UNIVERSITY OF GENOVA

PHD PROGRAM IN BIOENGINEERING AND ROBOTICS

Tactile motion perception across sensory contexts: from multisensory integration to visual deprivation.

by

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Thesis submitted for the degree of *Doctor of Philosophy* (XXXVIII cycle)

June 2026

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Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other university. This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and Acknowledgements. This dissertation contains fewer than 65,000 words including appendices, bibliography, footnotes, tables and equations and has fewer than 150 figures.

Anna Vitale

April 2026

Acknowledgements

First of all, I would like to thank my supervisor, Monica Gori, for giving me the opportunity to undertake this journey and for her guidance throughout my work.

I would also like to thank my co-supervisor, Maria Casado Palacios, and the UVIP group. A special thanks goes to the colleagues of my cohort, who showed me what it truly means to work with the support of a group - and, when needed, how not to work.

Finally, I am deeply grateful to Alessandro Moscatelli, my tutor, who taught me the importance of conducting rigorous analyses and helped me develop a more critical and thoughtful approach to research.

Abstract

Multisensory integration allows the brain to combine information from different sensory modalities to form a coherent and reliable representation of the environment. Among these interactions, vision and touch play a fundamental role in motion perception, sharing common computational principles and neural mechanisms for encoding orientation and direction. This thesis investigates visuo-tactile integration in motion perception and examines how motion-related information is processed when visual input is available and when it is absent.

In the first part of the work, we focus on visuo-tactile integration in sighted individuals. Using the RoMAT robotic platform, we investigated how visual and tactile motion cues interact when presented simultaneously. Specifically, we examined whether motion directions from vision and touch are integrated into a unified percept. Behavioural results show that perceived motion direction reflects a combination of visual and tactile inputs, indicating a flexible and salience-driven integration mechanism across sensory modalities.

These findings raised a fundamental question: how is motion perception shaped when visual input is no longer available? To address this issue, the second part of the thesis focuses on tactile motion perception in visually impaired individuals. To enable reliable and accessible assessment of orientation and motion perception in both sighted and blind participants, we developed a novel tactile device, the Tactile Knob (TaK). Using TaK, we demonstrated that tactile-based responses are equivalent to visually guided responses in sighted individuals and that visually impaired participants perform comparably to sighted controls when relying on touch alone.

Finally, we investigated tactile motion direction sensitivity in sighted, early-onset blind, and late-onset blind individuals by measuring just noticeable differences (JNDs) across different reference orientations. Results revealed comparable discrimination thresholds across groups, indicating that overall tactile motion sensitivity is not systematically altered by the absence of vision. However, a robust orientation-dependent effect emerged, with enhanced sensitivity for cardinal directions, revealing a tactile oblique effect in motion perception that is independent of visual experience and blindness onset.

Together, these findings provide new insights into the shared mechanisms underlying visual and tactile motion perception, highlight the flexibility of multisensory integration processes, and clarify how tactile motion perception is shaped in the absence of vision.

Key-words: Visual impairment, Vision, Touch, Multisensory, Perception, Multisensory Devices, Cross-sensory Calibration

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CHAPTER 1

Introduction

1.1 Multisensory perception and cross-modal interactions

Human perception relies on the continuous integration of information from multiple sensory modalities. In natural environments, objects and events typically generate concurrent signals across different sensory systems, including vision, touch, and audition. Rather than processing these inputs independently, the brain combines them to form coherent and reliable representations of the external world. This process, commonly referred to as multisensory integration, plays a fundamental role in perception, action, and decision-making, allowing organisms to reduce sensory uncertainty and generate robust estimates of environmental properties (Angelaki et al., 2009; Ernst & Bülthoff, 2004; Shams & Seitz, 2008; Stein, 1993). A large body of behavioural evidence has demonstrated that combining information across sensory modalities can improve perceptual performance. When redundant information is available, observers often exhibit increased accuracy, faster reaction times, and enhanced perceptual precision compared to unisensory conditions (Alais & Burr, 2004; Ernst & Banks, 2002). These benefits arise because each sensory modality provides a noisy and potentially ambiguous estimate of the same physical property. By integrating multiple estimates, the brain can reduce overall uncertainty and improve perceptual reliability. Normative accounts of multisensory perception formalize this process within Bayesian and maximum likelihood estimation (MLE) frameworks, which propose that sensory signals are combined according to their relative reliability, such that more precise signals exert greater influence on the final percept (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Körding & Wolpert, 2006). Under this framework, the integrated percept corresponds to a statistically optimal estimate that minimizes variance and maximizes precision. However, numerous studies indicate that multisensory integration is not a mandatory or automatic process but instead reflects a flexible and context-dependent computation. The degree of integration depends on multiple factors, including sensory reliability, spatial and temporal congruency,

