SD	$t_{obs}(11)$	p_{obs}	Cohen's d_{obs}	$p_{Holm;perm}$
1	6.505	5.383	4.186	$.002^{**}$	1.208	$.0048^{**}$
2	2.795	5.921	1.635	.130	0.472	.4210
3	0.507	4.192	0.419	.683	0.121	1.0000
4	1.496	4.326	1.198	.256	0.346	1.0000
5	0.599	2.190	0.947	.364	0.273	1.0000
6	-0.248	4.412	-0.194	.849	-0.056	.8606

Note. $p_{Holm;perm}$ > 1 is set to 1. $*p < .05$. $**p < .05$. $***p < .05$.

Table 3.2: Experiment 2 N-Back Statistics With Respect to the Previous Response

N-back	M	SD	$t_{obs}(11)$	p_{obs}	Cohen's d_{obs}	$p_{Holm;perm}$
1	12.725	9.609	4.587	$< .001^{***}$	1.324	$.0032^{**}$
2	7.048	7.539	3.238	$.008^{**}$	0.935	$.0012^{**}$
3	5.016	5.343	3.252	$.008^{**}$	0.939	$.0035^{**}$
4	4.006	4.016	3.456	$.005^{**}$	0.998	$.0057^{**}$
5	2.859	2.880	3.440	$.006^{**}$	0.993	$.0058^{**}$
6	1.323	3.378	1.356	.202	-0.392	.2074

Note. $p_{Holm;perm}$ > 1 is set to 1. $*p < .05$. $**p < .05$. $***p < .05$.

Table 3.3: Exp. 3 N-Back Statistics With Respect to the Previous Stimulus

N-back	M	SD	$t_{obs}(11)$	p_{obs}	Cohen's d_{obs}	$p_{Holm;perm}$
1	-1.733	6.677	-0.899	.388	-0.259	1.0000
2	0.892	3.587	0.861	.407	0.249	1.0000
3	-0.425	2.978	-0.494	.631	-0.143	.6754
4	1.488	3.592	1.435	.179	0.414	1.0000
5	-0.421	2.753	-0.530	.607	-0.153	1.0000
6	-0.242	1.246	-0.673	.515	-0.194	1.0000

Note. $p_{Holm;perm}$ > 1 is set to 1. $*p < .05$. $**p < .05$. $***p < .05$.

Table 3.4: Exp. 3 N-back Statistics With Respect to the Previous Response

N-back	M	SD	$t_{obs}(11)$	p_{obs}	Cohen's d_{obs}	$p_{Holm;perm}$
2	4.371	3.973	3.811	$.003^{**}$	1.100	$.0046^{**}$
4	4.003	3.596	3.856	$.003^{**}$	1.113	$.0074^{**}$
6	2.497	2.472	3.499	$.005^{**}$	1.010	$.0033^{**}$

Note. $p_{Holm;perm}$ > 1 is set to 1. $*p < .05$. $**p < .05$. $***p < .05$.

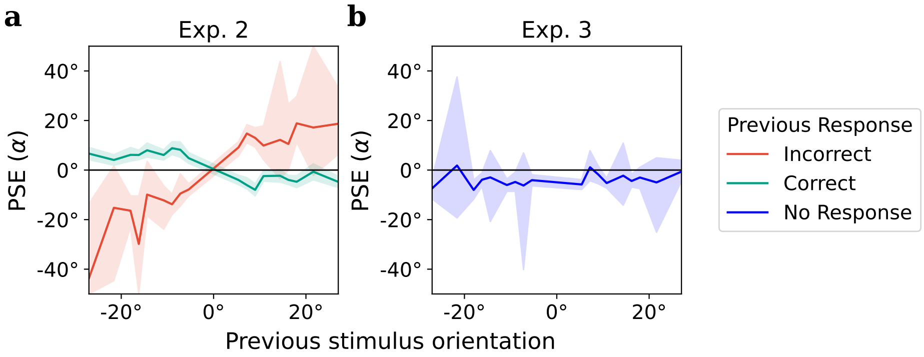

FIGURE 3.7: Bootstrapped estimates of the mean and 95% confidence intervals for the pse across different previous stimulus orientations in Experiments 2 and 3: **(a)** Experiment 2: Trials were categorized based on the accuracy of the previous response. For each category, 10,000 simulations were performed to calculate the bootstrapped mean and confidence interval. Trials following a correct response (represented by a green line) demonstrated an attraction effect on the current trial, unaffected by the orientation of the previous stimulus. Conversely, trials following an incorrect response exhibited a repulsive effect on the subsequent trial (red), and this repulsion appeared to amplify with the orientation of the previous stimulus. **(c)** Experiment 3: the bootstrapped PSE seems to be rather stable across different previous stimulus orientations, where no responses were required (blue).

3.3.3.2 Effect of Previous Trial Correctness and Orientation on the Serial Dependence Effect

We employed bootstrap methods to calculate means and confidence intervals, examining the impact of the correctness of the previous response and orientation on the serial dependence effect. In Experiment 2 (Figure 3.7a), by dividing the previous trial based on its correctness, we can see that different patterns of serial dependence effect can be observed for correct and incorrect responses. For the trials where the previous trial's response was correct (green), it shows an attractive serial dependence effect: when the previous stimulus was CCW, the bootstrapped PSE of the current trial was shifted towards the CW direction, meaning a CW stimulus was perceived as neutral, hence attracted towards the previous stimulus orientation, and *vice versa*. This attraction appears not to be affected by the previous stimulus orientation. On the contrary, the previous incorrect response showed a repulsive effect on the upcoming trial (red), in other words, the response of the current trial was repulsed away by the previous stimulus and attracted to the direction of the incorrect previous response. Although there seems to be increased variability between bootstrapped trials at the more extreme previous stimulus orientation, due to the decrease in a limited sample of incorrect trials with extreme stimuli, the bootstrapped mean and confidence interval still demonstrated a quite robust repulsion. In Experiment 3, the PSE was rather stable across all previous stimulus orientations when no responses were given (blue). These findings were in agreement with the previous analysis which shows that the attractive serial dependence effect was driven by the response.

3.4 Discussion

3.4.1 Superior Tactile Orientation Acuity at Proximal-Distal Axis

As mentioned earlier, in vision, a promising hypothesis to explain the evolutionary benefits of anisotropy in the orientation tuning of visual neurons is that matching the internal model of orientation distribution to the statistics of the external environment facilitates optimal statistical inference (Girshick et al., 2011; Harrison et al., 2023). Hence, it is reasonable to hypothesise that the observed tactile oblique effect, where proximal-distal orientation (with respect to the finger) shows significantly better acuity compared to oblique or medial-lateral orientations (Figure 3.3b), may have a similar origin. Although few studies have investigated the distribution of contact orientations during natural tactile tasks, it is plausible that the observed tactile oblique effect originates from a similar anisotropy in somatosensory neurons. This neural tuning would enable optimal inference when combining internal priors with external tactile stimuli.

Our current findings seem to support this hypothesis. First, in Experiment 1, no interaction was found between the exploration method and the reference orientation, suggesting that the observed oblique effect is not influenced by the additional cues or tactile gating effect associated with active exploration. Therefore, it is more likely to be an anisotropy embedded in the actual cortical processing of orientation information that was shared between the different touch methods, rather than an artifact due to other factors such as movement patterns or finger shapes; Second, Experiment 2 showed when a single stimulus was present and compared with an internal reference system, the same pattern of oblique effect was observed (Figure 3.4b), therefore further showing that the observed tactile oblique effect is not only touch-method independent but also paradigm-independent. The robustness of the tactile oblique effect observed in our study, together with neurophysiological evidence showing that SA1 peripheral fibres exhibit stronger responses to proximal–distal orientations (Khalsa et al., 1998), supports the view that this perceptual asymmetry may arise from anisotropies in somatosensory orientation tuning. And such anisotropy may reflect functional advantages similar to those proposed for the visual oblique effect.

This anisotropy observed in single-digit tactile tasks may also contribute to enhanced processing efficiency when multiple digits are involved. Previous findings in both humans (Hsiao et al., 2002) and animals (Fitzgerald et al., 2006) suggest that the receptive fields of orientation-selective neurons may span multiple digits. This arrangement likely aids in orientation perception during object handling, as it is common for an edge or pattern on a tool or object to contact multiple fingers simultaneously. Geometrically, an edge aligned with the finger's long axis makes proximal–distal contact with the fingertip and is therefore unlikely to contact adjacent finger pads due to hand anatomy. In contrast, an edge spanning multiple fingers is typically oriented orthogonally or diagonally to the digits, presenting a medial–lateral or oblique surface contact across them. Therefore, the superior acuity observed for proximal-distal orientations on a single fingerpad may compensate for the absence of input from neurons with cross-digit receptive fields, resulting in a more efficient encoding strategy. This proposal aligns with the theory that the anisotropy of neuronal tuning is matched to natural statistics to facilitate optimal perceptual inference (Girshick et al., 2011; Harrison et al., 2023). To validate this, future studies should examine orientation acuity across multiple digits to determine if the reduced acuity for oblique and medial-lateral orientations on a single finger is mitigated by the recruitment of multiple digits.

Although the anisotropy of orientation acuity seems to fit with our hypothesis, upon investigation of the orientation biases, it was found that the PSEs also differed significantly around the reference orientations, with the medial-lateral orientation biased towards CW direction when compared with the proximal-distal orientation (Figure 3.3a). This finding was not anticipated given the 2IFC design randomised sequence between reference and test stimuli in each trial. One possible explanation is that the observed bias could result from a recency effect, which describes the preference for more recent stimuli in a forced-choice paradigm (Mehrani & Peterson, 2015). In our Experiment 1, the observed clockwise (CW) bias reflects a tendency to favour the second stimulus over the first, particularly near medial-lateral orientations compared to proximal-distal ones. This could be due to inferior orientation acuity near the horizontal axis, leading to increased uncertainty, where more trials fell below the just-noticeable difference. Consequently, participants were forced to guess, amplifying the recency effect in comparison to the proximal-distal reference orientation. This would also explain why such a bias was not observed in Experiment 2. Despite a similar pattern of anisotropy in orientation acuity, each trial in Experiment 2 consisted of only a single stimulus presentation, thus preventing the systematic amplification of biases favouring either choice. This finding also indicated the importance of switching to the single stimulus design in Experiments 2 and 3, as the recency effect within each 2IFC trial would potentially mediate the investigation of the between-trial serial dependence effect.

3.4.2 Active Exploration Shows Better Orientation Acuity Than Passive

In Experiment 1, the active tactile perception showed a consistently better orientation acuity compared with passive tactile perception despite the reference axis (Figure 3.3b). The advantage of active perception aligns with previous research (Heller, 1984; Smith et al., 2009), confirming that the disadvantage of potential tactile gating during active exploration can be compensated by the various additional cues involved in active perception.

As mentioned earlier, compared to passive touch, active exploration introduces a series of additional spatial, intensity, and temporal cues. Spatially, the lateral movement across the grooved surface elicits activation in afferents across different sites on the fingertip. Regarding intensity, the forces applied to the skin differ from the passive condition, potentially resulting in higher stimulation intensity. Finally, unlike the passive condition, these spatial and intensity cues vary dynamically over time due to the non-linear nature of natural finger movement during active exploration. The presence of these additional cues already provides the brain with more information on which to base its decisions. For example, temporal cues can improve performance in tactile spatial tasks (Cascio & Sathian, 2001; Gamzu & Ahissar, 2001), and increasing the applied force can enhance tactile acuity (Jung et al., 2019). Moreover, there is evidence that these cues can be combined in an MLE-like manner, further improving sensitivity (Drewing & Ernst, 2006). Hence, the multifaceted advantages provided by these additional cues during active exploration may outweigh the suppression associated with tactile gating, resulting in the improved tactile performance observed in this study.

On top of the additonal cues, the active perception might also improve tactile orientation acuity via adaptation to the rapidly adapting (RA) afferents. Bensmaïa et al. (2006b) found that the ratio between SA1 response and RA response correlated with the tactile spatial acuity, where RA response is likely to act as a form of noise during fine spatial perception. As the active movement during active perception involves the participants' pad moving laterally across the grating surface, the mechanoreceptors are subject to vibratory stimulation, and since the RA fibre adapts quicker than the SA1 afferents (Leung et al., 2005), the reduced responsivity in RA afferents might help to amplify the ratio between SA1 and RA afferents, and hence improve the acuity in tactile spatial perception.

Furthermore, numerous neurophysiological studies indicate that active tactile perception is not merely an additive process to passive perception. Research suggests fundamental differences in cortical activation between the two exploration methods. For instance, Krupa et al. (2004) demonstrated not only layer-specific functional differences between active and passive touch in the rat somatosensory cortex, but also neuronal activation prior to direct contact. This anticipatory activity indicates a distinct difference in neuronal processing during active perception, likely mediated by top-down pathways. Similarly, studies in humans have shown distinct activation patterns in the somatosensory cortex using fMRI (Simões-Franklin et al., 2010).

3.4.3 Attractive Serial Dependence in Touch is Driven by the Previous Response

In Experiment 1, when separating the trials based on whether the average orientation of the previous 2IFC trial was CCW or CW to the average of the current trial, we noticed a significant shift in PSE that indicated a repulsive serial dependence effect (Figure 3.3c,d). This repulsive serial effect seems to contradict the findings in visual orientation perception (Fischer & Whitney, 2014), as well as the attractive tactile serial dependence effect in our previous study (Wang & Alais, 2024). However, the two-interval 2IFC design, while robust for investigating orientation acuity, is not optimal for serial dependence analysis due to its multiple stimulus presentations within one trial. Hence, in Experiment 2, we adopted a single stimulus paradigm to simplify the structure of each trial and better reveal the influence of the previous trial. As previous research had indicated that serial dependence can also arise from a motor response and lead to individual differences in serial dependence (Zhang & Alais, 2020), the active exploration condition was removed from Experiment 2 to reduce the number of factors and to keep the focus on serial dependence in tactile orientation processing.

Contrary to Experiment 1, an attractive serial dependence was found in Experiment 2. There is also no evidence of this attraction to the past being mediated by the reference orientation (Figure 3.5a). These results seemed encouraging as they demonstrated an attraction to the recent past in tactile orientation perception similar to its visual counterpart. However, further examination of the serial dependence effect with respect to the previous response showed an even larger attractive effect (Figure 3.5b, c). As the previous stimulus was unavoidably highly correlated with the previous response, it was unclear whether this attraction was driven by the stimulus *per se*, or by the post-perceptual processing/response.

To address this, in Experiment 3, we introduced an alternating response paradigm, where the participants were cued to respond on only every second trial. By doing so, we were able to separate the serial dependence effect of stimulus and response. When looking at the n-back serial dependence effect, we found that there was no significant serial dependence effect with respect to the previous stimulus. However, the attraction to the previous response can be found to be significant up to the 6-back response. Compared to Experiment 2, where the stimulus-driven attractive serial dependence effect is significant for 1-back trials and the response-driven effect is significant for up to 5-back trials, these results further highlight a robust and long-lasting attractive serial dependence effect driven by response-related or post-perceptual processing.

To further examine the complicated interplay between stimulus and response in the previous trial, we plotted the bootstrapped mean and confidence interval across different previous stimulus orientations (Figure 3.7). If the serial dependence effect were purely a perpetual effect, the PSE should not be affected by the correctness of the previous response. However, in Experiment 2, for the previous correct responses, attractive serial dependence was consistently observed across different levels of the previous stimulus orientations, with clear differences across stimulus orientations. For the previously incorrect stimulus, a repulsive serial effect was found. This distinction between correct and incorrect previous responses indicated that the serial effect could not be a purely perceptual effect. The fact that attractive serial dependence (green line) seems rather consistent across the different previous stimulus orientations with a narrow confidence interval further supports the post-perceptual decision origin of the attractive bias. For trials following an incorrect response, the repulsive PSE bias relative to the previous stimulus indicates that participants' current judgments were drawn toward their previous incorrect decision. Notably, both the mean bias and its confidence interval increased as the previous stimulus deviated further from the reference orientation. Because the task in Experiment 2 required participants to judge whether the stimulus was CW or CCW relative to the reference, larger deviations made the discrimination easier. Therefore, an incorrect response on highly discriminable (i.e., extreme) trials is more plausibly due to lapses (such as missed stimuli or motor response errors) rather than perceptual uncertainty. Consequently, the increasing magnitude of repulsive biases tied to the previous stimulus (or in other words, attraction toward the previous incorrect choice) may arise from a tendency to repeat the prior decision or motor response when perceptual information is absent, with the response process continuing to bias subsequent trials despite the lack of reliable sensory information.

Another possible explanation for the lack of serial dependence in Experiment 3 with respect to the stimulus could also be the observed tactile orientation serial dependence effect originating from processing in the visual cortex. Various studies have found evidence for the involvement of the visual cortex during tactile orientation perception (Hidaka et al., 2022; Hu et al., 2021; Krystallidou & Thompson, 2016; Lunghi & Alais, 2013; Merabet et al., 2007; Sathian & Zangaladze, 2002; van der Groen et al., 2013; Zangaladze et al., 1999; Zhang et al., 2005). In our previous study, we also found that the tilt aftereffect (TAE) in touch could be transferred crossmodally to vision (Wang & Alais, 2024). Given the critical role of the visual cortex in tactile orientation perception, the observed serial dependence effect in Experiment 2 could also be manifest during orientation perception in the visual cortex. And as post-perceptual processing of orientation information is critical in activating the visual cortex (Zangaladze et al., 1999), the trials where responses were not cued might not involve the orientation processing in visual cortical areas, and hence did not induce an attractive serial dependence effect in the next trial. However, as the origin of serial dependence in visual processing and the connection between the visual and somatosensory cortices are still not fully understood, this remains a hypothesis.

3.5 Conclusion

In this study, we conducted three experiments to investigate the intricate connection between the oblique effect, active exploration, and serial dependence in tactile orientation perception. By drawing analogies with visual orientation perception paradigms, we aim to better understand the tactile orientation processing mechanism and its similarity to visual orientation processing.

We demonstrated a robust tactile oblique effect that was independent of exploration methods (active vs passive) and paradigms (single-interval vs two-interval trials), with the proximal-distal axis showing superior orientation acuity compared to the oblique or medial-lateral axes. Additionally, we found that active exploration resulted in better orientation acuity across all reference axes. Finally, we demonstrated that the attractive serial dependence effect in touch is response-driven. These findings highlight the complexity of tactile orientation processing and its parallels with visual perception, offering new insights into the underlying mechanisms of somatosensory orientation processing and its similarities and differences relative to vision.

CHAPTER 4

Tactile Adaptation to Orientation Produces a Robust Tilt Aftereffect and Exhibits Crossmodal Transfer When Tested in Vision

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4.1 Introduction

Orientation is considered one of the most basic features in vision (Graham, 1989). It is extracted very early in visual processing by specialised neurons in the primary visual cortex (Hubel & Wiesel, 2004) and plays a vital role as one of the essential building blocks of visual perception. The receptive fields of neurons in the primary visual cortex (area V1) are narrowly tuned to the orientation of contours at a particular spatial scale. Collectively, the population of V1 neurons encodes all orientations over a wide range of spatial scales (De Valois & De Valois, 1988). Similar to vision, neurons in the early somatosensory cortex (areas S1 and S2) show an orientation selectivity. Although not as specialised or narrowly tuned for orientation as V1 neurons, the population of all orientation-tuned somatosensory neurons covers all orientations at a range of scales (Bensmaia et al., 2008; Bensmaïa et al., 2008; Hsiao et al., 2002). Given these similarities and considering the value of efficient sensory coding, it is natural to wonder whether there is a common processing of orientation between the visual and somatosensory modalities.