attentional allocation, and prior expectations about the causal relationship between sensory signals (Helbig & Ernst, 2007; Körding et al., 2007; Rohe & Noppeney, 2015). In particular, causal inference models propose that the brain must first estimate whether sensory signals originate from a common source before integrating them, and may partially or completely segregate signals that are unlikely to share a common cause (Körding et al., 2007; Shams & Beierholm, 2010). This framework explains why multisensory integration can range from optimal fusion to partial integration or sensory dominance, depending on the perceptual context.

At the neural level, multisensory integration is supported by distributed cortical and subcortical networks. Classical electrophysiological studies identified multisensory neurons in subcortical structures such as the superior colliculus, as well as in cortical association areas including the posterior parietal cortex and superior temporal sulcus (Stein & Stanford, 2008) These neurons exhibit characteristic integrative properties, such as enhanced responses to congruent multisensory stimuli. More recent neuroimaging and electrophysiological evidence has further demonstrated that cross-modal interactions are not restricted to higher-order areas but can also occur in early sensory cortices traditionally considered unimodal (Driver C Noesselt, 2008a; Ghazanfar C Schroeder, 2006; Kayser C Logothetis, 2007). These findings suggest that multisensory processing reflects a fundamental organizational principle of sensory systems, involving recurrent interactions across hierarchical processing stages.

Multisensory integration has been extensively investigated, and interactions between vision and touch represent a particularly important domain for understanding it. Both modalities provide detailed spatial information and play complementary roles in guiding object interaction, manipulation, and spatial behaviour. Critically, vision and touch also face similar computational challenges, particularly in motion perception, where sensory systems must reconstruct object motion from spatially distributed and inherently ambiguous signals. Investigating how visual and tactile signals are combined therefore provides a powerful framework for understanding the computational principles underlying multisensory perception.

1.2 Visuo-tactile interactions in spatial and motion perception

Among multisensory interactions, the integration of visual and tactile information represents a particularly important case for understanding how the brain combines signals conveying spatial and motion information. Both modalities encode fundamental spatial properties, including object position (DiCarlo James J., 2007; Klatzky C Lederman, 2011), orientation (Bensmaia, Denchev, et al., 2008; Bensmaia, Hsiao, et al., 2008; Furmanski & Engel, 2000), shape (Kubilius et al., 2016; S. J. Lederman & Klatzky, 1987), as well as material properties such as texture and compliance (S. J. , & K. R. L. Lederman, 2004). While vision samples information remotely through optical projections onto the retina, touch relies on direct mechanical interactions between objects and the skin. Despite these differences in sensory transduction, visual and tactile signals often convey information about the same physical properties and must therefore be integrated to support coherent perception and effective interaction with the environment.

Behavioural studies have demonstrated extensive visuo-tactile interactions in spatial perception. One of the most well-known examples is the rubber hand illusion, in which temporally and spatially congruent visual and tactile stimulation induces the illusory ownership of a prosthetic hand (Botvinick & Cohen, 1998). This illusion highlights the brain's ability to combine visual and tactile signals into a unified representation of body position, and critically depends on precise spatial and temporal correspondence between sensory inputs (Kammers et al., 2009). Similarly, visuo-tactile congruency paradigms have shown that visual stimuli can systematically bias tactile localisation, demonstrating that tactile perception is influenced by concurrent visual information and supporting the existence of shared multisensory spatial representations (Spence et al., 2004).

Visuo-tactile interactions have also been extensively investigated in the perception of surface properties, particularly texture. Tactile texture perception relies on spatiotemporal patterns of mechanoreceptor activation generated by relative motion between the skin and the surface (Hollins & Risner, 2000; Johansson & Vallbo, 1979). Vision and touch can provide partially redundant but also complementary information about texture, leading to modality-specific contributions depending on task demands. In some cases, tactile signals dominate perceptual judgments, consistent with the

modality appropriateness hypothesis, which proposes that sensory dominance depends on the relative reliability of each modality for the relevant perceptual dimension (Guest & Spence, 2003b, 2003a; Welch & Warren, 1980).

Beyond static spatial perception, visuo-tactile interactions play a particularly important role in motion perception. Both vision and touch encode motion through spatiotemporal patterns of activation across sensory receptors and rely on integrating local signals across space and time to reconstruct coherent motion trajectories (Pack & Bensmaia, 2015). Behavioural studies have demonstrated bidirectional interactions between visual and tactile motion signals. For example, tactile motion can bias visual motion perception when visual signals are ambiguous or degraded (Craig, 2006), while visual motion can systematically influence perceived tactile motion direction (Y.-C. Pei et al., 2013). These crossmodal influences indicate that motion signals are not processed independently within each modality but can interact to shape the final motion percept, suggesting the existence of shared or interacting computational mechanisms.

Neurophysiological evidence supports the existence of shared and interacting neural mechanisms underlying visuo-tactile motion processing. Electrophysiological studies in non-human primates have identified bimodal neurons in parietal and premotor areas that respond to both visual and tactile stimulation within overlapping spatial receptive fields (Graziano & Gross, 1993; Lanz et al., 2013; Murata et al., 1997). Importantly, these neurons encode stimuli in body-centred reference frames, enabling integration of visual and tactile information relevant for action. In humans, functional neuroimaging studies have revealed visuo-tactile interactions in fronto-parietal networks, including the intraparietal sulcus and premotor cortex, which are involved in spatial perception and sensorimotor control (Bremmer et al., 2001; Brozzoli et al., 2011; Makin et al., 2007). Critically, multisensory interactions have also been observed in cortical areas traditionally associated with visual motion processing. In particular, area MT/V5, a key region for visual motion perception, has been shown to respond to tactile motion stimulation, suggesting the existence of shared or convergent motion processing mechanisms across modalities (Hagen et al., 2002). Successful visuo-tactile integration requires the alignment of sensory signals encoded in different spatial reference frames. Visual motion is initially represented in retinotopic coordinates, whereas tactile motion is encoded in body-centred coordinates. Integrating these

signals therefore requires coordinate transformations that map sensory information into a common reference frame, a process supported by multisensory regions within the posterior parietal and premotor cortices (Driver & Noesselt, 2008b; Macaluso & Driver, 2005). These transformations enable the construction of coherent multisensory representations of object motion relative to the body. These findings challenge strictly modality-specific accounts of motion processing and support the idea that motion perception may rely on partially overlapping neural computations regardless of sensory modality.

While many studies have interpreted visuo-tactile interactions within Bayesian frameworks of optimal multisensory integration, research on motion perception within individual sensory modalities has highlighted additional computational properties that characterize how motion signals are represented. In both vision and touch, motion perception emerges from the integration of local spatiotemporal signals into coherent global motion percepts, a process that has been successfully described using vector-based models such as vector averaging and intersection-of-constraints mechanisms (Adelson & Movshon, 1982; Pack & Bensmaia, 2015; Y.-C. Pei et al., 2011). These models capture important aspects of how motion direction is encoded within each modality. The existence of these well-established unisensory motion integration mechanisms suggests that, in the multisensory domain, visuo-tactile motion perception may reflect not only the relative reliability of sensory signals, but also properties related to how motion information is represented and integrated within each modality. Considering these complementary perspectives may therefore provide a more complete account of how visual and tactile motion signals contribute to the final percept.

Importantly, the development and organisation of these multisensory representations are strongly influenced by sensory experience. Visual input plays a critical role in calibrating spatial perception across modalities, and its absence can alter the development and functional organisation of multisensory processing (Gori, 2015; Gori et al., 2010a). While these calibration processes have been extensively studied for spatial perception, their role in shaping visuo-tactile motion processing remains less well understood.