Various findings have accumulated in support of the view that orientation processing in visual and somatosensory modalities is linked. First, a number of studies using various brain imaging methods have reported occipital lobe (visual cortex) involvement during purely tactile tasks with both sighted and visual-impaired individuals (Merabet et al., 2004; Merabet et al., 2008; Prather et al., 2004; Sadato et al., 1996, 2004; Sathian & Zangaladze, 2002; Zangaladze et al., 1999; Zhang et al., 2004, 2005). These findings all point to the involvement of extrastriate visual cortex during the processing of a variety of tactile tasks. More importantly, they reveal that the spatial scale of the task feature regulates the degree of visual involvement: large features such as size, shape and orientation (macrospatial tactile scale) tend to activate the visual cortex whereas fine-grained or microspatial tasks (e.g., texture and roughness, for which somatosensory neurons are specialised) do not. One interpretation is that macrospatial tactile information is passed onto the visual cortex because vision is more specialised for such information, and that this occurs in a top-down manner, possibly as visual imagery (Merabet et al., 2004; Prather et al., 2004; Sathian et al., 1997; Stoesz et al., 2003; Zangaladze et al., 1999; Zhang et al., 2005).

Several neuroimaging studies have shown the involvement of extrastriate visual cortex during tactile orientation discrimination (macrospatial task) which is absent during fine tactile spatial frequency discrimination (microspatial task). Evidence for this comes from a positron emission tomography (PET) (Sathian et al., 1997) study and a functional magnetic resonance imaging (fMRI) (Zhang et al., 2005) study which found that orientation discrimination produced a significant task-specific activation in extrastriate visual cortex compared with a tactile texture discrimination. Stronger evidence comes from a transcranial magnetic stimulation (TMS) (Zangaladze et al., 1999) study which showed that TMS applied over the extrastriate visual area significantly impaired participants' ability to discriminate grating orientation (macrospatial) but did not affect grating texture (microspatial) discrimination. In an interesting asymmetry, TMS applied over somatosensory cortex had a severe impact on both tasks – suggesting the visual cortical component for the grating orientation task originated from somatosensory cortex. These results suggest differing processing pathways for micro- and macro-spatial tactile tasks: while both require the somatosensory cortex, macrospatial tasks such as orientation also require the involvement of visual cortex. Behavioural data complementing these findings come from a perceptual learning study of grating orientation which showed tactile-to-visual transfer of orientation learning (Hu et al., 2021). Together, these findings support the hypothesis that tactile orientation information is passed on to the extrastriate visual cortex, presumably to exploit vision's finer orientation acuity.

There is another line of evidence implicating connections between the somatosensory cortex and early visual cortex, including area V1. Neuronal recordings in rats have found primary somatosensory cortex (S1) and primary visual cortex (V1) carry similar amounts of information during purely tactile tasks, and V1 responses correlate strongly with task performance (Vasconcelos et al., 2011). In humans, one study found activation in V1 and deactivation in extrastriate visual cortex during a tactile dot spacing task (Merabet et al., 2007). Complementing this, psychophysical studies show that visual contrast sensitivity for grating stimuli is improved when paired with a tactile grating that is congruent with the visual stimulus. Critically, varying the relative orientation between the gratings reveals the crossmodal facilitation has a very tight orientation tuning, implying an interaction at the earliest cortical stage where orientation tunings are tightest (van der Groen et al., 2013). Another study found a similarly tight orientation tuning between touch and vision in a visual suppression paradigm in which visual gratings were less suppressed when paired with a congruent or near-congruent tactile grating (Lunghi & Alais, 2013). These findings support the possibility of direct connections between primary visual and somatosensory cortices, such as those documented in rodent brain (Henschke et al., 2014; Massé et al., 2016), and hence an early integration of visual and tactile orientation information. Thus, while there is a considerable accumulation of evidence documenting visual-tactile interactions for orientation tasks, it is not clear at which cortical stage these interactions occur.

Adaptation and aftereffects often serve as valuable tools for investigating underlying neural mechanisms through behavioural experiments. In multisensory research, numerous studies have utilized the adaptation paradigm to investigate various combinations of visual, tactile and auditory modalities (Domenici et al., 2022; Ehrenstein & Reinhardt-Rutland, 1996; Konkle et al., 2009; Tonelli et al., 2017; Xiao et al., 2021). Specifically, motion aftereffects have been shown to be transferable between vision and touch, offering behavioural support for the hypothesis of a shared representation of motion (Konkle et al., 2009). Therefore, establishing a similar crossmodal adaptation effect for orientation perception could provide additional behavioural evidence for the proposed common processing mechanism of orientation information between touch and vision. The tilt aftereffect (TAE) is an old and well-known visual aftereffect that has revealed much about visual orientation mechanisms (Gibson & Radner, 1937). The TAE occurs when a tilted stimulus is presented for a prolonged period, causing nearby orientations to appear repelled away from the adaptor's orientation. These perceptual repulsion effects are linked to corresponding changes in the cortical responses of V1 neurons (Dragoi et al., 2000; Jin et al., 2005). These adaptation-induced neural changes, similar to many other visual aftereffects (Clifford et al., 2000), are traditionally explained by a simple fatigue model in which neurons preferring the adaptor orientation show reduced responsivity after adaptation, increasing the relative response strength to nearby orientations. In recent years, several studies have tried to explore orientation adaptation in somatosensation. A tactile TAE has been demonstrated on the palm of the hand using a two-point stimulation method (Hidaka et al., 2022), and visual adaptation to tilted gratings biases perception of subsequent two-point tactile orientation stimuli on the forehead (Krystallidou & Thompson, 2016). In addition, combining tactile and visual surround gratings is found to increase the visual tilt illusion (Pérez-Bellido et al., 2018). These exciting findings all point to the similarity in adaptation effect between the two modalities, which further supports the hypothesis of a close connection between the two modalities in orientation processing. However, a few important aspects have not been comprehensively investigated in the above-mentioned studies which motivate our current study. To date, there has been no systematic demonstration of tactile and crossmodal orientation aftereffects within the same paradigm. By testing whether the same tactile stimulus could lead to a tactile TAE and a crossmodal TAE when tested in vision, and whether a visual TAE can be transferred between vision and touch, it could help demystify whether the orientation adaptation effect is just a result of separate but analogous processing in different cortical areas, or whether it arises from the same process (i.e., tactile orientation information being processed in the visual cortex).

Moreover, besides the negative adaptation effect, another form of bias induced by the previous stimulus, namely serial dependence, has also been reported in visual orientation perception

(Fischer & Whitney, 2014). Unlike neural adaptation, which is believed to be low-level and repulsive, serial dependence in visual orientation has been reported to be mostly attractive, with the stage at which it occurs still under extensive debate (Bliss et al., 2017; Cicchini et al., 2018, 2024; Fornaciai & Park, 2018; Manassi & Whitney, 2022; Manassi et al., 2023; Murai & Whitney, 2021; Pascucci et al., 2019, 2023; Samaha et al., 2019). Serial dependence has not yet been reported in tactile orientation perception, nor compared to its visual counterpart. Given the close connection between vision and touch in orientation perception, it would be hypothesised that tactile orientation perception might also exhibit similar serial dependence. By including a test sequence in our studies, we aim to further explore the intricate mechanism of temporal influence on orientation perception in both modalities.

Given the ample evidence pointing to the common orientation processing mechanism between the two modalities, we hypothesised that tactile orientation perception on the finger pad would exhibit a similar TAE to its visual counterparts. Additionally, we posited that if tactile orientation information is indeed processed in the visual cortex, adaptation in one modality would be transferable to the other. We conducted two experiments: Experiment 1 tested TAE in touch, while Experiment 2 examined crossmodal TAE by testing for transfer in both directions. Our results reveal a robust tactile TAE and also show that adaptation effects can transfer between modalities in an asymmetrical way, where tactile adaptors bias subsequent visual perception, but not vice versa. These results provide concrete evidence of touch and vision engaging common orientation mechanisms, while the asymmetricity of adaptation transfer is informative about the links underlying visual-tactile orientation interactions. In addition to the main findings, we also took a closer look at how the adaptation effect changes after the adaptation phase by further examination of the trial-by-trial variability during the test phase. We found a similar asymmetrical intramodal serial dependence effect between the test trials, which provides additional insights into the potential source of this asymmetricity.

4.2 Methods

4.2.1 Participants

Participants were all young adults (first/second-year psychology students from the University of Sydney) recruited through the Sydney University psychology SONApsych research participation system, and were given course credit for their participation. Informed consent was obtained from all participants prior to the commencement of the experiment. 14 naïve participants participated in Experiment 1, 12 females and two males. 22 naïve participants participated in Experiment 2, 16 females and six males. All participants reported being right-hand dominant with no recent history of damage to the right index finger and no history of damage or diseases of the nervous system. Participants also reported having a normal or corrected-to-normal vision, which is collected as part of the SONA pre-screening process. This research was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048), and all methods were carried out in accordance with relevant guidelines and regulations.

4.2.2 Apparatus and Stimulus

The tactile stimulus used in all experiments was a 3D printed (Ultimaker 3D printer) disk with a grating pattern on its upper surface whose orientation could be rotated with an Arduino Uno microcontroller. The model of the grating disk was designed using FreeCAD. It has a diameter of 30 mm and is composed of a triangular wave with a 6 mm spatial period and a peak-to-trough amplitude of 2.5 mm (see Figure 4.1c). The microcontroller is controlled by an Arduino Uno Board via MATLAB and can rotate the disk with a resolution of 1.8°/step. The disk was housed in a 3D printed box on which the subject rested their hand. The disk was presented to the subject through an aperture on top of the box and the presentation period was controlled by raising the disk into position for a fixed period and then lowering it back inside. A cardboard cover was placed over the device to prevent participants from seeing the tactile stimulus. In Experiment 1, three sets of tactile stimulus orientations were employed

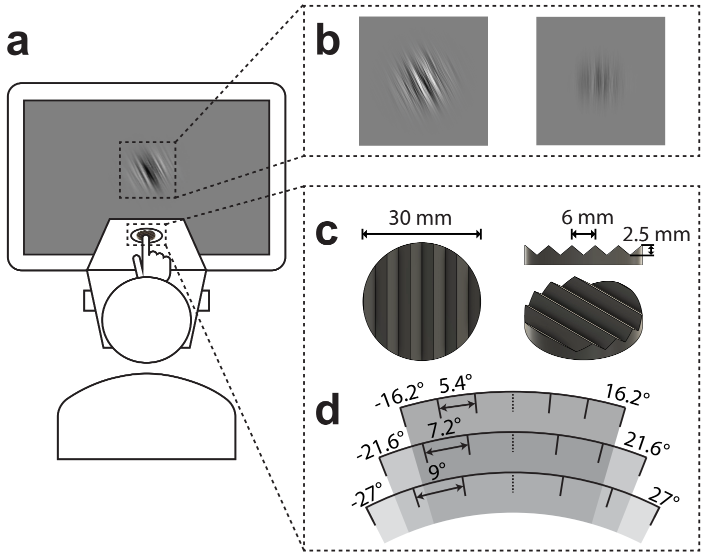

FIGURE 4.1: **(a)** Experimental setup. The tactile stimuli were presented via a device positioned in front of the screen and the instructions and visual stimuli were presented on the screen. **(b)** Examples of adaptation (left image) and test (right image) visual stimulus used in Experiment 2. Both types of stimuli were orientation-filtered pink noise with different RMS contrast levels (adaptation: 0.300, test: 0.018), oriented at $-27°$ or $27°$. **(c)** Illustration of the tactile grating used in both experiments. **(d)** The three sets of tactile stimulus orientations used in Experiment 1. To deal with the large variability in orientation sensitivity among different participants, three sets of stimulus orientations with the same mean and varying range were used in Experiment 1 as shown in the figure ($-16.2°$ to $16.2°$, $-21.6°$ to $21.6°$ or $-27°$ to $27°$), each set consisted of six different orientations ($5.4°$ gap, $7.2°$ gap or $9°$ gap, respectively). For each participant, one of the three sets would be selected based on their performance in the preliminary experiment, such that their performance would be in a reasonable range for psychometric function fitting. In Experiment 2, only the largest set ($-27°$ to $27°$ with $9°$ gap) was used.

(refer to Figure 4.1d). This approach was adopted to account for the substantial variability in orientation acuity among participants, and the selection of the specific set was based on each participant's performance in the preliminary test. In Experiment 2, only the largest set was used to simplify the process.

Visual stimuli used in Experiment 2 were generated using a MATLAB image processing toolbox (Wang et al., 2022), and presented using Psychophysics Toolbox extensions (Brainard,

1997) on a Dell OptiPlex 7440 Display (1920×1080 pixels, $60\,\mathrm{Hz}$ refresh rate). Visual adaptation and test stimuli in these experiments (see Figure 4.1b) were orientation-filtered noise patterns (pink noise, filtered with a Gaussian orientation filter with bandwidth ($\sigma = 5°$), with a 2D Gaussian kernel applied to the noise pattern to generate a smooth roll-off at the edge. In Experiment 2, condition VT, the root-mean-squared (RMS) contrast for the visual adaptor was 0.3, oriented at $-27°$ and $27°$. In Experiment 2, condition TV, the RMS contrast for the test stimuli was 0.018, with six different orientations around vertical ($-1.8°$ to $1.8°$, with $0.4°$ gap, excluding $0°$).

4.2.3 Data Analysis

4.2.3.1 Exclusion Criteria

As the bias estimation depends on reliable psychometric function fitting for each participant under all conditions, it is crucial for participants to perform within a reasonable percentage of correctness range. Hence, we excluded participants with a low percentage of correct performance (<65%). In Experiment 1, the criterion was applied to the overall performance of the participant since only one condition was presented in the experiment, all 14 participants passed this assessment and were included in the analysis. For Experiment 2, the criterion was applied for each condition separately, and six out of the 22 participants were excluded, as their performance in at least one of the conditions was below the 65% cutoff.

4.2.3.2 Psychometric Function Fitting

Psychometric functions were fitted for each participant and each adaptor orientation separately using the Bayesian hierarchical model from Palamedes toolbox (Prins, 2023):

$$\Psi(x;\mu,\sigma,\gamma,\lambda) = \gamma + (1-\gamma-\lambda)F(x;\mu,\sigma) \tag{4.1}$$

The function $F(x;\mu,\sigma)$ is a cumulative Gaussian function where $\mu =$mean and $\sigma =$standard deviation. γ and λ represent the guess rate and the lapse rate. These parameters correspond to the disparity between the asymptotes of the psychometric function and the ideal performance levels of 0% and 100%, respectively. Point of subjective equality (PSE) was obtained as the mean of the cumulative Gaussian function (μ, 50% rightward response), which was used as a measure for bias in orientation judgement (positive: leftward bias, negative: rightward bias).

4.2.3.3 Permutation Test

We used a non-parametric permutation test to evaluate the biases in the PSEs. The observed statistics (t_{obs}) were obtained through paired-sample t-tests comparing the PSEs of the actual participants' data under different adaptor orientations. Then, 10,000 permutations of the empirical PSEs were generated by randomly swapping the PSEs under different adaptor conditions. The p-value of the permutation test is calculated as the proportion of t statistics from the permuted distribution that is more extreme than the observed statistics($|t_{permutation}| \geq |t_{obs}|$).

For each condition, as multiple trials were tested after the adaptation, and similar permutation tests were performed for each test trial, we used the Holm-Bonferroni method (Abdi, 2010b) to correct for family-wise error rate. The adjusted p-value is calculated by sorting the permuted p-value in each condition in ascending order, and multiplying the p-value by the number of tests (C) in the condition minus the rank(i) and plus one. The formula is as follows:

$$p_{holm} = (C - i + 1)p_{perm} \tag{4.2}$$

where an adjusted p-value larger than one is set to one.

4.2.3.4 Generalised Linear Mixed Effects Model (GLMM)

The serial dependence effects were analysed using GLMM, as further dividing each participant's data based on previous stimulus in addition to adaptor orientations would result in insufficient data for proper psychometric function fitting, and lead to unreliable PSE estimates.

The model was fitted with the raw trial-by-trial data, following the principle of Moscatelli et al. (2012) The first test trial after each adaptation phase was excluded in this analysis as there is no 1-back test trial (the previous test trial was prior to the preceding adaptation phase, which is separated with the test trial by 60 s/10 s for initial and top-up adaptation, and would not be appropriate for serial dependence analysis).

We employed MATLAB's Statistics and Machine Learning Toolbox to fit the GLMM. The model was fitted using a binomial distribution and probit link function, applying the maximum likelihood method with Laplace approximation. We included the three fixed effects, to account for the previous and current stimulus, as well as the adaptor orientation. We also included the subject as a random effect to account for the differences in sensitivity and overall internal biases for each participant. The GLMM model is presented in Wilkinson notation below:

$$\begin{aligned} \mathit{Response} \sim 1 + \mathit{Current\ Stimulus} + \mathit{Adaptor\ Orientation} + \mathit{Previous\ Stimulus} \\ + (\mathit{Current\ Stimulus} \mid \mathit{Subject}) \end{aligned} \tag{4.3}$$

Notice that the previous stimulus orientations used in the actual GLMM were in degrees. However, for clarity, in the graphical illustration (Figure 4.7) the previous stimulus was simplified to left or right.

4.2.4 Design and Procedure

4.2.4.1 Experiment 1: Tactile Tilt Aftereffect

Participants sat in front of a screen with their right hand resting on top of a box containing the tactile device. A schematic plot is shown in Figure 4.1a. Each session began with a preliminary test lasting approximately five minutes to determine for each participant which of the three orientation ranges was best suited to their tactile orientation acuity to ensure a better-fitting psychometric function (Figure 4.1d). This also acted as a practice block to familiarise the participant with the task. The main test contains six blocks, with adaptor orientations (left vs. right) alternating between blocks, and the order is counterbalanced between subjects. Each trial began with the tactile grating rising from inside the box to the level of the participant's fingertip already rotated to the adaptor orientation used for that block. Participants passively felt the orientation for the duration of the adaptation phase (30 s for initial adaptation, 5 s top-ups thereafter). After the adaptation phase, and a gap of 500 ms, the

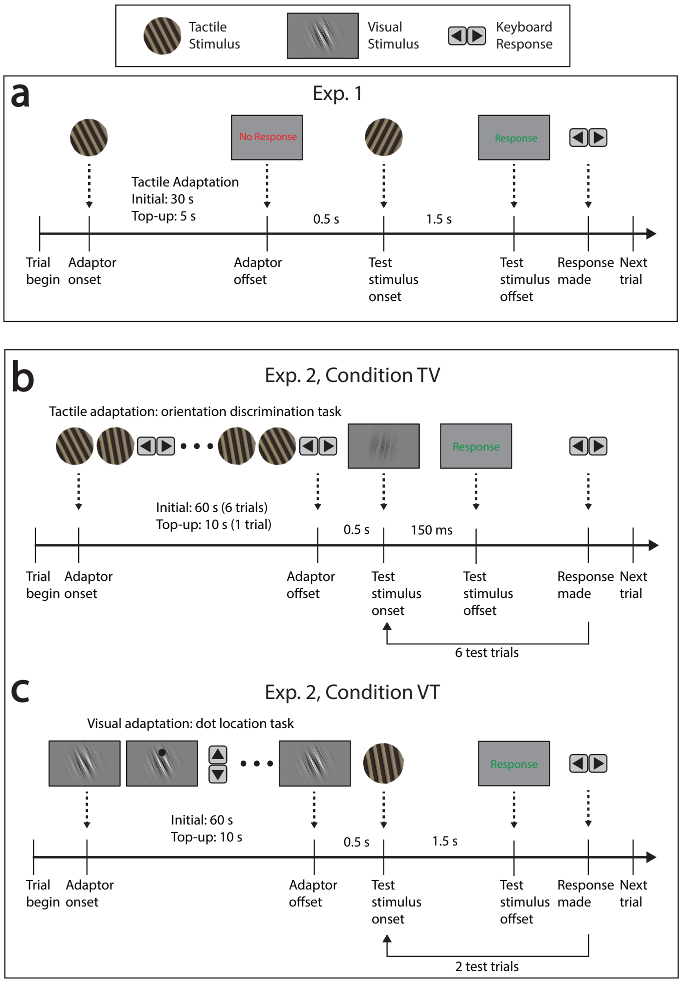

FIGURE 4.2: Procedures for Experiment 1 and Experiment 2: **(a)** Experiment 1: the experiment consisted of two phases, an adaptation phase (initial:30 s, top-up: 5 s) and a test phase. During the adaptation phase, participants were cued to passively feel the orientation of a tilted grating ($-27°$ or $27°$) without making a response by the "No Response" text on the screen. During the test phase, one of the six test stimulus orientations was presented for 1.5 s. Participants were then cued by the "Response" text on the screen to respond using the arrow keys on the keyboard to indicate whether the perceived orientation was left or right of the vertical (proximal-distal) axis. **(b)** Experiment 2, Condition 1: tactile adaptation, visual test (TV): during the adaptation phase (initial: 60 s, top-up: 10 s), participants were cued to perform multiple tactile orientation discrimination tasks, with the pseudo-randomised tactile stimulus that sits around either $-27°$ (leftward adaptation condition) or $27°$ (rightward adaptation condition), after which participant went through the test phase that consisted of a sequence of six visual test stimuli, with each stimulus presented for 150 ms. **(c)** Procedure for Experiment 2, Condition 2: visual adaptation, tactile test (VT): during the adaptation phase (initial: 60 s, top-up: 10 s), participants were instructed to fixate on the orientation-filtered pink noise pattern ($-27°$ or $27°$), during which they were also instructed to perform a dot location task, to ensure their fixation was on the visual adaptor. After this, participants went through the test phase which consisted of a sequence of two tactile test stimuli, with each test stimulus presented for 1.5 s.

test stimulus was then presented to the participant through the tactile device for 1.5 s, and the participant was cued to passively feel the orientation of the test stimuli with their fingertip, and then report whether the stimulus orientation was left (anticlockwise) or right (clockwise) compared to vertical (proximal-distal orientation) by pressing the arrow keys with the other hand (see Figure 4.2a).

4.2.4.2 Experiment 2: Visuotactile Crossmodal Tilt Aftereffect

Experiment 2 consisted of two consecutive sessions, each testing a different condition: tactile adaptation, visual test (TV) and visual adaptation, tactile test (VT). The order of the two conditions was counterbalanced between participants. Both conditions consisted of an adaptation phase followed by a test phase.

In Condition TV, in order for the participant to focus their attention on resolving the tactile orientations during the adaptation phase, which is thought to be critical in deploying the visual cortical process in tactile contexts (Sathian & Zangaladze, 2002). A 2IFC orientation discrimination task was introduced as the adaptation task: two tactile orientations were presented in succession, with each presentation lasting five seconds. Participants responded on the keyboard whether the second orientation was more towards the left or right of the first. All adaptation stimuli were pseudo-randomly drawn from four orientations (18°, 23.4°, 30.6°, 36°, left or right based on the block). At the beginning of each block, a sequence of six adaptation trials was performed, adding up to 60 seconds of initial adaptation. After each visual test sequence, another top-up adaptation trial was conducted, which accounted for 10 seconds of top-up adaption (see Figure 4.2b) For each block, the average of the pseudo-randomised adaptation trial stimulus orientation was -27°or 27°, alternating between blocks and counterbalanced between subjects.

In the VT condition, the visual adaptation phase contained a dot location task designed to keep the participant's attention on the adaptation stimulus. The dot appeared randomly in an upper or lower location multiple times during the adaptation period and the participant responded to the dot location with the keyboard every time they saw the dot, as shown in Figure 4.2c.

In both conditions, a test trial was presented immediately after the adaptation phase to test for the TAE. However, to accommodate the different nature of visual and tactile perception and the longer time needed to determine the tactile orientation, the test stimuli were presented for different durations in each condition (visual test: 150 ms, tactile test: 1.5 s). To evaluate the potential confound introduced by different time courses of testing, additional test trials were given after the first trial to test the change in TAE after the initial test. In Condition TV, five additional test trials were conducted (six test trials in total, See Figure 4.2)b), and in Condition VT, one additional test trial was conducted (two test trials in total, See Figure 4.2c).

4.2.5 Divisive Normalisation Model

To try and explain the mixed results in the visual adaptation, tactile test condition (VT), we used a simple divisive normalisation model to simulate the population response of neurons in the visual cortex. This simplified illustrative model was inspired by some published data (Carandini & Heeger, 2011; Solomon & Kohn, 2014; Wissig & Kohn, 2012).

The CRF (summation field) and normalisation field (suppression field) tuning of each of the orientation-selective neurons is simulated with Von Mises functions (see Figure 4.8a):

$$r(\theta) = c + a * e^{b*[cos(\theta - \theta_{pref}) - 1]} \tag{4.4}$$

where c is an offset representing the base response, a is the peak height of the summation field/normalisation field, and b is a parameter that controls the bandwidth of the summation field/normalisation field. θ_{pref} stands for the preferred orientation of the neuron.

The adaptation effect $a(\theta_{pref})$ to a neuron with preferred orientation θ_{pref} was simulated with the complement of the Von Mises function, with different strength (k) applied to the summation field and normalisation field, and the strongest drive were observed at the adaptor orientation $\theta_{adaptation}$ (Figure 4.8b and d). The adaptation effects were then multiplied with the summation field and suppression field to obtain the tuning after adaptation (Figure 4.8c and e):

$$a(\theta) = 1 - k * e^{b_{adapt}*[cos(\theta_{pref} - \theta_{adaptation}) - 1]} \tag{4.5}$$

The normalised response r_j of the neuron j was calculated by dividing the CRF response (weighted sum of drive to the summation field $\sum_k \omega_{ik} I_k$, where I_k was the non-normalised response of the neuron k in the summation field), divided by the normalisation signal (weighted sum of drive to the normalisation field $\sum_k \alpha_{jk} I_k^m$). Constant σ was added to the denominator to avoid division by zero. n and p are exponents to account for non-linearity:

$$r_j = \gamma \frac{(\sum_k \omega_{ik} I_k)^n}{\sigma^n + (\sum_k \alpha_{jk} I_k^m)^p} \tag{4.6}$$

The population response was obtained by fitting a Von Mises function to the normalised responses of all the simulated neurons with different preferred orientations. The centre of the Von Mises function, representing the peak response, was used as the simulated perceived orientation (see Figure 4.8f).

4.3 Results

Two experiments were conducted to assess the tactile tilt aftereffect (TAE) and the transfer of TAE between vision and touch. Figure 4.1 illustrates the experimental setup and example stimuli. Participants underwent an adaptation phase in which tilted stimuli (Experiment 1: tactile; Experiment 2, Condition 1: tactile, Condition 2: vision) were presented for a prolonged duration (Experiment 1: 30 s, Experiment 2: 60 s). Following this, test stimuli were presented either in the same modality (Experiment 1: tactile) or different modalities (Experiment 2, Condition 1: visual; Condition 2: touch). Participants then indicated their responses by judging the orientation of the stimulus with respect to the vertical axis (proximal-distal direction in touch). Psychometric functions were fitted for each participant under each adaptor orientation (left vs. right). The point of subjective equality (PSE) was obtained from the fitted psychometric functions and was used as the measure of adaptation-induced orientation bias, with positive values indicating a leftward bias and negative values indicating a rightward bias. The TAE is then quantified by the difference in PSE ($\Delta PSE = PSE_{right} - PSE_{left}$) between the two adaptor orientations (left vs. right), where positive values indicate a repulsive TAE and negative values indicate an attractive shift. See Methods for more details.

4.3.1 Robust Repulsive Tilt Aftereffect (TAE) in Touch

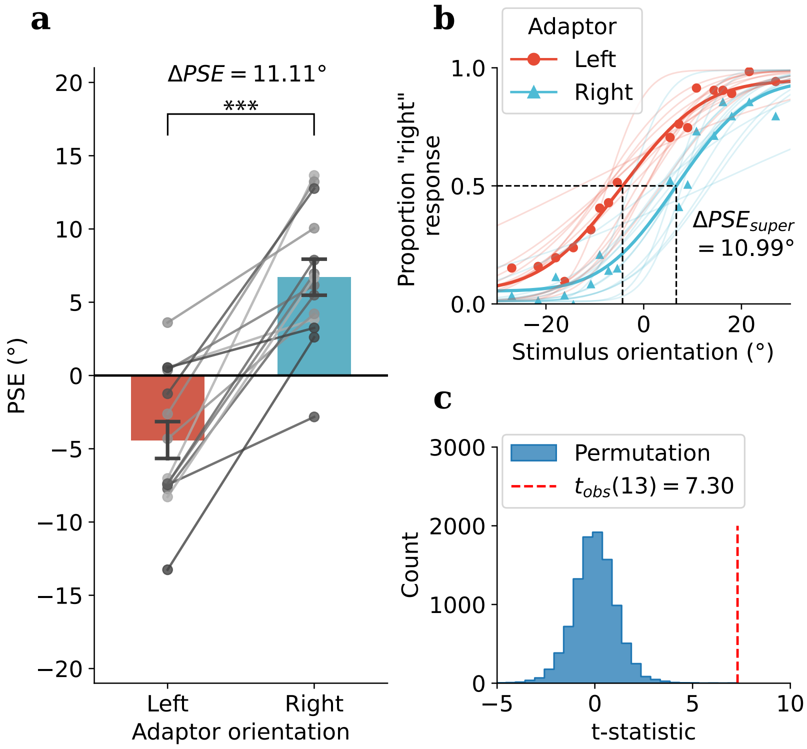

FIGURE 4.3: Experiment 1: Tactile TAE results: **(a)** Group average of PSEs following leftward ($-27°$, red bar) and rightward (27°, blue bar) tilted tactile adaptor, PSEs for individual participants are shown as grey dots. Error bars denote standard errors. **(b)** Psychometric functions for each adaptor orientation (super-subject: bold lines, individual participants: faint lines). **(c)** A permutation test was used to assess the difference between PSEs under each adaptor orientation. The histogram of the t-statistics from 10,000 permutations of the PSEs is shown in blue, while the observed t-statistic is represented by the red dashed line, $p_{perm} < .0001^{***}$.

Experiment 1 investigates whether adaptation to somatosensory orientation will produce a TAE, similar to what is observed in the visual system. The experiment consists of two phases: an adaptation and a test phase (Figure 4.2a). During the adaptation phase, participants were instructed to passively feel the orientation of a tilted tactile grating (-27°or 27°) without making any response. After adaptation, a test stimulus was presented (a rotated version of the same tactile grating), and participants indicated whether the test grating was oriented left or right with respect to the proximal-distal direction.

A permutation test on the PSE difference between leftward and rightward adaptor conditions (Figure 4.3) revealed a robust repulsive perceptual shift from the adaptor orientation (mean $\Delta PSE = 11.11°$, $SD = 5.70$, $t_{obs}(13) = 7.30$, $p_{obs} < .001$, Cohen's $d_{obs} = 1.83$, $p_{perm} < .0001^{***}$). The tactile TAE was strong and reliable and was present at the individual level for all 14 participants (Figure 4.3a, grey dots and lines represent individual participants). A post hoc power analysis was carried out using G*Power, based on an observed effect size of 1.83 and a sample size of 14, yielded an estimated power of 99.99%.

4.3.2 Crossmodal Transfer of Orientation Adaptation From Touch to Vision

In the previous experiment, we successfully demonstrated a robust TAE in tactile orientation perception, similar to its visual counterpart. Given the close connection established by prior research in orientation perception between the two modalities, we aimed to investigate whether adaptation in one modality would induce TAE in the other modality.

Participants were tested in two conditions in Experiment 2: tactile adaptation, visual test (TV) and visual adaptation, tactile test (VT); In the TV condition, similar to Experiment 1, participants were first adapted using the tilted tactile grating during the adaptation phase. In order for the participant to focus their attention on resolving the tactile orientations, which is thought to be critical in deploying the visual cortical process in tactile contexts (Sathian & Zangaladze, 2002), participants were adapted through a series of pseudo-randomized two-interval-forced-choice (2IFC) tactile grating orientation discrimination trials with stimuli centred around the adaptor orientation (-27°or 27°), alternating between blocks and counter-balanced between subjects (see Method section for more details). After the adaptation period (initial: 60 s, top-up: 10 s, see Figure 4.2b), participants were then tested in vision using orientation-filtered pink noise stimuli (Figure 4.1b). After each tactile adaptation phase, a series of six visual test trials were presented in the test phase. Psychometric functions were fitted separately for each trial (i.e., all first-trial responses, all second-trial responses, etc) for each participant. The PSEs from the first-trial data (immediately after adaptation) were used to assess the adaptation effect (as shown in Figure 4.4), and the remaining five trials in the

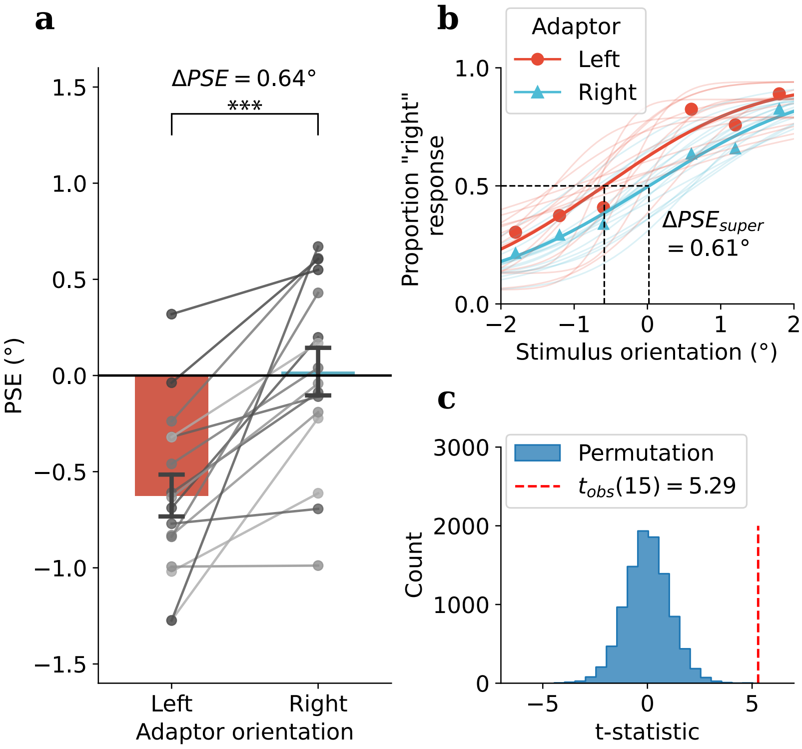

FIGURE 4.4: Experiment 2, Condition 1: Tactile Adaptation, Visual Test (TV) results: **(a)** Group average of PSEs in visual test following leftward (average -27°, red bar) and rightward (average 27°, blue bar) tilted tactile adaptor, individual participant PSEs were shown as grey dots. **(b)** Psychometric functions for each adaptor orientation (super-subject: bold lines, individual participants: faint lines). **(c)** A permutation test was used to assess the difference between PSEs under each adaptor orientation. The histogram of the t-statistics from 10,000 permutations of the PSEs is shown in blue, while the observed t-statistic is represented by the red dashed line, Holm-Bonferroni correction was applied to the permuted p-value, $p_{Holm;perm} = 0.0006^{***}$.

test phase were used to examine how the adaptation effect changed over time (Discussed in more detail in the last part of the Results section).

Similar to Experiment 1, a significant difference in PSE was observed between leftward and rightward tactile adaptation conditions (mean $\Delta PSE = .64, SD = .49$, $t_{obs}(15) = 5.29$, $p_{obs} < .001$, Cohen's $d_{obs} = 1.32$, $p_{holm;perm} = .0006^{***}$, see Figure 4.4), which clearly shows that the TAE can transfer crossmodally from somatosensation to vision. Again, the repulsive effect was robust and evident at the individual level for all 16 participants, even though its magnitude was substantially smaller than the within-modality tactile TAE (Figure 4.4a). A post hoc power analysis was carried out using G*Power, based on an observed effect size of 1.32 and a sample size of 16, yielded an estimated power of 99.85%.

4.3.3 Asymmetry in Crossmodal Tilt Aftereffect: Visual Adaptation Does Not Bias Tactile Orientation Perception

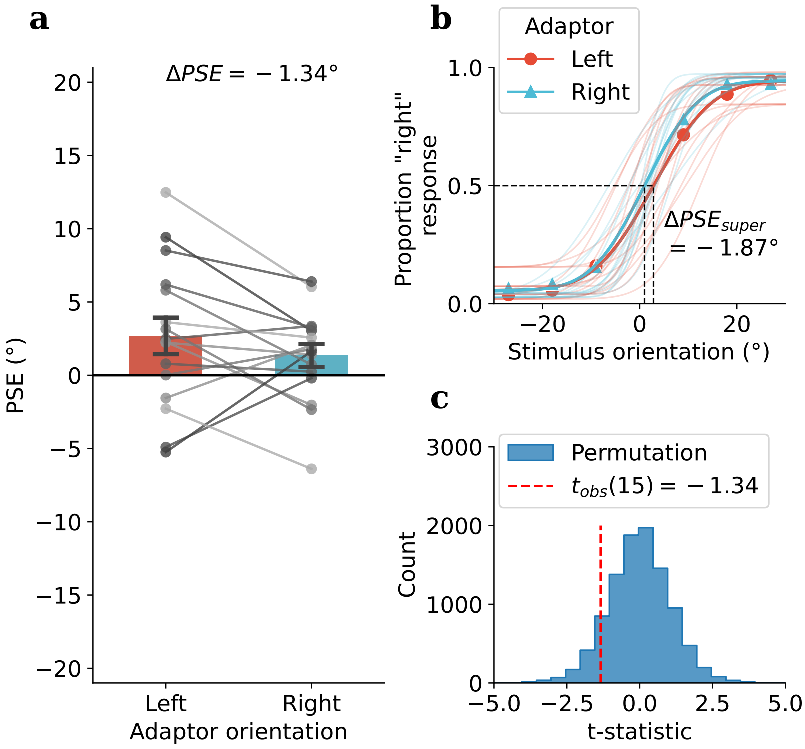

FIGURE 4.5: Experiment 2, Condition 2: Visual adaptation, Tactile test (VT) results: **(a)** Group average of PSEs in the tactile test following leftward (-27°, red bar) and rightward (27°, blue bar) tilted visual adaptor, individual participant PSEs were shown as grey dots. Error bars denote standard errors. **(b)** Psychometric functions for each adaptor orientation (super-subject: bold lines, individual participants: faint lines). **(c)** A permutation test was used to assess the difference between PSEs under each adaptor orientation. The histogram of the t-statistics from 10,000 permutations of the PSEs is shown in blue, while the observed t-statistic is represented by the red dashed line, Holm-Bonferroni correction was applied to the permuted p-value, $p_{Holm;perm} = 0.20$.

In the second condition of Experiment 2, we tested the crossmodal transfer of orientation adaptation in the other direction — from vision to touch. Participants were adapted using either a leftward tilted (-27°) or rightward tilted (27°) orientation filtered pink noise pattern (see Figure 4.1b for an example). A dot discrimination task on the stimulus (see Figure 4.2c) was employed in the adaptation phase to make sure the participant fixated on the visual adaptor. After the adaptation phase, participants were then tested in touch using the tactile grating. Each test phase consists of two trials, and the responses of the first trial were used to evaluate the crossmodal TAE here. And surprisingly, different from the previous condition, no significant difference in PSE was found between the two adaptor orientations (mean $\Delta PSE = -1.34°$, $SD = 4.06°$, $t_{obs}(15) = -1.32$, $p_{obs} = 0.20$, Cohen's $d_{obs} = -0.33$, $p_{holm;perm} = 0.20$, see Figure 4.5). A post hoc power analysis was carried out using G*Power, based on an observed effect size of -0.33 and a sample size of 16, yielded an estimated power of 23.54$\%$.

4.3.4 Trial-by-Trial Variability in Crossmodal Tilt Aftereffect and Asymmetrical Serial Dependence

In Experiment 2, the adaptation phase had the same duration for both TV and VT conditions. However, a notable difference was that the test stimulus presentation time for tactile was 1.5 s — 10 times longer than that for visual test (150 ms). This difference in test duration can be attributed to the higher sensitivity of vision (mean orientation bandwidth $\sigma = 1.29°$, obtained from the fitted cumulative Gaussian psychometric functions) compared to somatosensory perception ($\sigma = 7.84°$). To account for the difference in stimulus presentation time, we decided to incorporate a sequence of test trials in the test phase following each adaptation phase. This approach allows us to examine the time course of changes in TAE after adaptation more comprehensively (see Figure 4.2b and 4.2c).