Investigating visuo-tactile motion perception therefore provides a valuable opportunity to examine how multisensory systems combine signals that already reflect complex computations within each sensory modality, and how sensory experience contributes to shaping these mechanisms.

1.3 Motion perception as a computational problem across sensory modalities

Motion perception relies on integrating spatially and temporally distributed sensory signals to derive coherent estimates of object motion. In the visual system, this process begins with local measurements, such as the responses of direction-selective neurons in early visual cortex, which encode motion within restricted receptive fields (Movshon & Newsome, 1996; Rust et al., 2006). However, these local measurements are inherently ambiguous. This ambiguity is well illustrated using drifting gratings, which are sinusoidal patterns consisting of alternating light and dark bars moving across space and commonly used to study motion perception. When a drifting grating is observed through a limited spatial aperture, only the component of motion perpendicular to the orientation of the bars can be uniquely determined, while an infinite number of possible motion directions remain compatible with the local sensory input. This phenomenon, known as the aperture problem, reflects the fact that each local motion signal constrains the possible motion of the stimulus without uniquely specifying it (Adelson & Movshon, 1982; Weiss et al., 2002).

Resolving this ambiguity requires combining information from multiple motion signals to estimate a single global motion direction. Several computational rules have been proposed to explain how this integration occurs. One influential model is the intersection-of-constraints (IOC) rule, which computes global motion as the unique velocity vector located at the intersection of the constraint lines defined by individual motion components (Adelson & Movshon, 1982; Weiss et al., 2002). This solution corresponds to the veridical motion direction, as it represents the only motion consistent with all local measurements simultaneously. In contrast, the vector average (VA) model computes global motion as the weighted average of the normal motion vectors associated with each component. Graphically, this corresponds to a point in velocity space located midway between the component motion vectors. Unlike the IOC

solution, the vector average does not necessarily correspond to the true physical motion but often provides a good approximation of perceived motion direction.

A third proposed mechanism is feature tracking (FT), in which motion perception is derived from tracking identifiable features within the stimulus, such as corners or intersections between contours. In certain stimuli, such as plaid patterns, the FT and IOC solutions coincide, and both correspond to the veridical motion direction (Weiss et al., 2002). However, psychophysical studies have shown that human perception does not always follow a single rule. Depending on stimulus properties such as contrast, speed, and spatial configuration, perceived motion may correspond to the IOC solution, the vector average, or intermediate estimates between these predictions (Rust et al., 2006; Weiss et al., 2002). These findings suggest that motion perception does not rely on a fixed deterministic rule but reflects flexible computations that depend on stimulus reliability and sensory uncertainty.

To account for these observations, probabilistic models have proposed that motion perception can be understood as a statistical inference process. Within Bayesian frameworks, the visual system combines noisy sensory measurements with prior expectations about motion to estimate the most probable velocity. In this formulation, local motion signals provide likelihood functions over possible velocities, while prior assumptions, such as a preference for slower motion, bias the final estimate toward more probable solutions (Weiss et al., 2002). The resulting percept corresponds to the velocity that maximizes the posterior probability distribution. Importantly, this framework naturally explains why perceived motion can deviate from the physically correct IOC solution under conditions of uncertainty, such as low contrast or noisy sensory input.

Importantly, analogous computational principles have been observed in tactile motion perception. As in vision, tactile motion is encoded through sequential activation of mechanoreceptors across the skin, and global motion direction must be reconstructed by integrating local motion signals. Neurophysiological and behavioural studies have demonstrated that neurons in somatosensory cortex respond selectively to global motion direction and that tactile motion perception can be described using models similar to those developed for visual motion integration (Pack & Bensmaia, 2015; Y.-C. Pei et al., 2011). These findings suggest that motion perception relies on canonical

computational strategies that operate across sensory modalities, despite differences in sensory receptors and input signals.