Similarly, psychometric functions were fitted for each of the remaining trials after adaptation, and permutation tests were performed to examine the TAE for each trial after adaptation, with p-values adjusted using the Holm-Bonferroni procedure. In Condition 1 (TV), as stated earlier, a significant repulsive TAE was observed in the first visual test trial after tactile adaptation. However, this effect seems to diminish quickly after the first test trial, with no significant biases observed in the remaining trials (see Figure 4.6a). In condition 2 (VT), no significant

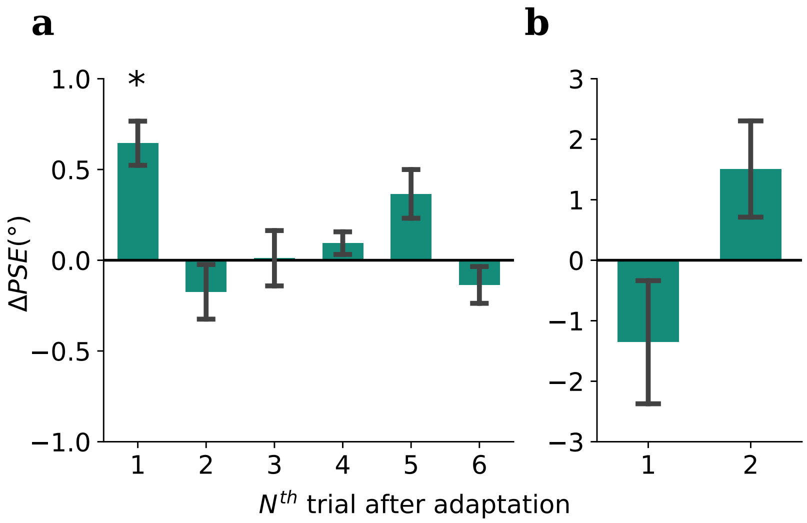

FIGURE 4.6: Experiment 2 results: **(a)** Condition 1, tactile adaptation, visual test (TV): after each adaptation phase, a sequence of six test trials were performed, the detailed analysis for the first trial immediately after adaptation was shown in Figure 4.4, similar permutation test were performed for all six trials, and the permuted p-values were corrected using Holm-Bonferroni procedure. A significant repulsive TAE was found for the 1st trial ($p_{Holm;perm} = .0006^{***}$, see Figure 4.4), while subsequent trials yielded non-significant p-values of $p_{Holm;perm} = .58, p_{Holm;perm} = .95, p_{Holm;perm} = .73, p_{Holm;perm} = .07, p_{Holm;perm} = .58$, respectively. Error bars denote standard errors. **(b)** Condition 2, visual adaptation, tactile test (VT): no significant TAE was observed for either the 1st or the 2nd trial after adaptation, $p_{Holm;perm} = .20, p_{Holm;perm} = .15$ respectively.

biases were observed for either the first test trial after adaptation or the second one (see Figure 4.6b).

TABLE 4.1: GLMM Model Statistic for Remaining Test Trials (2nd to 6th Following Adaptation), in Condition 1 (TV) of Experiment 2.

						95% CIs	
Name	Estimate	SE	t	df	p	Lower	Upper
(Intercept)	0.106	0.053	2.000	7196	0.046*	0.002	0.210
Current Stimulus	0.538	0.044	12.314	7196	< 0.001***	0.453	0.624
Previous Stimulus	-0.100	0.013	-7.895	7196	< 0.001***	-0.124	-0.075
Adaptor Orientation	-0.023	0.033	-0.714	7196	0.476	-0.087	0.041

In Condition 1 (TV), the absence of a TAE in the second and subsequent trials could simply be due to recovery from adaptation over time. However, it could also be a result of the adaptation

TABLE 4.2: GLMM Model Statistic for the Second Test Trial (Following Adaptation), in Condition 2 (VT) of Experiment 2.

						95% CIs	
Name	Estimate	SE	t	df	p	Lower	Upper
(Intercept)	-0.115	0.103	-1.121	2876	0.262	-0.316	0.086
Current Stimulus	0.084	0.010	8.656	2876	< 0.001***	0.065	0.103
Previous Stimulus	0.010	0.002	5.571	2876	< 0.001***	0.006	0.013
Adaptor Orientation	-0.057	0.067	-0.844	2876	0.399	-0.188	0.075

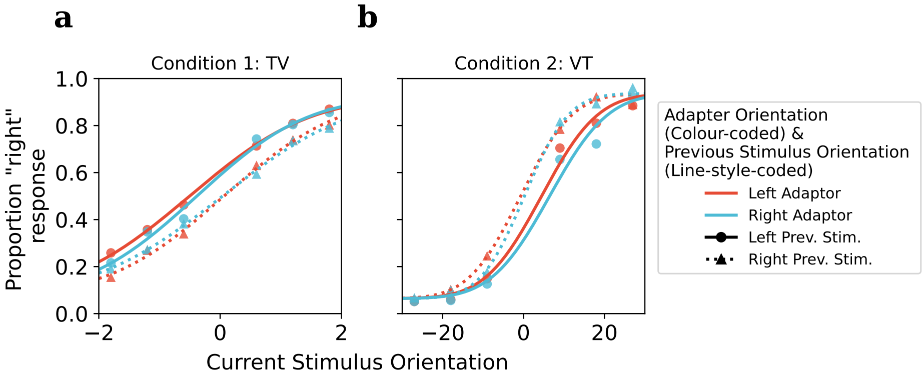

FIGURE 4.7: Super-subject psychometric functions as a graphical illustration of serial dependence and TAE in Experiment 2. Psychometric functions were differentiated by adaptor orientation (colour-coded, with blue indicating a leftward adaptor and red indicating a rightward adaptor) and previous stimulus orientation (denoted by solid and dotted lines, where solid lines represent a leftward previous stimulus and dotted lines represent a rightward previous stimulus). Previous stimuli were categorised based on their direction for this plot (left vs. right), while the actual orientation in degrees was used in the Generalised Linear Mixed Model (GLMM) analysis. **(a)** Condition 1: tactile adaptation, visual test (VT): a repulsive serial dependence (indicated by the horizontal shift in psychometric function between solid and dotted lines, i.e., the difference in PSEs between leftward and rightward previous stimulus conditions). However, no crossmodal TAE was observed (no visible shift between red and blue lines within each previous stimulus condition, i.e., similar PSE for leftward and rightward adaptors), as confirmed by GLMM results. **(b)** Condition 2: visual adaptation, tactile test (VT): an attractive serial dependence was observed from the plot, but no TAE was observed, as also confirmed by GLMM results.

effect being mediated by the percept of the previous test trial, a serial dependence (Cicchini et al., 2018; Fischer & Whitney, 2014; Kiyonaga et al., 2017) effect might be operating in addition to the adaptation (especially given that we tested a sequence of test trials).

To evaluate the potential biases caused by serial dependence using PSEs, the trials need to be further divided based on 1-back stimulus orientation, which would lead to insufficient data points for proper psychometric function fitting. Hence, we instead used Generalised Linear Mixed Effect Model (GLMM) to evaluate the potential influence of serial dependence (Moscatelli et al., 2012). In Condition 1 (TV), the GLMM was fitted with data from the 2nd to 6th visual test trials from all participants. For Condition 2 (VT), GLMM was fitted for the 2nd tactile test trial. See the Methods section for details on the GLMM.

The results indicate that both the current stimulus and previous stimulus were significant predictors for the remaining test trials in Conditions 1 and 2 (see Table 4.1 for Condition 1 (TV) and Table 4.2 for Condition 2 (VT). However, no significant difference in response was observed between the two adaptor orientations, for both TV and VT conditions. For graphical illustration purposes, we fitted a super-subject psychometric function for each combination of adaptor orientation and 1-back stimulus orientation direction (see Figure 4.7). The significant serial dependence (difference in PSE between solid lines and dotted lines) and non-significant TAE (difference in PSE between blue and red lines) can also be clearly visualised in the figure. However, surprisingly, both the GLMM and the super-subject psychometric function have shown an asymmetry in the direction of the serial dependence between conditions, with TV showing repulsive serial dependence ($\beta = -0.10$, $t(7196) = -7.90$, $p < .001^{***}$) and VT indicating attractive serial dependence ($\beta = 0.01$, $t(2876) = 5.57$, $p < .001^{***}$).

4.4 Discussion

In this study, we used the classic tilt aftereffect paradigm to test adaptation to orientation in the somatosensory system. Our first goal was to determine whether a TAE would occur in the touch domain (Experiment 1) and whether it would exhibit the repulsive tuning that is observed in the visual TAE. Our second goal, motivated by accumulating cortical and behavioural evidence for visual-somatosensory interactions (Merabet et al., 2004; Merabet et al., 2008; Prather et al., 2004; Sadato et al., 1996, 2004; Sathian & Zangaladze, 2002; Zangaladze et al., 1999; Zhang et al., 2004, 2005), was whether any adaptation to orientation would transfer crossmodally between vision and touch (Experiment 2). In Experiment 1 we successfully demonstrated a robust tactile TAE using a tactile grating which displayed the typical repulsive effect observed with the visual TAE. The tactile TAE was robust and observable reliably at the level of the individual in all participants (Figure 4.3). Experiment 2 tested whether there is a crossmodal transfer of adaptation effect between the two modalities, and revealed an interesting asymmetry in which tactile adaptation to orientation induced a repulsive TAE when tested in vision, yet adaptation to visual orientation did not generate a tactile TAE. We also examined the time course of crossmodal adaptation and found the repulsive tactile-to-vision TAE diminished quickly and was no longer significant after the first trial in the visual test sequence. Finally, we examined whether there were serial dependence effects in the test sequences used in the crossmodal conditions (Experiment 2). In another curious asymmetry, serial dependence was found in both VT and TV conditions, however, it was a repulsive effect for visual test sequence and an attractive effect for tactile test sequence.

The significant tactile TAE found in Experiment 1 is in agreement with a very recent report using a different paradigm to study tactile orientation. Hidaka et al. (2022) presented orientation on the palm of the hand using a two-point stimulation task. The alignment of two points was sufficient to produce a percept of orientation and adaptation to this stimulus produced a robust TAE. Somewhat surprisingly, these are the first two published studies to document a purely tactile TAE (i.e., adapting and testing with tactile stimuli). While our study is focused primarily on crossmodal transfer of adaptation, Hidaka et al. (2022) made important observations regarding somatosensory orientation processing. They showed that the TAE transfers from the palm to the back of the hand in a "see-through" manner following rotation around the longitudinal axis of the hand, and TAE is also preserved in hand-centred coordinates following rotation in the horizontal plane. These findings suggest that tactile orientation is represented in a hand-centred reference frame rather than a world-centred one. Our results complement Hidaka et al. (2022)'s report by adding that orientation on the fingertip also produces a TAE that is very robust and apparent at the individual level in all participants. Importantly for our purposes, the robust tactile TAE we observed confirms the feasibility of using the same tactile stimulus settings to explore crossmodal TAEs between touch and vision in Experiment 2.

Our second experiment examined crossmodal transfer of orientation adaptation between touch and vision, testing for both vision-to-touch and touch-to-vision transfer. As shown in Figure 4.4, there was a very clear effect of tactile adaptation to orientation on the fingertip transferring to vision and causing orientation repulsion on visual test stimuli. The effect was very reliable and was present at the individual level in all participants. This result is consistent with the literature reviewed in the Introduction showing behavioural evidence of common processing mechanisms for visual and tactile orientation. For example, a tactile grating combined with a visual surround grating increases the magnitude of the tilt illusion (Pérez-Bellido et al., 2018), showing a clear orientation interaction, and visual-tactile orientation interactions have been shown to exhibit surprisingly tight orientation tunings (Lunghi & Alais, 2013; van der Groen et al., 2013), possibly due to the increased perceptual precision that arises from integration of multisensory cues (Alais & Burr, 2019). Despite these behavioural findings, and a host of neural findings supporting visual-tactile interactions (Sathian & Zangaladze, 2002; Sathian et al., 1997; Zangaladze et al., 1999), the crossmodal transfer of adaptation did not occur in the reverse direction. As shown in Figure 4.5, there is no evidence of transfer of visual orientation adaptation to tactile orientation perception. There is no definitive explanation for this null result (which we consistently observed during several pilot experiments testing various parameters), although we consider several possibilities below.

4.4.1 Potential Explanation for Asymmetry in Crossmodal TAE and Implications for Crossmodal Connections

As a first observation, it is clear that orientation signals from the two modalities in our study were not simply combined in the manner of Bayesian maximum likelihood estimation (MLE) integration. MLE fusion of multisensory signals does occur and is well documented in the perception of audio-visual spatial location (Alais & Burr, 2004) and visual-tactile size (Ernst & Banks, 2002), but in this instance, the effect is unlikely to arise from MLE integration. The reason for this may relate to the very different orientation sensitivities in touch and vision, with orientation discrimination in touch being much poorer than in vision. Behavioural studies show that human orientation discrimination in vision is typically well below 1° for a wide range of spatial frequencies and can be as low as $0.3°$ – $0.5°$ in the most sensitive range (Burr & Wijesundra, 1991; Regan & Beverley, 1985; Vázquez et al., 2000). This is around 10 times better than human orientation discrimination in touch where the best-reported estimates are $4.2°$ – $5.4°$ for static and passively applied stimuli on the finger pad (Dodson et al., 1998). Our behavioural observations are consistent with these neural findings in that we found a mean bandwidth for visual orientation of $1.29°$ (average value of σ from the fitted psychometric functions) and a mean bandwidth for tactile orientation of $7.84°$. These perceptual results reflect single-unit neurophysiological data recorded from primates. In the primary visual cortex, most neurons are orientation-tuned and the full bandwidth is typically in the range of $30°$ - $40°$ (Shapley et al., 2003). In the somatosensory cortex, neurons selective for orientation on individual finger pads are found in S1 and across multiple fingers in S2 (Hsiao et al., 2002). An example of an S1 neuron with a "sharp tuning" is shown in Hsiao et al. (2002) and has a full bandwidth of about $50°$. In the second somatosensory cortical area (S2) the average orientation tuning bandwidth is $63°$ (Fitzgerald et al., 2006). Given these marked differences in orientation precision, an MLE framework would always predict that vision would dominate visual-tactile orientation perception. Thus, in the TV condition (where we found a strong transfer of tactile orientation adaptation to vision), a Bayesian fusion model would predict little change in post-adaptation orientation as vision would be by far the higher-weighted input. Thus, vision would be expected to dominate orientation perception regardless of the adapted state of tactile orientation neurons, yet against this, we found a strong TAE in the TV condition. Conversely, the MLE fusion model would predict a strong TAE in the VT condition, as the adapting stimulus was visual and thus in a vision-dominated fusion model the adapted state of visual neurons should be clearly evident, yet we did not observe a TAE.

Another consideration is that there may have been a genuine TAE in the VT condition but it was simply missed. Neural and methodological factors could both contribute to this possibility. As mentioned earlier, Konkle et al. (2009) demonstrated the shared representation of motion in vision and touch through a similar crossmodal adaptation paradigm, where the adaptation effect was transferable in both directions (Konkle et al., 2009). Compared to Konkle et al. (2009), one noticeable limitation in the current study is the unmatched spatial localisation of the visual and tactile stimuli. Although the tactile devices were placed right in front of the screen to keep them as close as possible spatially, the grating disk was in a different plane than the visual stimulus. This arrangement was dictated by hardware limitations and ergonomic considerations. In contrast, Konkle et al. (2009) decided to place the tactile stimulus behind the monitor, superimposing the visual stimulus on top of it. Hence, one potential source of the asymmetry could be the different planes of stimulus in space, leading to different populations of neurons being adapted and tested. One potential improvement in future experiments would be to recreate the task in a virtual reality environment and then spatially collocate the visual and tactile stimuli.

The differences in the spatial frequency and structure of the tactile and visual stimuli could also lead to a weak or undetectable TAE in the VT condition. The visual stimuli used in the current experiment consisted of orientation-filtered pink noise; this was chosen to target a broader group of visual neurons with diverse spatial frequency tuning. Currently, there is limited knowledge regarding whether the connections between touch and vision are spatial-frequency specific. Furthermore, in natural perception, while the spatial frequency of the same object changes depending on the distance to the eye, the tactile spatial frequency always remains the same. By using orientation-filtered pink noise, we aimed to provide a better chance of involving tactilely adapted visual neurons in the VT condition, maximising the likelihood of adapting visual neurons involved in tactile orientation perception. Similarly, in the TV condition, the aim was to maximise the possibility of involving tactile-adapted neurons during visual testing. However, while broader spatial-frequency tuned visual neurons could be recruited by the pink noise during visual adaptation and testing, the strength of adaptation within each specific spatial-frequency range is weaker as a trade-off. Consequently, despite the success in the TV condition, this weaker TAE might be buried under the noise during tactile testing in the VT condition.

Besides, given the markedly different orientation bandwidths, detecting evidence of orientation repulsion following visual adaptation could be challenging. Visual adaptation typically produces a visual TAE on the order of $1°$ – $2.5°$ (Gibson, 1937; Harris & Calvert, 1989). In the tactile system, where the level of orientation precision is much lower ($\sigma = 7.84°$), the effect of visual adaptation might simply be too small to be reliably detected. This is also compounded by the fact that aftereffects are relatively brief and decay over time, returning continuously towards their unadapted baseline. This makes it difficult methodologically to measure the tilt aftereffect as measurements in touch generally take more time than in vision. In vision, it is easy to flash a brief test grating and quickly probe the adapted state of the orientation system but in touch, this is usually a much slower process. In our experiment, the tactile grating was presented for a duration of 1.5 s in the test condition and it is possible there may have been a transfer of orientation adaptation from vision to touch in the VT condition but it dissipated and fell below the threshold during test trials as participants felt the stimulus and arrived at their decision about its orientation. If the decay of the aftereffect was a critical factor in our failure to observe the transfer of orientation adaptation from vision to touch, it remains possible that it could be obtained under different test conditions using briefer tactile test trials. Supporting the possibility that we simply missed a genuine TAE in the VT transfer condition is the fact that this same condition has been successfully demonstrated by Krystallidou and Thompson (2016), although they tested tactile orientation on the forehead and used a two-point test stimulus. It remains to be seen whether the same effect would be obtained when testing as we did, on the finger pad with oriented gratings and we propose that brief tactile test stimuli would likely improve the probability of detecting the effects of visual orientation adaptation in touch.

By contrast, the transfer of orientation adaptation from touch to vision was robust. How this would arise neurally is not well established. One possibility is that tactile-visual interactions for orientation are mediated by imagined or visualised orientation when engaged in touching tactile orientation, a suggestion made by Sathian and Zangaladze (2002). Indeed, multiple studies have shown visual imagery is capable of inducing aftereffects through top-down recruitment of the visual cortex (Finke & Schmidt, 1978; Ganis & Schendan, 2008; Winawer et al., 2010). Particularly, Mohr et al. (2009, 2011) showed that mental imagery alone was sufficient to produce orientation-specific adaptation in the extrastriate visual cortex (V3-V4) and elicit a consequent visual TAE. Thus, if tactile orientation were to interact with vision through visualising the felt orientation (Sathian & Zangaladze, 2002), it would still provide a possible means for the transfer of orientation adaptation from touch to vision that we observed in the visual test condition.

Interestingly, Ganis and Schendan (2008) showed that mental imagery and perception produce opposite-signed adaptation effects in face perception (with the imagery effect being attractive). Mohr et al. (2009) studied TAEs with imagined visual stimuli and found a similar result: while imagined lines produced the classic direct TAE (repulsion of orientations near the adapted orientation), they found the indirect TAE (where orientations far from adaptation are tested) had the opposite sign to the standard attractive effect elicited directly from visual adaptation. This also seems to coincide with our results in the visual-to-tactile condition, which though not significant, did point to an attractive TAE while testing in touch (Figure 4.5), although further work would be needed to establish this concretely. It seems that the top-down recruitment of the visual cortex might lead to the opposite adaptation effects (attraction), but the cause of this is not clear yet, possibly it has to do with the differences in neural mechanisms between bottom-up and top-down recruitment of the primary visual cortex.

Another possibility is that the adaptation effect transfers via direct connections between primary cortices for touch and vision. This notion is appealing and sits well with recent challenges to the traditional view that the primary cortices are strictly unimodal and well segregated from each other (Ghazanfar & Schroeder, 2006; Schroeder & Foxe, 2005). Direct interactions between primary sensory cortices have been well documented in rodents (Iurilli et al., 2012; Sieben et al., 2013, 2015), however corresponding studies in primates show that direct projections between primary cortices are quite sparse (Cappe et al., 2009; Cappe & Barone, 2005; Clavagnier et al., 2004; Falchier et al., 2002; Rockland & Ojima, 2003) and primates probably rely more on multisensory interactions in areas beyond primary cortices. This view squares with evidence for tactile input to the extrastriate visual cortex during tactile orientation discrimination such as Sathian et al. (1997)'s PET study and Zhang et al. (2005)'s fMRI study showing orientation discrimination elicited significant task-specific activations in the extrastriate visual cortex, and a TMS study by Zangaladze et al. (1999) showing the same area was critical to discriminating tactile grating orientation.

4.4.2 Adaptation and Serial Dependence Acting as Competing Mechanisms

In Experiment 2, the GLMM analysis on the remaining test trials (excluding the initial trial) reveals contrasting intramodal serial dependence effects in the two conditions. These serial effects were present while no crossmodal TAE was found in these remaining trials by the GLMM modal. Serial dependence has been widely studied in vision (for review, see Pascucci et al. (2023), Cicchini et al. (2024) and Manassi et al. (2023)), with orientation being one of the first visual features that have been looked at (Fischer & Whitney, 2014). In condition VT, we were able to show an attractive intramodal serial dependence in the tactile orientation task, which is first up-to-date, and also seems to coincide with our hypothesis that the tactile orientation judgment shares a very similar processing mechanism as vision. In Condition TV, we did not observe a classical attractive serial dependence, on the contrary, we found a repulsive intramodal serial effect, which is very interesting.

Although the serial dependence effect has been widely reported in a wide variety of visual perceptual tasks, ranging from low-level features such as orientation (Fischer & Whitney, 2014) and numerosity (Cicchini et al., 2018) to high-level features such as faces (Liberman et al., 2014), aesthetic perception (Kim et al., 2019), and attractiveness (Xia et al., 2016), there are still heated debates regarding the stage of the perceptual process from which it originates and its direction. On the one hand, many believe that the serial dependence effect is an attractive perceptual bias (as opposed to a repulsive neuronal adaptation effect), without the need for a previous response (Fornaciai & Park, 2018) or decision (Manassi & Whitney, 2022; Murai & Whitney, 2021), and is tuned for low-level properties such as location (Fischer & Whitney, 2014) and feature similarity (Cicchini et al., 2018). On the other hand, there is also another line of arguments suggesting that the observed attractive serial bias cannot be a low-level process (Kim et al., 2020) and originates from post-perceptual processing, modulated by memory (Bliss et al., 2017), decision (Pascucci et al., 2019), and confidence (Samaha et al., 2019). On top of these, various studies also reported a mixture of attractive and repulsive effects (Alais et al., 2017; Bliss et al., 2017; Fornaciai & Park, 2019a; Pascucci et al., 2019; Sadil et al., 2023; Sheehan & Serences, 2022; Zhang & Alais, 2020). One hypothesis that attempts to unite these mixed results is that the observed serial bias originates from two competing mechanisms: a lower-level repulsive sensory adaptation effect presented right after the previous percept, and an attractive serial dependence that manifests throughout higher-order post-perceptual processing. The observed direction of the perceptual biases is considered to be a combination of these two competing mechanisms (Bliss et al., 2017; Pascucci et al., 2023). Previous studies also indicated that the strength of attractive serial dependence is dependent on the reliability of the current percept, in particular, the attractive effect is greater when the current precept lacks reliability (hence more weight is put on the recent perceptual history to optimise the current percept (Cicchini et al., 2018)). And in our experiment, orientation perception is much more reliable in vision ($\sigma = 1.29°$) compared to touch ($\sigma = 7.84°$). In condition TV, with the more reliable visual orientation judgment, the weight on the previous percept should be lower, which should lead to a weaker attractive serial effect. Besides, the immediate response cue after the brief presentation of visual test stimuli (150 ms) might be too early for the attractive serial dependence to manifest in the higher-order post-perceptual processing, which together could lead to the observed classical sensory-driven repulsive effect. It would also be able to explain the quick diminishing of crossmodal TAE in Condition TV: the visual neurons that were crossmodally adapted by tactile adaptor could be re-adapted intramodally by the visual test stimuli, and hence diminishing the touch-to-vision crossmodal TAE in the subsequent test trials.

In condition VT, tactile orientation judgment would potentially rely more on the previous percept due to the lack of reliability, and the much longer presentation time (1.5 s) would provide more time for higher-order post-perceptual processing, hence showing a stronger attractive intramodal serial effect at the time of cued response. The absence of vision-to-touch crossmodal TAE in this condition can also be attributed to this lack of reliability in tactile orientation judgment, as the effect of the weak repulsive crossmodal sensory adaptation being overpowered by the stronger attractive influence of perceptual history due to high uncertainty in perception, and fits with our suggestion that the hint of an attractive effect in our vision-to-touch TAE condition (Figure 4.5), and provides a good theoretical framework to motivate a reinvestigation of this condition in future studies to clarify whether there is a genuine attractive effect or not.

4.4.3 Divisive Normalisation Between Modalities Leads to a Combination of Repulsive and Attractive Effects

Figure 4.5 shows a mix of attractive and repulsive biases among participants for condition VT. These effects might simply reflect noise in a genuine null condition, but they might also indicate a genuine mixture of adaptation-induced attractive and repulsive biases. Some studies in vision have reported attractive adaptation shifts with certain paradigms (Patterson et al., 2013; Wissig & Kohn, 2012), although repulsive effects are more common. One flexible model used to explain adaptation effects is the divisive normalisation model and it can explain the difference in the direction of adaptation-induced bias across many different sensory adaptation paradigms (Carandini & Heeger, 2011; Solomon & Kohn, 2014; Wissig & Kohn, 2012). At the neuronal level, divisive normalisation is proposed to work by taking a given neuron's activation from within its own receptive field (Classical Receptive Field - CRF) and dividing it (i.e., normalising it) by the sum of activation from neurons arranged in a larger suppressive surround field (normalisation pool). The net effect is that stimulation in the normalisation field down-regulates the neuron's response. Phenomena such as surround suppression observed in V1 can be explained by divisive normalisation as extending the stimulus extent into the surround field reduces a neuron's response (Carandini & Heeger, 2011). Divisive normalisation has been used to model many perceptual and neurophysiological effects and is also thought to play a role in multisensory integration (Carandini & Heeger, 2011). Hence it may play a role in how orientation information is transferred from somatosensory to the visual cortex. We tried to simulate a divisive normalisation model based on these principles where an orientation-selective visual neuron has a normalisation field with a broader orientation range compared to the CRF. We were able to show that the sign of the adaptation effect – whether attractive or repulsive – could vary based on the relative strength of the adaptation drive to the CRF and normalisation field (see Figure 4.8). It has been shown that during tactile processing there are both a top-down suppressive pathway through the visual hierarchy and an ascending excitatory pathway that directly influences V1 (Merabet et al., 2007). This supports the possibility of a normalisation arrangement between these two types of signals as in this study, and as found more generally, top-down projections tend to be diffuse and provide surround suppression (Nassi et al., 2013; Rockland, 2022). Additionally, Sathian has shown the significant variability in connection strength between visual and somatosensory cortical areas across individuals based on their visual history, potentially attributed to crossmodal plasticity (Sathian, 2005). Hence, the mixed attractive and repulsive adaptation effect observed in condition VT could potentially be attributed to experience-related differences in the relative strength of suppressive and excitatory signals among participants. However, the model and simulation here were only for illustrative purposes to demonstrate the possible explanation of the observed behaviour; future research with actual neuronal recording might help confirm this hypothesis.

Furthermore, despite the common perception of normalisation as a static computation in our model, recent studies have demonstrated that a dynamic normalisation model with temporally changing normalisation weights can better capture the dynamic nature of transient behaviour in visual neurons (Mikaelian & P. Simoncelli, 2001; Westrick et al., 2016). This insight could potentially contribute to explaining the mixed results observed in our experiment. Specifically, the temporal contingency of adapting stimuli has been shown to influence whether the normalisation signal weakens or strengthens (Aschner et al., 2018). The adaptation paradigm in our experiment, involving multiple testing, differs in temporal contingencies between conditions (varying in the number of test trials and test trial durations between conditions VT and TV). These differences might be the source of the asymmetrical TAE and serial dependence effects observed between the touch and vision modalities. However, further investigation is required to comprehensively understand these dynamics.

4.4.4 Conclusion

In the current study, we found that adaptation to a tactile grating presented to the finger pads produced a robust, repulsive TAE, analogous to what is observed in vision after adaptation to a visual grating. We also explored the transfer of orientation adaptation between vision and touch. Adaptation to tactile orientation produced a very robust TAE when tested in vision that was reliable at the level of individual participants. This result is consistent with mounting neural evidence of common processing of visual and tactile orientation in the extrastriate

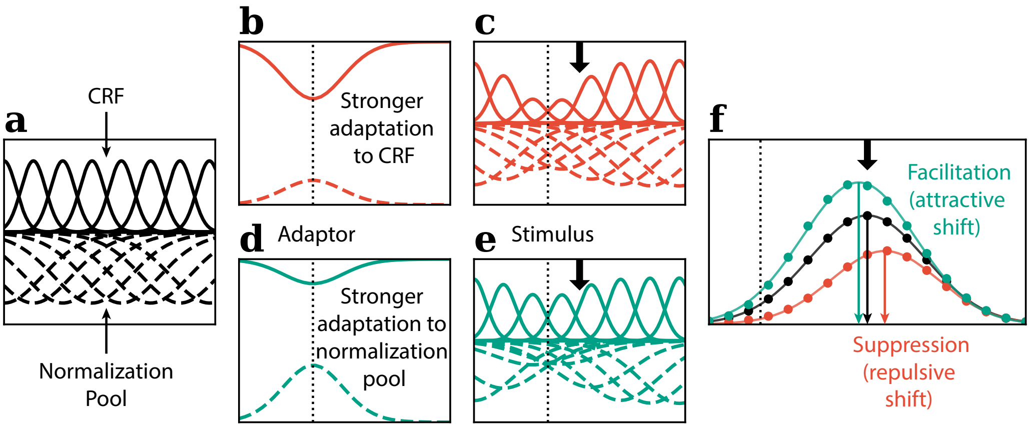

FIGURE 4.8: Illustration of the Divisive Normalisation Model. **(a)** CRF and normalisation pool prior to adaptation. **(b-c)** Stronger adaptation to the CRF **(d-e)** stronger adaptation to the normalisation signal **(f)** Stronger adaptation to the CRF leads to classic repulsive TAE with suppression effect on the population response, while stronger drive to the normalisation signal lead to attractive adaptation and facilitating effect in the population response, which could potentially explain the asymmetrical crossmodal TAE results in our experiment.

cortex. However, in an asymmetrical result, we found no evidence of transfer of orientation adaptation in the other direction, from vision to touch. We propose that the failure to find an effect of visual orientation adaptation when test in touch is inconclusive and should be interpreted with caution. It is inconsistent with a behavioural report of vision-to-touch transfer of orientation adaptation (albeit for test stimuli presented on the forehead rather than the finger pad). We conjecture that our rather long tactile stimulus presentation time may have prevented effective measurement of transferred orientation adaptation and recommend future studies employ brief test trials to better capture the ephemeral and decaying nature of orientation adaptation. It is also possible that the poor precision of tactile orientation perception relative to vision adds to the difficulty of capturing vision-to-touch transfer of orientation adaptation. We also looked at the intramodal serial dependence effect within the test sequence and found a similar asymmetrical serial dependence effect. Which could be a competing mechanism that mediates the crossmodal TAE, and provides another alternative explanation for the asymmetrical crossmodal transfer of TAE. Finally, we propose that a divisive normalisation model could explain our inconclusive findings in the case of vision-to-touch transfer as both attractive and repulsive shifts can be induced by the adaptor depending on the nature of the surround field. Thus our null result might reflect roughly equivalent numbers of subjects showing a repulsive or an attractive effect.

Despite these caveats, we have demonstrated two key findings: (i) for the first time we have shown a purely tactile TAE on the finger pads, and (ii) we show clear evidence of crossmodal transfer of adaptation from touch to vision, complementing an earlier report of transfer from vision to touch. The first result complements neural work in primates showing orientation selectivity in S1 neurons and indicates that neural interactions among S1 cells with adjacent orientation preferences interact similarly to those observed in the visual cortex. The second result adds to mounting neural and behavioural evidence of common processing of visual and tactile orientation.

CHAPTER 5

Tactile and Visual Spatial Frequency Perception Follows Optimal Integration but Is Not Affected by Spatial Proximity

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Tactile and Visual Spatial Frequency Perception Follows Optimal Integration but Is Not Affected by Spatial Proximity

5.1 Introduction

Spatial frequency, which describes how often surface structures change periodically in space, is a key aspect of human perception. In vision, spatial frequency perception enables the visual system to efficiently extract features from complex scenes by processing different spatial scales through dedicated frequency channels (Kauffmann et al., 2014; Lamb & Yund, 1996; Sachs et al., 1971). This function is supported by spatial frequency-selective neurons, which are found throughout the visual hierarchy, from ganglion cells (Kelly, 1975) to cortical neurons (De Valois & De Valois, 1988; Foster et al., 1985). In the primary visual cortex (V1), the receptive fields of neurons can be modelled as Gabor filters, narrowly tuned to specific orientation and spatial frequency (Pollen & Ronner, 1983). These neurons respond optimally to stimuli matching their preferred orientation and spatial frequency. Through the combined population response of neurons with diverse tuning properties, V1 processes visual elements like contours and shapes across different frequency bandwidths (De Valois & De Valois, 1988).

In somatosensory perception, spatial frequency also plays a crucial role in sensory processing, as objects and surfaces encountered through touch exhibit both low spatial frequency features (such as shape) and high spatial frequency features (such as texture or roughness). Research on the receptive field properties of primary somatosensory neurons indicates that Gabor-like filtering of spatial variations in cutaneous afferent signals contributes to roughness perception (Hsiao et al., 1993). And a substantial amount of somatosensory neurons have been shown to be tuned to specific spatial frequencies (Bourgeon et al., 2016). These findings demonstrate that the neural basis and processing mechanisms of spatial frequency perception are highly similar between touch and vision.

In the natural environment, it is rare for our perceptual system to depend only on unisensory information. Instead, the brain typically receives multiple streams of information from different sensory modalities simultaneously. Therefore, it is crucial for the brain to utilise the multisensory stream of information to enhance precision and resolve ambiguous perceptions. One prominent framework used to model multisensory integration is the Maximum Likelihood Estimation (MLE) model (Landy et al., 1995). The MLE model suggests that the brain combines sensory information in a statistically optimal manner, where the integrated multisensory percept is a weighted linear combination of cues from different modalities. The weight of each sensory input is proportional to its reliability, resulting in a more precise percept than individual unisensory estimates. This optimal cue combination has been validated across a wide range of behavioural studies, including visual-auditory (Alais & Burr, 2004) and visual-vestibular (Fetsch et al., 2010), etc. Specifically, MLE integration has been shown in various features between tactile and vision (Ernst & Banks, 2002; Helbig & Ernst, 2007a; Helbig et al., 2012). In addition, a series of studies highlight the close connection between vision and touch (Lunghi & Alais, 2013; Sathian et al., 1997; van der Groen et al., 2013; Wang & Alais, 2024). Hence, it is of interest to examine whether spatial frequency, as a fundamental aspect of both systems, integrates in an MLE fashion.

Despite the MLE model's success in explaining many cases of multisensory integration, it sometimes fails to account for observed behavioural data. On the one hand, there were tasks that demonstrated a suboptimal integration between two modalities, such as audiovisual integration of temporal rate and audiovisual integration of spatial location cues (Arnold et al., 2019). On the other hand, there were also scenarios where a supralinear combination of multisensory information has been found, where the bimodal performance exceeded the statistical optimal linear combination of the two unimodal signals, like the integration of visual and tactile orientation information in rats (Nikbakht et al., 2018). There were also scenarios where the MLE prediction did not align well with the weightings of different modalities (Meijer et al., 2019). Moreover, in tactile-visual texture and roughness perception, where spatial frequency plays a key role, findings have been mixed: evidence has been found that supports both the two modalities being separate and independent (Guest & Spence, 2003; Roberts et al., 2024; Whitaker et al., 2008) or being an integrated system (Jones & O'Neil, 1985; Lederman et al., 1986) in processing the texture information. These findings together highlight the need for a deeper understanding of the rules governing multisensory integration. And specifically, in the context of spatial frequency perception.

Another key principle of multisensory integration is the spatial rule, which suggests that optimal integration occurs when cues from different modalities are spatially colocalised (Kadunce et al., 2001; Stein & Stanford, 2008). This principle stems from neurophysiological studies on the receptive field properties of single multisensory neurons (Kadunce et al., 2001; Stein & Stanford, 2008; Stein et al., 1989), and has been widely supported by evidence from a wide range of behavioural tasks (for reviews, see Spence (2013)). Specifically, it has been demonstrated in spatial distance judgement between vision and touch (Gepshtein et al., 2005). From an evolutionary perspective, the spatial rule and temporal rule (where optimal integration occurs when signals overlap in time, see Section 2.3) seem to both reflect how the brain infers whether inputs from different senses share a common cause. By evaluating the spatial and temporal correlations between signals, the brain can determine whether they originate from the same event, and thus whether integrating them will yield perceptual benefits (Parise & Ernst, 2016; Parise et al., 2012). However, there is also substantial evidence from behavioural tasks that do not follow this pattern. Spence (2013) argues that the validity of the spatial rule is task-dependent; it tends to hold when spatial location information is relevant to the task, but often fails for tasks that do not require spatial information, such as identification and temporal judgment. The contradictory behavioural findings suggest that multisensory integration may not be confined to multisensory neurons that exhibit optimal responses to overlapping cues. Instead, there may be other concurrent pathways and alternative mechanisms that contribute to the complex interactions between multisensory cues.

As a localised feature, the judgment of spatial frequency is generally considered to be largely independent of spatial location in both vision and touch. However, in vision, the localised receptive fields of primary sensory neurons lead to spatial frequency processing being location-dependent (Williams et al., 1982). In touch, although spatial location is not explicitly required for the task, spatial attention has been shown to play a critical role in the processing of spatial frequency information (Sathian & Burton, 1991). Hence, it remains an open question whether spatial frequency integration adheres to the spatial principle.

In this study, we aim to test whether MLE integration occurs between vision and touch in spatial frequency perception and to examine whether spatial frequency integration follows the spatial rule. By exploring the interplay between these modalities, we seek to better understand the conditions under which multisensory integration is successful.

5.2 Methods

5.2.1 Participants

A total of 51 participants were recruited for our study. Twenty-six participated in Experiment 1 and 25 participated in Experiment 2. All participants reported being right-hand dominant with no recent history of damage to the right index finger and no history of damage or diseases of the nervous system. This research was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048), and all methods were carried out in accordance with relevant guidelines and regulations. Participants were first and second-year psychology students from the University of Sydney, recruited through the Sydney University Psychology SONApsych research participation system and were given course credit for their participation. Informed consent was obtained from all participants prior to the commencement of the experiment.

Six participants were excluded from Experiment 1 due to exceptionally low performance (<70% in at least one of the five conditions) to ensure sufficient data quality for reliable psychometric function fitting and parameter estimation

Similar exclusion criteria were applied to Experiment 2: one participant was excluded for not completing the test due to personal reasons, and five were excluded due to exceptionally low performance.

5.2.2 Apparatus and Stimulus

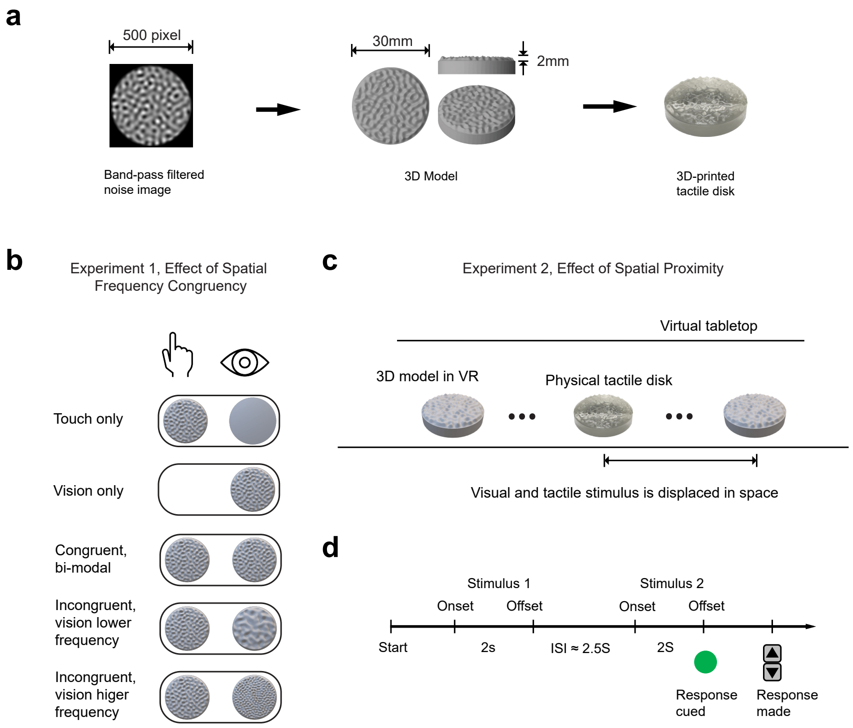

FIGURE 5.1: Experimental stimuli, conditions and procedures. **a** From left to right: Band-pass filtered noise image, 3D model generated from the noise image used as the visual stimulus, and the corresponding 3D-printed tactile stimulus. **b.** Example of conditions for Experiment 1: Effect of Spatial Frequency Congruency. Five different conditions were tested in Experiment 1: two uni-modal conditions (touch-only and vision-only) and three bi-modal conditions (congruent bi-modal, incongruent with vision at a lower frequency, and incongruent with vision at a higher frequency). **c.** Demonstration of conditions in Experiment 2: Effect of Spatial Proximity. In Experiment 2, the visual stimulus was displaced horizontally from the physical stimulus to investigate the effect of spatial proximity on multisensory integration. The virtual device was replaced with a large (10 m wide) white virtual tabletop to minimise the potential for any spatial reference to provide additional cues to the participants.

5.2.2.1 Visual Stimulus

Visual stimuli used in the experiment were 3D models of circular disks with textured noise patterns. An example of the stimulus is shown in Figure 5.1a. The surface texture was created using a MATLAB toolbox (Wang et al., 2022), by passing white noise images of 500×500 pixels through 2D Gaussian band-pass filters. The surface textures of the disks were controlled by varying the peak frequencies of the band-pass filters, such that each stimulus disk had a different range of spatial frequency components. The seven stimulus disks used in the experiment had spatial frequencies ranging from 0.200 to 0.600 cycles/mm (see Figure 5.2), selected from a larger set of printed disks based on pilot results to ensure an appropriate level of difficulty for both the tactile and visual tasks. A 2D circular cosine ramp was then applied to the square noise pattern to create a smooth roll-off. The textured patterns were then converted to a 3D object using MATLAB and Blender using the intensity of the grey-scale image as elevation.

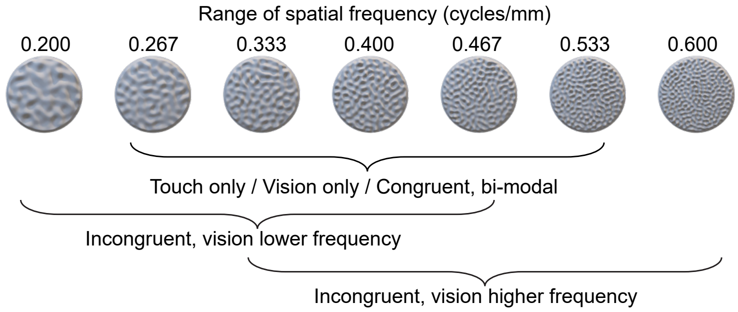

FIGURE 5.2: The figure displays 3D models of all stimulus disks used across conditions, with spatial frequencies ranging from 0.200 to 0.600 cycles/mm (corresponding to spatial wavelengths of approximately 5.000 to 1.667 mm).

5.2.2.2 VR Setup

The visual stimulus was presented to participants via an HTC Vive Pro Eye VR head-mounted display (HMD), with a resolution of 1440×1600 pixels per eye (2880×1600 pixels combined), a $90\,\mathrm{Hz}$ refresh rate, and 110° field of view, with integrated Tobii eye tracking technology. The HMD was driven by the Dell XPS 8950 desktop equipped with an NVIDIA RTX 3070

GPU and a 12th Gen Intel Core i7-12700K 3.60 GHz CPU. A Vive Tracker was used to ensure spatial alignment between the virtual and physical stimuli. The positions of the HMD and Vive Tracker were tracked using two HTC Vive Base Stations 2.0 within a $3m \times 3m$ calibrated workspace.

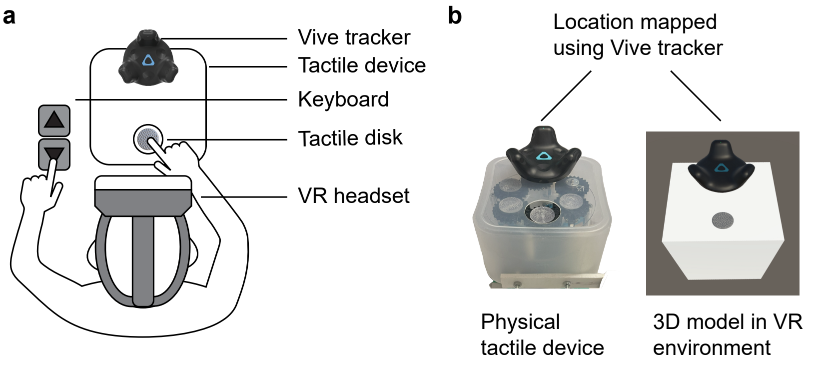

FIGURE 5.3: Experimental setup and apparatus. **a.** Experimental Setup: Participants were seated in front of the tactile device while wearing a VR headset. Tactile stimuli were delivered using an Arduino-controlled device, while visual stimuli were presented through the VR headset. **b.** Left: Tactile device. Right: Device and stimulus presentation in VR. The physical device's location was tracked using the Vive tracker, ensuring that the 3D model was rendered in the virtual environment at the same position. This alignment allowed the visual and tactile stimuli to be spatially co-localised.

5.2.2.3 Tactile Stimulus

The tactile disks used in this experiment were fabricated using a Formlabs Form 3 industrial resin 3D printer. The author created the design for the 3D models and the disks were printed at the Sydney Manufacturing Hub. Formlabs Clear V4 photopolymer resin was used as the printing material, with both the layer height and lateral resolution set to $25\,\mu m$ to ensure high surface texture quality.

5.2.2.4 Tactile Device

The 3D-printed textured disks were presented using a custom Arduino-controlled device. Five tactile disks were attached to a platform, which could be rotated by a stepper motor to position one disk underneath an aperture on top of the device. The tactile stimulus could then be delivered by raising and lowering the platform with a servo motor (Figure 5.3a). Additionally, the orientation of each disk could be adjusted by rotating another stepper motor. A Vive Tracker was fixed on top of the device, providing positional data that allowed the visual stimulus to be mapped onto the physical device in the VR environment.

5.2.2.5 Experimental Environment and Visual-Tactile Spatial and Temporal Synchronisation

The experiment was implemented in Unity 2021.3.16f1 using the SteamVR plugin. 3D models of the tactile disks were imported into the virtual environment. Spatial colocalization of the virtual (visual) and physical (tactile) stimuli was achieved using a Vive Tracker, which provided real-time coordinates of the physical device. The relative positions of the physical stimulus disk, tactile device, and Vive Tracker were measured in reality and replicated in the virtual environment. The Vive Tracker's position was recalibrated during the initialisation of the testing environment, and again following any system failure or whenever a participant reported noticeable drift in the virtual alignment. Virtual stimuli were rendered in real time to match the physical locations. Experimental control was implemented via C# scripts and Arduino code. Temporal synchronisation between the physical and virtual stimuli was achieved through serial communication between the computer and Arduino, with the visual stimulus triggered once the Arduino sensor detected that the tactile disk had reached the designated height (Figure 5.3b).

5.2.3 Procedure

5.2.3.1 Experiment 1: Visuotactile Integration of Surface Spatial Frequency

Five different spatial frequency congruency conditions were tested in Experiment 1: two uni-modal conditions (vision-only and touch-only), and 3 bi-modal conditions (Congruent, Vision Lower Frequency and Vision Higher Frequency), as shown in Figure 5.1b.

The experiment followed a classic two-interval forced-choice (2IFC) paradigm. In the visual-only, tactile-only, and congruent bimodal conditions, the same set of five disks was used as the test stimulus in 2IFC trials, presented in vision, touch, or both, respectively. In the two incongruent bimodal conditions, the tactile stimulus was presented simultaneously with a visual stimulus of incongruent spatial frequency (one step lower or higher than the tactile stimulus; see Figure 5.1b). The reference stimulus in each 2IFC trial was a disk with a spatial frequency of 0.400 cycles/mm. The test and reference stimuli were presented sequentially in counterbalanced and randomised orders. Different conditions were also randomised and intermingled between trials. After both stimuli were presented, participants were cued to compare their spatial frequencies and respond. A typical trial is shown in Figure 5.1d.

5.2.3.2 Experiment 2: Spatial Incongruence on Visuotactile Integration

Experiment 2 aimed to investigate the effect of spatial proximity on visuotactile integration of spatial frequency. It followed a similar 2AFC design to the bimodal, congruent spatial frequency condition in Experiment 1. However, in the test trials, the visual stimulus was displaced horizontally from the tactile stimulus, and the 3D model of the device was covered by a large 10m-wide virtual tabletop, eliminating any visual reference for the spatial location of the visual stimuli (see Figure 5.1c.).

5.2.4 Data analysis and MLE model prediction

5.2.4.1 Data Cleaning

In both experiments, trials with response time (RT) exceeding two standard deviations above the mean (Exp 1: RT > 2.91 s, Exp 2: RT > 2.24 s) were considered anomalies and removed from the analysis. This exclusion aimed to remove trials in which participants were disrupted by external events or experienced lapses. The exclusion method (z-score method) was based on the recommendations of Berger and Kiefer (2021), which should minimise the bias introduced by outlier trials.

5.2.4.2 Psychometric function fitting

The cumulative Gaussian psychometric function was fitted for every participant under each condition. The mean (μ or point of subjective equality, PSE) and standard deviation (σ, slope) of the cumulative Gaussian function can be used to quantify the sensitivity and bias in the participant's spatial frequency perception respectively. With a higher σ representing worse sensitivity, and PSE representing the estimated testing stimulus frequency at which it is perceived the same as the reference stimulus(0.400 cycles/mm).

5.2.4.3 MLE prediction

The MLE integration model proposes that the bimodal estimation of spatial frequency is a weighted average of the unimodal inputs, with weights determined by the reliability of each modality. Specifically, the weights are inversely proportional to the variance of the unimodal sensory inputs (σ^2), such that more reliable cues contribute more to the combined estimate:

$$\hat{S_{vt}} = w_v \hat{S}_v + w_t \hat{S}_t \tag{5.1}$$

Where $\hat{S}$ represents the perceived stimulus and w represents the weights, which can be calculated as:

$$w_v = \frac{1/\sigma_v^2}{1/\sigma_v^2 + 1/\sigma_t^2} = \frac{\sigma_t^2}{\sigma_v^2 + \sigma_t^2} \tag{5.2}$$

$$w_t = \frac{1/\sigma_t^2}{1/\sigma_v^2 + 1/\sigma_t^2} = \frac{\sigma_v^2}{\sigma_v^2 + \sigma_t^2} \tag{5.3}$$

The MLE integration model also predicts that the variance for the bi-modal condition

$$\sigma_{vt,prediction}^2 = \frac{\sigma_v^2 \sigma_t^2}{\sigma_v^2 + \sigma_t^2} \tag{5.4}$$

For the incongruent bi-modal condition, the PSE can also be predicted based on the MLE model. AS PSE denoted where the test and reference stimulus were perceived as equal

($\hat{S}_{vt,ref} = \hat{S}_{vt,test}$), hence we could get:

$$\hat{S}_{vt,ref} = w_v \hat{S}_{v,test} + w_t \hat{S}_{t,test} \tag{5.5}$$

In the incongruent bi-modal condition, the spatial frequency of each test stimulus pair in the visual modality was always either lower or higher by Δf in spatial frequency compared to touch, hence for the incongruent condition where vision had a lower frequency, we assume, for simplicity, that unimodal estimates are unbiased and that sensory integration follows linearity in the frequency space, we could then get

$$\hat{S}_{vt,ref} = w_v(\hat{S}_{t,test} - \Delta f) + w_t \hat{S}_{t,test} \tag{5.6}$$

And:

$$\hat{S}_{vt,ref} = \hat{S}_{t,test} - w_v \Delta f \tag{5.7}$$

Hence, the PSE for incongruent, vision lower frequency condition, defined as the tactile test stimulus at which the perceived bimodal estimate is equal to the reference stimulus, can be calculated using the MLE model as follows:

$$PSE_{MLE,v<t} = \hat{S}_{vt,ref} + w_v \Delta f = (w_v \widehat{PSE}_v + w_t \widehat{PSE}_t) + w_v \Delta f \tag{5.8}$$

Similarly, for incongruent, vision higher frequency condition, we could get:

$$PSE_{MLE,v>t} = \hat{S}_{vt,ref} - w_v \Delta f = (w_v \widehat{PSE}_v + w_t \widehat{PSE}_t) - w_v \Delta f \tag{5.9}$$

And for congruent bi-modal conditions:

$$PSE_{MLE,v=t} = w_v \widehat{PSE}_v + w_t \widehat{PSE}_t \tag{5.10}$$

5.3 Results

5.3.1 Experiment 1: Visuotactile Integration of Surface Spatial Frequency

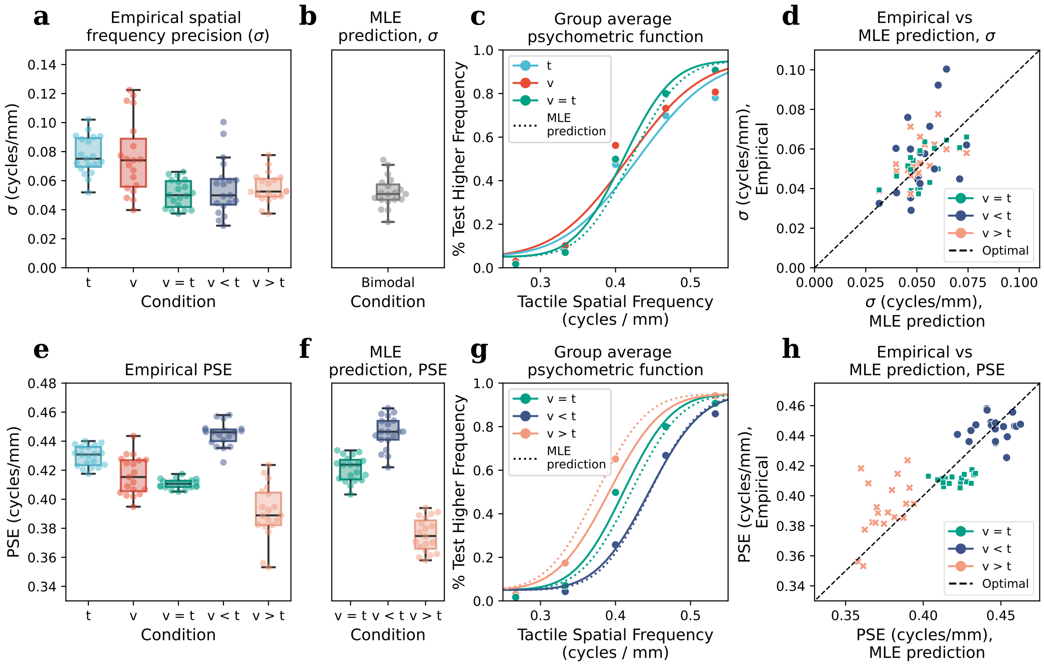

FIGURE 5.4: Experiment 1: Visuotactile Integration of Spatial Frequency. **a.** Boxplot of spatial frequency precision (σ) across all empirical conditions in Experiment 1. *Post hoc* comparisons indicate that all three bimodal conditions exhibit better precision than either of the two unimodal conditions. **b.** MLE prediction of bimodal spatial frequency precision. No significant differences were found between the MLE predictions and the three bimodal conditions. **c.** Group-averaged psychometric functions for the two unimodal conditions and the congruent bimodal condition, along with the MLE-predicted psychometric function for the congruent bimodal condition (dotted line). The congruent bimodal condition and the MLE prediction exhibit greater precision than the unimodal conditions, as indicated by the steeper slopes. **d.** Empirical σ were plotted against MLE prediction, and a significant relationship was found between the two. No significant effects were found between different bi-modal conditions. **e.** Boxplot of PSE across all empirical conditions. **f.** MLE prediction of PSE. **g.** Group-averaged psychometric functions for the three empirical bi-modal conditions and corresponding MLE prediction. **h.** Empirical PSE against MLE prediction. Both MLE prediction and congruency conditions were found to predict the empirical values significantly.

Experiment 1 aims to investigate whether the brain integrates spatial frequency information from vision and touch in a statistically optimal manner. Participants were tested under five different congruency conditions: visual-only, touch-only, congruent bi-modal, incongruent (visual lower frequency), and incongruent (visual higher frequency). Maximum likelihood estimation (MLE) model predictions were computed for each participant based on their uni-modal performance. These predictions included both spatial frequency precision (σ) for the biases (PSE) for bi-modal conditions (see the Methods section for further details).

5.3.1.1 Effect of Congruency Condition on Spatial Frequency Precision

A repeated-measures analysis of variance (RMANOVA) was conducted to test the main effect of congruency conditions on spatial frequency acuity (σ). Mauchly's test indicated that the assumption of sphericity was violated ($\chi^2(14) = 63.053$, $p < .001$). Therefore, a Greenhouse-Geisser correction was applied. The main effect of congruency condition was significant after correction ($F(2.182, 39.283) = 18.113$, $p < .001$, $\eta_p^2 = .502$).

Post hoc pairwise comparisons using the Holm-Bonferroni correction revealed that spatial frequency precision was significantly better for all three bi-modal conditions (congruent bi-modal, incongruent with visual lower frequency, and incongruent with visual higher frequency) as well as the MLE prediction, compared to either of the uni-modal conditions (vision-only, touch-only). No other significant pairwise comparisons were found (see Table 5.1 for detailed statistics). See Figure 5.4a and b for boxplot of empirical and MLE predicted σ.

In addition to the RMANOVA, A multiple linear regression was conducted to examine whether the MLE prediction and bimodal congruency conditions significantly predict the empirical data (Figure 5.4d). For the regression analysis, bimodal congruency conditions ($v = t$, $v < t$, $v > t$) were coded as the difference between visual and tactile spatial frequencies (0, -0.067, 0.067 cycles/mm respectively) such that it is a continuous variable. The overall regression model was significant, $R^2 = 0.224$, $F(2, 54) = 7.798$, $p = 0.001$, indicating that MLE prediction and congruency conditions explain a significant portion of the variance in the empirical data. The regression coefficients revealed that MLE prediction was a significant predictor of empirical σ ($b = 0.624$, $\beta = 0.473$, $SE = 0.157$, $t(54) = 3.949$,

$p < .001$). However, the congruency condition was not a significant predictor of empirical spatial frequency precision (σ) ($b = -0.001$, $\beta = -0.006$, $SE = 0.030$, $t(54) = -0.047$, $p = .963$).

These findings strongly support the hypothesis of multisensory integration of spatial frequency information between vision and touch. All bimodal conditions exhibited significantly better precision than either unimodal condition, highlighting the facilitative effect of combining multisensory cues. Furthermore, the lack of significant differences between the MLE predictions and the three bimodal conditions suggests that the experimental results align well with the MLE model. Additionally, regression analysis indicated that congruency had no effect on spatial frequency precision, further reinforcing the MLE integration hypothesis.

5.3.1.2 Effect of Congruency Condition on Biases in Spatial Frequency Perception

To further test whether the incongruence of tactile and visual stimulus would lead to biases in spatial frequency perception, and whether the biases (PSE) can be predicted with the MLE model, another RMANOVA was conducted to test the main effect of congruency conditions on PSE. As the predicted PSEs were MLE predictions based on linear combinations of empirical PSEs, Mauchly's test cannot be conducted due to collinearity between conditions. Instead, John, Nagao and Sugiura (JNS) test of sphericity (Abdi, 2010a) was conducted and indicated that the assumption of sphericity was violated ($\chi^2_v(27) = 1099.009$, $p < .001$). And a Greenhouse-Geisser correction was applied. The main effect of congruency condition was significant after correction ($F(2.506, 45.108) = 102.853$, $p < .001$, $\eta^2_p = .851$).

Figure 5.4 e and f show the boxplots for PSE across all conditions, and the statistics for the *post hoc* comparisons are detailed in Table 5.2. Several key comparisons are as follows: The incongruent, vision-lower-frequency condition was found to have a PSE larger than all other empirical conditions, while the incongruent, vision-higher-frequency condition had a PSE lower than all other conditions. The PSE for the empirical congruent bimodal condition was significantly higher than the MLE prediction. No significant difference was found between the incongruent, vision-lower-frequency condition and its MLE prediction, which confirms the

MLE prediction. Additionally, the empirical incongruent, vision-higher-frequency condition had a PSE significantly higher than its MLE prediction.

The analysis of biases (PSEs) in spatial frequency perception also supports the hypothesis of MLE integration of spatial frequency cues between touch and vision, as the PSEs for incongruent conditions were found to shift according to the incongruent visual stimulus. However, for the incongruent, vision-higher-frequency the MLE model appears to underestimate the biases, while for congruent bi-modal conditions the MLE model seems to overestimate the biases. The implication of these particular finding will be discussed in detail in the Discussion section.

A multiple linear regression analysis was also conducted for PSE, and the overall regression model was significant ($R^2 = 0.802$, $F(2, 54) = 109.323$, $p < 0.001$). The regression coefficients revealed that both MLE prediction ($b = 0.393$, $\beta = 0.124$, $SE = 0.124$, $t(54) = 3.158$, $p = .003$) and congruency condition ($b = -0.191$, $\beta = -0.420$, $SE = 0.071$, $t(54) = -2.693$, $p = .009$) significantly predicted the empirical PSE.

The results of the regression analysis on PSE also support the MLE integration model, as the MLE prediction significantly predicted the empirical PSEs in all bimodal conditions. Additionally, the empirical PSE was significantly shifted by the incongruent visual frequency, complementing the findings from the previous RMANOVA on PSE.

5.3.1.3 Effect of Congruency Condition on Response Time

To better understand the difference in sensory processing between each congruency condition, an RMANOVA was performed to test the effect of congruency condition on response time. Mauchly's test indicated that the assumption of sphericity was violated ($\chi^2(9) = 28.519$, $p < .001$), and a Greenhouse-Geisser correction was applied. The main effect of congruency condition was significant after correction ($F(2.470, 44.465) = 35.081$, $p < .001$, $\eta_p^2 = .661$). indicating that response times varied across conditions.

Post hoc comparisons using the Holm-Bonferroni correction showed that response times in the touch-only condition were significantly slower than all other conditions, and the vision-only

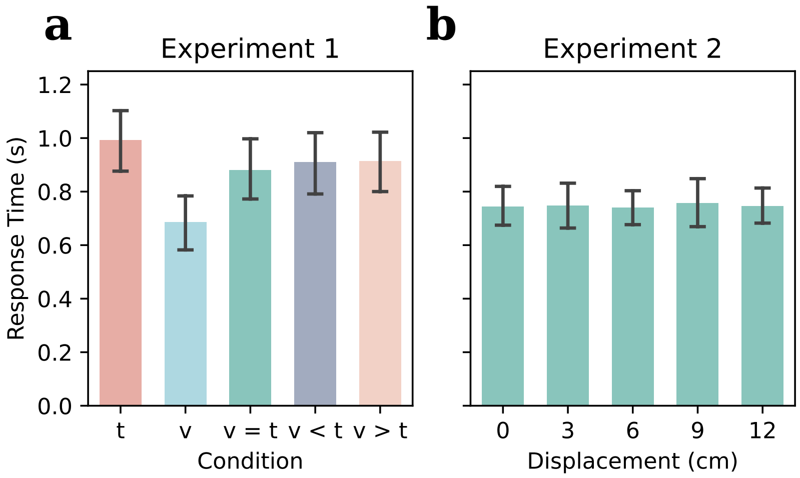

FIGURE 5.5: Experiment 1: effect of congruency condition on response time. **a.** Bar plot of mean response time (RT) across congruency conditions in Experiment 1. The tactile-only condition had significantly longer RTs compared to all other conditions, while the vision-only condition had the shortest RTs. **b.** Bar plot of mean RT across congruency conditions in Experiment 2. No significant main effect of spatial proximity on RT was found.

conditions were significantly faster than all other conditions. No significant difference was found in response time between the three bimodal conditions. See Table 5.3 for detailed statistics.

5.3.2 Experiment 2: Effect of Spatial Proximity on Visuotactile Integration of Spatial Frequency Cue

Experiment 2 aims to investigate whether spatial proximity affects the integration of spatial frequency cues between vision and touch. This experiment consists only of bimodal trials with congruent visual and tactile spatial frequencies. However, the visual stimulus was horizontally displaced from the tactile stimulus at five different distances to examine whether spatial proximity influences the integration of spatial frequency cues from the two modalities.

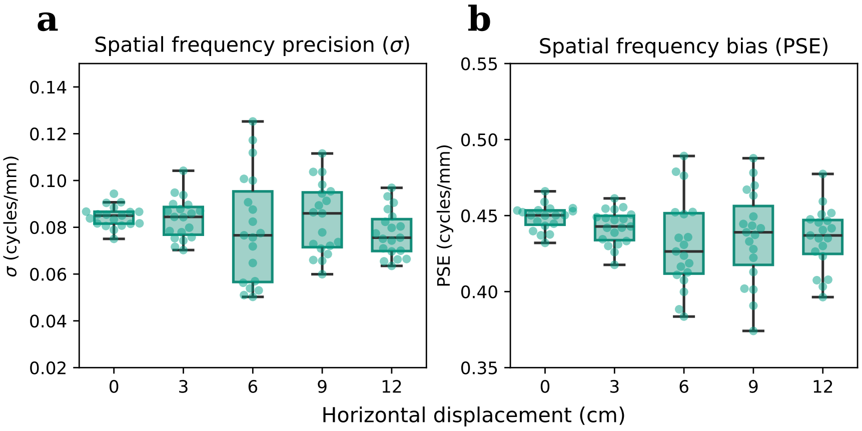

FIGURE 5.6: Experiment 2: effect of spatial proximity on visuotactile integration of spatial frequency. **a.** Boxplot of spatial frequency precision (σ) across five different horizontal displacements. No significant effect of spatial proximity on spatial frequency precision was found. **b.** Box plot of biases in spatial frequency perception (PSE) across five different horizontal displacements. A significant main effect was found, but no pairwise comparisons were significant.

5.3.2.1 Effect of Spatial Proximity on Spatial Frequency Precision

A repeated-measures ANOVA was conducted to test the main effect of spatial proximity on spatial frequency precision (σ). Mauchly's test indicated that the assumption of sphericity was violated ($\chi^2(9) = 38.096, p < .001$). Therefore, a Greenhouse-Geisser correction was applied. The main effect of spatial proximity was not significant after correction ($F(1.810, 32.578) = 1.973$, $p = .159$, $\eta_p^2 = .099$). To further understand whether the spatial frequency precision of the bimodal perception was affected by spatial proximity, a Bayesian RMANOVA was performed, and the Bayes factor indicated anecdotal evidence in favour of the null hypothesis, $BF_{10} = 0.543$. Figure 5.6a shows the boxplot of spatial frequency precision (σ) at different horizontal displacement levels.

5.3.2.2 Effect of Spatial Proximity on Biases in Spatial Frequency Perception

As all test stimuli in Experiment 2 were congruent in spatial frequency, no systematic differences in bias (PSE) in perceived spatial frequency were expected. Another repeated-measures ANOVA was conducted to test the effect of spatial proximity on PSEs. Mauchly's test indicated that the assumption of sphericity was violated ($\chi^2(9) = 27.261$, $p = .001$). The main effect of spatial proximity on PSE after Greenhouse-Geisser correction is significant ($F(2.693, 48.477) = 3.196$, $p = .036$, $\eta_p^2 = .151$). However, *post hoc* tests with Holm-Bonferroni correction find no significant difference between any pair of displacement conditions (see Table 5.4). The Bayes factor indicated anecdotal evidence in favour of the alternative hypothesis, $BF_{10} = 0.543$.

5.3.2.3 Effect of Spatial Proximity on Response Time

Similar to Experiment 1, an RMANOVA was conducted to examine the effect of spatial proximity on response time. Mauchly's test indicated that the assumption of sphericity was not violated ($\chi^2(9) = 5.213, p = .816$). No significant main effect of displacement on response time was found ($F(4, 72) = 0.133$, $p = .970$, $\eta_p^2 = .007$).

Overall, despite the inconclusive results in PSE analysis, the analysis of spatial frequency precision and biases found no clear evidence that spatial proximity affects the degree of visuotactile integration of spatial frequency cues. Furthermore, the absence of differences in response time across displacement conditions provides additional support for the notion that spatial proximity does not influence the sensory processing of bimodal information.

5.4 Discussion

5.4.1 Visuo-tactile Integration of Spatial Frequency Cue Follows Optimal Integration

In Experiment 1, we demonstrated that spatial integration between vision and touch follows the MLE rule, with bimodal conditions showing better precision than unimodal conditions. The MLE model successfully predicted the improvement in spatial frequency precision under the bimodal condition. Additionally, the PSE analysis revealed that when incongruent visual and tactile frequencies were presented, the bimodal perception fell between the individual unimodal perceptions. Regression analysis on spatial frequency precision and bias also finds that MLE prediction significantly accounts for the empirical data, which also supports the model.

While the overall results largely align with the MLE framework, some findings deviate from its predictions. Specifically, in the high visual-frequency condition, the MLE model overestimated the visual weight, predicting a PSE lower than empirically observed. Conversely, in the congruent bimodal condition, the model predicted a higher PSE than was obtained. These discrepancies likely arise because spatial-frequency processing is nonlinear in both vision and touch, and these nonlinearities are not equivalent across modalities. As a result, mismatches in their sensitivity profiles may cause the relative weighting of each modality to vary across the spatial-frequency domain.

Nonlinear behaviour in contrast sensitivity is well documented, with human contrast sensitivity varying nonlinearly across different spatial frequency ranges (Campbell & Robson, 1968; Hall & Hall, 1977; Pointer & Hess, 1989). Similarly, evidence from somatosensory perception indicates that tactile spatial sensitivity also varies nonlinearly across different frequency ranges, with an optimal range of spatial frequencies at which sensitivity is maximised (Hsiao et al., 1993). Besides, there were also various studies that suggest temporal cues can influence tactile spatial acuity (Cascio & Sathian, 2001; Gamzu & Ahissar, 2001). In an active exploration setting like the current experiment, changes in the spatial frequency of surface texture are likely to alter the rate of temporal cues received by mechanoreceptive afferents in the glabrous skin of the fingertip as the finger moves across the tactile stimulus. Previous studies have demonstrated nonlinear behaviour in tactile spatial acuity across different vibratory frequencies (Bensmaïa et al., 2006a) and tactile spatial perception, such as orientation acuity, could be influenced by the introduction of such temporal cues during active exploration (Wang & Alais, 2025a). Therefore, variability in temporal information may also contribute to the overall nonlinearity observed across different frequency ranges.

In Experiment 1, we also found evidence of nonlinearity in tactile and visual frequency perception, with significant differences in PSE between vision-only, tactile-only, and congruent bimodal conditions (see Figure 5.4e and Table 5.4). The difference in PSE between the two unimodal conditions and the congruent bimodal conditions suggests that, firstly, there might be nonlinearity in sensitivity at different frequencies, and secondly, the sensitivity profile might also differ between the two modalities. The nonlinear sensitivity across the spatial frequency space implies that each modality's weight may change across frequency ranges, depending on its reliability at a given spatial frequency, rather than remaining constant. This nonlinearity could explain the overestimation observed in the MLE model for congruent bimodal and incongruent higher frequency visual conditions.

Another possibility for the observed PSE being less affected by vision at vision higher frequency condition compared to the model prediction is the influence of the central tendency effect, as suggested by Aston et al. (2021). In the experimental design, incongruent trials were interleaved with the other three conditions (vision-only, touch-only, and congruent bimodal). The trial sequence was pseudorandomised to ensure an equal number of trials for each condition within each experimental block. Additionally, the average of all trials in a block was centred around the reference spatial frequency (0.4 cycles/mm), with more than half of the visual and tactile stimuli (including all reference stimuli and part of the testing stimuli) also set at 0.4 cycles/mm. As a result, participants' perceptions and decision-making may have been biased toward the average stimulus. This could explain the observed difference between the MLE prediction and the empirical PSE for the incongruent conditions. Even though the integration of incongruent vision and tactile cues drives bimodal perception away from the tactile stimulus and towards the visual stimulus (which has a higher or lower spatial frequency), the central tendency effect would also pull the bimodal perception and decision towards the average stimulus (which equals the reference stimulus of 0.4 cycles/mm). This, in turn, could reduce the shift in the PSE. In the Bayesian framework, this central tendency could also be viewed as a prior distribution with its mean at the reference stimulus, thereby influencing the posterior distribution of the bimodal perception accordingly.

5.4.2 Integration of Spatial Frequency Cue is not Affected by Spatial Proximity

Unlike the findings of Gepshtein et al. (2005), our results from Experiment 2 found no evidence that supports the hypothesis that spatial proximity affects integration. This discrepancy may arise from several factors, offering a valuable opportunity to explore the underlying mechanisms of multisensory cue integration.

One key factor that might lead to the difference between the two studies is the tasks and features tested. As Spence (2013) suggested, spatial proximity effects are less likely when tasks do not require spatial location information. In Gepshtein et al. (2005)'s study, the integrated feature was inter-surface distance, which required participants to focus on the location of surfaces and engage spatial attention. In contrast, our study examined spatial frequency perception, which is a localised feature that does not inherently depend on spatial location information; This could explain the absence of a spatial proximity effect.

Besides, Takahashi et al. (2009) also found that the brain integrates visual and tactile signals in an optimal fashion during tool use, even when there is a large spatial offset between the visual signal of the object at the tool tip and the tactile signal from the hand. However, this integration was reduced when the visual signal was moved away from the tool tip. This finding provides strong evidence suggesting that spatial proximity itself might not be the determining factor in whether information from different modalities is integrated. Instead, spatial proximity appears to provide information that helps the brain determine whether cues from different modalities originate from the same source. Complementing this hypothesis, the benefit of a common source in multisensory integration between vision and touch has been demonstrated by Helbig and Ernst (2007b).

Another consideration that further supports this hypothesis is that different integration mechanisms may be recruited depending on the nature of the task. Sathian and Zangaladze (2002) demonstrated that distinct patterns of brain activation occur when participants attend to different features within the same tactile stimulus. Specifically, orientation processing engaged the visual cortex, whereas spatial frequency perception did not. Similarly, orientation also requires awareness and reference to the location of the stimulus, where spatial frequency perception does not. Complementing this, Stoesz et al. (2003) also finds macrospatial features (large-scale features like shape, size and orientation) elicit different brain activity when compared to microspatial features (smaller, localised features like texture). Together, these findings suggest that there might be differential deployment of the visual system in tactile tasks.

Another interesting finding that seems to support the hypothesis that the integration of visual and tactile spatial frequency occurs at later stages comes from the discrepancy in response times across different congruency conditions in Experiment 1. Previous research has shown that human observers can detect combinations of multisensory signals more quickly than when each signal is presented individually (Hecht et al., 2008). However, in Experiment 1, we observed a different pattern: the vision-only condition was consistently faster in response time compared to the bimodal conditions, while the tactile-only condition was consistently slower (see Figure 5.5a). This finding seems to suggest that for spatial frequency information, unimodal information may first be processed independently and only combined at higher cognitive hierarchical levels. This could explain the slower yet more precise bimodal perception compared to the vision-only condition. Furthermore, the independent processing of unimodal information before integration may also account for the lack of effect of spatial proximity on integration. The facilitative effect of multisensory integration might arise from higher-level cognitive processes, where the information is more abstract and not tied to a specific receptive field location. The response time results in Experiment 2 also support this, as no significant difference was found in response times across different displacements (Figure 5.5b). This also seems to suggest that similar integration processes occur despite the discrepancy in spatial locations, with no evidence of an additional facilitative effect when the stimuli were colocalised. One limitation of the current experiment is that displacement was varied only horizontally (left–right) and within a limited range. This choice was partly due to the fact that movements along the other two axes (front–back and up–down) would result in larger changes in participants' viewing position relative to the visual stimuli, potentially altering the effective spatial frequency. Future studies could address this limitation by systematically manipulating vertical and depth displacements, while controlling for viewing distance, to investigate whether spatial location influences crossmodal integration over a broader range of positions.

One limitation of the current experiment is that displacement was varied only horizontally (left–right) and within a limited range. This was partly because movements along the other two axes (front–back and up–down) would produce larger changes in participants' viewing position relative to the visual stimuli, potentially altering the effective spatial frequency. Future studies could address this limitation by systematically manipulating vertical and depth displacements, while incorporating changes in viewing distance into the MLE model, to investigate whether spatial location influences crossmodal integration along other dimensions.

5.5 Appendix

TABLE 5.1: Experiment 1: Post Hoc Comparisons of Spatial Frequency Precision Across Frequency Congruency Conditions

		Mean Difference	SE	df	t	Cohen's d	p_{holm}
t	v	0.001	0.006	18	0.201	0.079	1.000
	v = t	0.026	0.003	18	9.771	1.669	$< .001$
	v < t	0.022	0.004	18	6.131	1.398	$< .001$
	v > t	0.022	0.002	18	9.335	1.410	$< .001$
	MLE	0.025	0.003	18	9.475	1.601	$< .001$
v	v = t	0.025	0.005	18	4.827	1.590	0.001
	v < t	0.021	0.006	18	3.279	1.319	0.033
	v > t	0.021	0.006	18	3.746	1.331	0.013
	MLE	0.024	0.004	18	6.152	1.522	$< .001$
v = t	v < t	-0.004	0.004	18	-1.040	-0.271	1.000
	v > t	-0.004	0.002	18	-1.917	-0.259	0.499
	MLE	-0.001	0.002	18	-0.532	-0.068	1.000
v < t	v > t	1.854×10^{-4}	0.004	18	0.050	0.012	1.000
	MLE	0.003	0.004	18	0.809	0.203	1.000
v > t	MLE	0.003	0.002	18	1.303	0.191	1.000

Table 5.2: Experiment 1: Post Hoc Comparisons of PSE Across Spatial Frequency Congruency Conditions

		Mean Difference	SE	df	t	Cohen's d	p_{holm}
t	v	0.013	0.003	18	3.857	1.189	0.005
	v = t	0.019	0.002	18	11.889	1.716	< .001
	v < t	−0.015	0.002	18	−7.426	−1.375	< .001
	v > t	0.038	0.004	18	8.497	3.453	< .001
	v = t, MLE	0.009	0.002	18	4.293	0.787	0.003
	v < t, MLE	−0.016	0.002	18	−7.022	−1.475	< .001
	v > t, MLE	0.054	0.003	18	15.533	4.907	< .001
v	v = t	0.006	0.003	18	1.895	0.527	0.149
	v < t	−0.028	0.004	18	−8.005	−2.565	< .001
	v > t	0.025	0.004	18	6.358	2.263	< .001
	v = t, MLE	−0.004	0.002	18	−2.666	−0.402	0.047
	v < t, MLE	−0.029	0.005	18	−5.818	−2.665	< .001
	v > t, MLE	0.041	0.002	18	17.144	3.718	< .001
v = t	v < t	−0.034	0.002	18	−17.662	−3.092	< .001
	v > t	0.019	0.004	18	4.416	1.737	0.002
	v = t, MLE	−0.010	0.002	18	−5.274	−0.929	< .001
	v < t, MLE	−0.035	0.002	18	−14.113	−3.191	< .001
	v > t, MLE	0.035	0.002	18	14.113	3.191	< .001
v < t	v > t	0.053	0.004	18	12.189	4.828	< .001
	v = t, MLE	0.024	0.003	18	9.325	2.163	< .001
	v < t, MLE	−0.001	0.003	18	−0.362	−0.100	0.722
	v > t, MLE	0.069	0.003	18	21.222	6.283	< .001
v > t	v = t, MLE	−0.029	0.004	18	−7.439	−2.666	< .001
	v < t, MLE	−0.054	0.006	18	−9.136	−4.928	< .001
	v > t, MLE	0.016	0.004	18	4.186	1.454	0.003
v = t, MLE	v < t, MLE	−0.025	0.004	18	−6.372	−2.263	< .001
	v > t, MLE	0.045	0.002	18	21.081	4.120	< .001
v < t, MLE	v > t, MLE	0.070	0.005	18	14.113	6.382	< .001

Table 5.3: Experiment 1: Post Hoc Comparisons of Response Time Across Frequency Congruency Conditions

		Mean Difference	SE	df	t	Cohen's d	p_{holm}
t	v	0.308	0.040	18	7.627	1.205	< .001
	v = t	0.113	0.025	18	4.447	0.442	0.002
	v < t	0.083	0.028	18	2.929	0.326	0.038
	v > t	0.079	0.026	18	3.001	0.309	0.038
v	v = t	−0.195	0.025	18	−7.868	−0.762	< .001
	v < t	−0.224	0.033	18	−6.861	−0.878	< .001
	v > t	−0.229	0.031	18	−7.414	−0.896	< .001
v = t	v < t	−0.030	0.024	18	−1.230	−0.116	0.469
	v > t	−0.034	0.015	18	−2.250	−0.133	0.112
v < t	v > t	−0.004	0.017	18	−0.263	−0.017	0.795

TABLE 5.4: Experiment 2: Post Hoc Comparisons of PSE Across Horizontal Displacement Conditions

		Mean Difference	SE	df	t	p_{holm}
0	3 cm	0.006	0.003	18	2.472	0.189
	6 cm	0.018	0.007	18	2.725	0.125
	9 cm	0.013	0.007	18	1.879	0.536
	12 cm	0.014	0.005	18	2.987	0.079
3 cm	6 cm	0.011	0.006	18	1.845	0.536
	9 cm	0.006	0.005	18	1.180	1.000
	12 cm	0.008	0.004	18	1.801	0.536
6 cm	9 cm	−0.005	0.007	18	−0.697	1.000
	12 cm	−0.004	0.005	18	−0.697	1.000
9 cm	12 cm	0.001	0.005	18	0.250	1.000

CHAPTER 6

General discussion

One of the primary goals of our perceptual system is to construct an accurate and reliable representation of the ever-changing, information-rich external world. Yet, for a long time, research in sensory perception focused on isolated modalities and static, independent trials (Alais et al., 2010). With growing evidence in recent years highlighting the importance of multisensory and temporal context in shaping perception, it becomes both important and compelling to adopt a holistic and dynamic approach to the study of sensory processing.

Orientation and spatial frequency are among the most fundamental spatial features in somatosensory perception. As in vision, they serve as building blocks for more complex spatial attributes (Hsiao, 2008; Hsiao et al., 1993; Pruszynski & Johansson, 2014) and are processed early in the perceptual hierarchy (Bourgeon et al., 2016; Hsiao et al., 2002; Pruszynski & Johansson, 2014). More importantly, striking similarities have been observed between somatosensation and vision in their underlying neural processing mechanisms (Bourgeon et al., 2016; Hsiao et al., 2002), especially concerning orientation and analogous behavioural patterns have also been demonstrated in both modalities (Appelle, 1972; Essock et al., 1992).

Hence, this thesis aimed to investigate the effects of multisensory and temporal context on two low-level spatial features, orientation and spatial frequency, using a psychophysical approach. By examining the complex interactions between the visual and somatosensory modalities, as well as the influence of temporal context across modalities, the goal was to gain a deeper understanding of the multiple pathways involved in the multisensory processing of these features, and to explore the potential for shared or common mechanisms underlying their perception.

6.1 Summary of Findings

In Chapter 3, the characteristics of tactile orientation perception were examined through a series of three experiments. Experiment 1 (Tactile Orientation Acuity) investigated the interaction between the tactile oblique effect and the exploration method (passive vs. active) using a two-interval forced-choice (2IFC) paradigm. It demonstrated the existence of an anisotropy in tactile orientation perception at the fingertip that was independent of exploration method, with the proximal-distal direction showing consistently superior acuity compared to the oblique and medial-lateral directions. In Experiment 2 (Tactile Orientation Serial Dependence), the tactile oblique effect was replicated using a single-interval binary task, and a systematic attractive serial dependence effect was observed. Finally, Experiment 3 (Tactile Orientation Serial Dependence with Alternating Responses) revealed that the attractive serial dependence effect was driven by post-perceptual processing rather than by the stimulus *per se*.

In Chapter 4, we extended our exploration of the influence of temporal and multisensory context on orientation perception in the second study. In Experiment 1 (Tactile Tilt Aftereffect), we examined another type of perceptual history effect, orientation adaptation, in tactile orientation perception using a tilt aftereffect (TAE) paradigm. This experiment revealed a tactile TAE similar to the classic TAE observed in vision. In Experiment 2 (Visuotactile Crossmodal Tilt Aftereffect), we demonstrated an asymmetrical transfer of the orientation adaptation effect: adaptation in touch produced a TAE in vision, but the reverse—visual adaptation affecting tactile perception—was not observed. Additionally, when examining the intramodal serial dependence effect, a similar asymmetry was found: the visual test sequence showed a repulsive serial effect, whereas the tactile test sequence showed an attractive serial effect.

Finally, in Chapter 5, the multisensory integration of another low-level spatial feature, spatial frequency, was investigated in a virtual reality (VR) environment. In Experiment 1 (Visuotactile Integration of Surface Spatial Frequency), unisensory, congruent bimodal, and incongruent bimodal perceptions of spatial frequency were experimentally tested. It was demonstrated that multisensory integration of spatial frequency followed the predictions of statistically optimal Maximum Likelihood Estimation (MLE). In Experiment 2 (Effect of Spatial Proximity on Visuotactile Integration of Spatial Frequency Cue), it was shown that this integration did not conform to the spatial principle, as no effect of spatial proximity on integration was observed.

6.2 Analogy of Tactile and Visual Low-Level Spatial Feature Processing

One important implication of the experimental findings is the similarity between the two modalities. In Chapter 3, both the oblique effect and the serial dependence effect were demonstrated in the tactile domain. In Chapter 4, a robust TAE was also observed in touch. All of these disparate phenomena were initially demonstrated in vision (Appelle, 1972; Fischer & Whitney, 2014; Gibson, 1937), and were successfully replicated in this thesis. While these analogous behaviours may not appear surprising, they nevertheless underscore a crucial insight into the processing of spatial features across visual and tactile modalities: the mechanisms involved are likely highly similar, with the possibility of shared processes across these different modalities.

Indeed, prior neurophysiological findings provide a solid basis for this speculation: both orientation selectivity (Bensmaia et al., 2008; Bensmaïa et al., 2008; Hsiao et al., 2002; Pollen & Ronner, 1983) and spatial frequency selectivity (Bourgeon et al., 2016; Pollen & Ronner, 1983) are critical receptive field properties of primary sensory neurons in both modalities, indicating similar processing stages and mechanisms at the single-neuron level for these low-level spatial features.

Hence, part of the goal of this thesis is to further extend the behavioural evidence supporting this hypothesis. Specifically, the oblique effect has been shown to originate from the distribution and tuning bandwidth of orientation-selective neurons (Li et al., 2003; Mansfield, 1974). Functionally, in vision, it has been hypothesised that such anisotropy enables the embedding of natural scene orientation statistics, acting as a prior distribution within a Bayesian framework and facilitating the efficient coding of orientation information at early processing stages (Harrison et al., 2023). The observed paradigm-independent and exploration-method-independent tactile oblique effect, along with neurophysiological evidence that slowly adapting type 1 (SA1) fibres exhibit a biased response toward the proximal-distal axis (Khalsa et al., 1998), suggests an analogous mechanism and evolutionary origin of the oblique effect in touch.

Moving on to the effect of temporal context, it appears that the similarity between vision and touch persists. In Chapter 4, a robust tactile TAE was replicated experimentally. As a well-studied and well-understood behavioural paradigm, the TAE has been widely adopted to probe the underlying orientation adaptation mechanisms in vision. The replicated robust TAE has provided behavioural evidence for two key similarities in tactile orientation perception to vision. First, it confirms that tactile orientation-selective neurons experience similar suppression after prolonged adaptation. Second, the population coding of orientation in touch appears similar to that in vision, where suppressed responses near the adaptor orientation lead to a repulsive bias in the perception of subsequent stimuli (Jin et al., 2005). This finding, along with several other behavioural studies on similar orientation adaptation effects in touch (Hidaka et al., 2022; Krystallidou & Thompson, 2016; Pérez-Bellido et al., 2018), complements previous neurophysiological findings on the representation of orientation information in the somatosensory cortex (Bensmaia et al., 2008; Bensmaïa et al., 2008; Hsiao et al., 2002), and demonstrates the universality of orientation-selective neuronal properties.

Serial dependence is another type of perceptual history effect that has gained increasing attention in recent years. In Chapter 3, the serial dependence effect was systematically tested and demonstrated for the first time in somatosensory orientation perception. However, further analysis and the results of Experiment 3 (Tactile Orientation Serial Dependence with Alternating Responses) suggest that the origin of this attractive bias may arise from post-perceptual processing. This finding aligns with several studies in vision research and argues against a purely perceptual origin of the serial dependence effect (Bliss et al., 2017; Ceylan et al., 2021). The implications for the processing stage and origin of the serial dependence effect are discussed in detail in Section 6.4. Nevertheless, the behavioural similarity observed across the two modalities reinforces the idea of shared mechanisms in orientation processing at later stages of processing.

6.3 Multiple Potential Pathways for Multisensory Interactions in Spatial Feature Processing

The analogous processing of low-level spatial features raises an important question: are the pathways for spatial features in the two modalities always parallel, and if not, at what stage do they converge? The experimental findings in this thesis seem to point to the existence of feature-dependent pathways.

In Chapter 4, an asymmetrical crossmodal transfer of the TAE has been observed between touch and vision: tactile adaptation induces a TAE in visual perception, but visual adaptation does not elicit a TAE in touch. This asymmetry reveals two important insights into orientation processing in somatosensory and visual modalities. First, contrary to the traditional view that unisensory information is processed independently and only integrated in higher-order multisensory brain areas (Stein & Stanford, 2008), the transfer of adaptation effect suggests that the same population of neurons must be involved in the unisensory processing of orientation information in both vision and touch. This is supported by neuroimaging studies showing activation in visual cortical areas during purely tactile tasks (Sathian & Zangaladze, 2002; Sathian et al., 1997; Zangaladze et al., 1999; Zhang et al., 2005). Secondly, the absence of a tactile TAE following visual adaptation suggests an asymmetric crossmodal transfer, indicating an unequal bidirectional connectivity between the two modalities. Although multiple potential mechanisms underlying this asymmetry are discussed in Chapter 4, the finding nonetheless highlights crossmodal involvement during unisensory tasks, indicating processing beyond simple unisensory pathways and convergence in higher-order cortical areas. Furthermore, an asymmetry was also observed in the intramodal serial dependence effects within the test sequences: visual testing trials exhibited a repulsive bias, whereas tactile testing trials showed an attractive bias. This finding once again points to non-parallel processing between the two modalities, suggesting distinct mechanisms or stages of influence underlying serial dependence in vision and touch.

The above findings indicate a complex interaction between the visual and somatosensory cortices during orientation perception, potentially occurring at multiple stages. In contrast, the psychophysical evidence presented in this thesis suggests that spatial frequency information is integrated differently, likely at later stages of processing. Specifically, the integration of visual and tactile spatial frequency information follows the predictions of the Maximum Likelihood Estimation (MLE) model, however, this statistically optimal integration is not affected by the spatial proximity between the two stimuli. As previously summarised in Section 2.3.1.1, the spatial principle of multisensory integration is grounded in the receptive field properties of multisensory neurons. Spence (2013) suggest that task-dependent violations of the spatial principle may arise from differential processing in the ventral and dorsal pathways. Indeed, positron emission tomography (PET) studies have demonstrated task-specific activations of the visual ventral and dorsal pathways during tactile tasks (Prather et al., 2004). This further supports the hypothesis of multiple potential pathways for crossmodal interaction.

Taken together, the findings of this thesis highlight the intricate relationship between the tactile and visual sensory systems. While there is a striking similarity in how spatial features are encoded and processed across modalities, crossmodal interactions are highly feature-dependent. This underscores the complexity and flexibility of multisensory integration, shaped not only by shared encoding principles but also by distinct processing pathways and task demands across the perceptual hierarchy. It also further underscores the importance of adopting a multisensory perspective when examining somatosensory perception.

6.4 Perceptual History Differentially Impacts Perceptual and Post-Perceptual Processing

Another critical dimension in adopting a holistic view of somatosensory perception is its temporal context. In Chapter 3, an attractive serial dependence effect was observed for the first time in somatosensory perception, further supporting the universality of this phenomenon across sensory modalities. However, the findings also suggest that this attractive bias is most likely driven by post-perceptual processes, as it was absent when participants were not cued to respond. This finding aligns with various results in vision, where the attractive bias is thought to emerge during post-perceptual processing or within working memory. In the absence of such processes, the dominant effect observed is typically repulsive, reflecting low-level neuronal adaptation (Bliss et al., 2017; Ceylan et al., 2021; Fornaciai & Park, 2019a; Sadil et al., 2023; Zhang & Alais, 2020). The empirical findings of the current thesis further confirm the presence of an attractive effect arising from post-perceptual processing. Moreover, by extending this effect from vision to somatosensation, the results suggest that serial dependence may be a canonical phenomenon across sensory modalities, providing additional support for its origin in working memory.

However, when considered alongside the complex cross-cortical recruitment of visual areas during tactile perception, the multisensory temporal context adds an additional layer of complexity to the system. In Chapter 4, we examined intramodal serial dependence within a crossmodal adaptation paradigm. A striking and noteworthy finding was that the serial dependence effect and classical neuronal adaptation do not appear to be simply additive. Instead, the results suggest a more complex interaction between these two distinct yet intertwined processes. Specifically, prolonged adaptation to tactile orientation induced a robust repulsive effect in the subsequent visual test sequence, alongside an inter-trial repulsion within the visual modality. Conversely, visual orientation adaptation did not transfer to touch; however, an attractive intramodal serial dependence effect was observed within the tactile test sequences. These empirical findings demonstrate that classifying serial dependence effects solely based on the direction of the bias is insufficient. Instead, they support the view that behavioural biases likely arise from the combination and interaction of multiple temporal integration mechanisms operating at different stages of processing. The direction and strength of these biases depend on stimulus features and the temporal profile of the stimuli, and the task demand of the post-perceptual processing.

6.5 Limitations and Future Outlook

Although the current thesis aimed to examine tactile and multisensory processing of low-level spatial features under rigorous experimental control, several limitations remain that warrant further investigation.

The first limitation arises from the experimental setup used in Chapter 3 and Chapter 4. Due to the design constraints of the tactile device, only one testing disk with a fixed spatial frequency could be used during the exploration of orientation. As a result, a series of pilot experiments were conducted to select a specific spatial frequency for the main studies. However, as shown in previous research and supported by the current findings, tactile spatial acuity varies significantly across individuals and is influenced by factors such as fingertip size and age (Peters & Goldreich, 2013; Peters et al., 2009). And in Chapter 5, evidence suggests that tactile perception of spatial frequency may not be linear across the entire range. Given the close relationship between orientation and spatial frequency, it would be worthwhile to extend the exploration to a broader range of spatial frequencies in future studies. By varying both spatial frequency and orientation, the reliability or variance of the tactile and visual orientation stimuli could be systematically manipulated by varying the spatial frequency. This would enable the modelling of temporal context effects within a Bayesian framework, and to understand the underlying computational model of the temporal integration.

Besides, Chapter 3 also examined how tactile orientation perception differs between active and passive conditions. In the passive condition, the disk was raised to press into the participant's fingertip and remained static during stimulus presentation, whereas in the active condition participants stroked their finger along the disk surface to perceive its orientation. When combined with the oblique effect conditions, the empirical findings in Chapter 3 offered valuable insights into the mechanisms underlying tactile orientation perception. However, improvements to the current apparatus could further disentangle the multiple factors that differentiate passive and active perception. Previous studies have shown that variables such as contact force (Papetti et al., 2017) and vibratory frequency (Bensmaïa et al., 2006a) during tactile perception can substantially affect perceptual performance. Thus, enhancing the apparatus to record and replay the contact forces and movement paths generated during active exploration would enable direct comparison across three conditions: (1) passive static stimulation, (2) active perception, and (3) passive perception with force and movement replayed. Such a design would help isolate the potential effect of temporal cues, intensity cues, and tactile gating mechanisms involved in active exploration.

In addition, in the empirical studies of Chapter 4, although efforts were made to closely align the visual and tactile stimuli, they were presented on different spatial planes. As described in that chapter, this spatial misalignment may have contributed to the asymmetrical crossmodal transfer of the TAE. To address this issue in the final empirical study of the thesis, the tactile device was upgraded to accommodate multiple tactile disks, and a virtual reality (VR) environment was implemented to achieve precise spatial colocalisation of visual and tactile stimuli. In future studies, replicating such experiments in a tightly controlled VR environment would be a worthwhile direction, as it better mimics the dynamic and active nature of tactile and multisensory perception in natural settings.

Another important finding in the empirical section of this thesis is the influence of temporal context and its intertwining effects. Although efforts were made to dissociate different stages of sensory processing, both through experimental design and data analysis, sensory perception, post-perceptual processing, and response execution are inherently continuous and difficult to separate by a purely behavioural paradigm. In Chapter 3, an alternating-response paradigm was used to dissociate perception from response in order to test whether serial dependence is driven by perceptual or decisional processes. Although the interleaved response and no-response trials separated response and response-associated motor movement from perception, knowing in advance whether a response would be required could still influence activity in primary somatosensory cortex through top-down attentional modulation (Mima et al., 1998). Introducing a condition with a randomly cued response requirement would further isolate and control for such attentional effects. It would also be worthwhile to combine behavioural tasks with high-temporal-resolution neuroimaging techniques, such as EEG, to better capture the neural signatures of these biases across different processing epochs. This approach could help to more accurately characterise the temporal profile of perceptual history effects across the full sequence of processing stages.

6.6 Conclusion

This thesis set out to investigate the mechanisms of tactile and multisensory processing of low-level spatial features, with a particular focus on orientation and spatial frequency. Across a series of psychophysical experiments, it revealed both shared and distinct principles underlying visual and tactile perception, as well as the complex influence of temporal context on perceptual history effects. The findings contribute to a growing body of evidence supporting the significance of the effect of multisensory and temporal context on somatosensory perception. By extending these phenomena into the somatosensory domain, this work has not only deepened our understanding of somatosensory perception, it has also highlighted the need for an integrative, dynamic and holistic model to fully understand sensory perception. It is hoped that this thesis has made a contribution that will inspire future efforts to further advance the frontiers of sensory research.

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