Together, these findings highlight that motion perception relies on computational mechanisms that integrate ambiguous local signals into coherent global motion representations, and that similar principles operate in both vision and touch. However, most of this knowledge derives from studies conducted within individual sensory modalities. Whether these modality-specific motion computations are preserved, modified, or interact when motion information is available simultaneously across different senses remains an open question. Investigating how visual and tactile motion signals are combined therefore provides a critical opportunity to determine how multisensory integration operates when the signals themselves arise from complex and potentially ambiguous computational processes.

1.4 Visual experience as a calibrating signal for tactile motion perception

Sensory experience plays a critical role in shaping how information from different sensory modalities is integrated and how individual sensory systems develop and function. Although adults often combine redundant multisensory information in a near-optimal fashion, converging evidence from developmental and neurophysiological studies indicates that multisensory integration is not fully mature at birth but emerges gradually through experience-dependent mechanisms (Lewkowicz, 2000; Nava et al., 2024; Sann & Streri, 2007). Animal studies have shown that multisensory neurons fail to develop typical response properties when cross-modal experience is disrupted during early development. For example, neurons in the superior colliculus of animals deprived of cross-modal experience fail to exhibit multisensory response enhancement, highlighting the critical role of sensory experience in the development of multisensory processing (Wallace et al., 2004). Converging evidence in humans further demonstrates that early atypical sensory experience can lead to long-lasting changes in cross-modal interactions, consistent with the existence of sensitive periods during which multisensory systems are particularly dependent on experience (Badde et al., 2020; Putzar et al., 2007).

Importantly, multisensory interactions during development may serve not only to combine redundant sensory signals, but also to calibrate sensory systems while the body and sensorimotor mappings are still developing. According to the cross-sensory

calibration hypothesis, one modality may provide a reference signal that helps establish and refine the representations of another modality (Burr & Gori, 2011). Within this framework, multisensory interactions may result in modality dominance rather than improved perceptual precision, reflecting an ongoing calibration process rather than reliability-weighted integration. This perspective helps explain developmental findings showing strong cross-modal influences and modality dominance in children despite the absence of the precision benefits typically associated with optimal multisensory integration (Barutchu et al., 2010; Gori et al., 2010b; Nardini et al., 2010).

Within this calibration framework, visual experience is thought to play a particularly important role in shaping tactile spatial representations. In the spatial domain, vision provides stable and externally referenced information about object orientation and motion, whereas touch must derive comparable spatial information from patterns of activation across the skin and transformations between reference frames. If vision contributes to calibrating tactile spatial representations during development, then early visual deprivation should selectively affect tactile perceptual functions that rely on spatial reference frames typically informed by visual input. Evidence supporting this prediction comes from studies of individuals with congenital visual impairment. Despite extensive tactile experience, congenitally blind individuals show impairments in specific tactile spatial tasks, such as orientation discrimination, whereas performance in other tactile domains, such as size perception, can remain intact or even enhanced relative to sighted individuals (Gori et al., 2010b). Crucially, individuals who experienced vision early in life but lost it later do not necessarily show the same impairments, suggesting that even limited early visual input may be sufficient to establish or stabilize tactile spatial representations.

These findings indicate that visual experience contributes to the developmental tuning of tactile spatial processing, rather than functioning solely as a redundant sensory input available for online integration. Within this framework, studying individuals with different visual experience provides a valuable opportunity to investigate how visual input contributes to the development and organization of tactile perceptual mechanisms. By comparing tactile perception in individuals with congenital and acquired blindness, it becomes possible to dissociate perceptual processes that depend on visual calibration from those that emerge independently of vision.

This approach is particularly relevant for motion perception. As discussed in the previous section, motion perception requires reconstructing global motion from inherently ambiguous local sensory signals and relies on spatial reference frames that specify motion direction relative to the external world (Adelson & Movshon, 1982; Pack & Bensmaia, 2015; Weiss et al., 2002). If visual experience contributes to calibrating these spatial representations, its absence could influence how motion signals are processed within the tactile modality. For example, visual deprivation could alter tactile motion sensitivity, directional anisotropies, or the integration of local motion signals into coherent global percepts. Investigating tactile motion perception in individuals with impaired visual experience therefore provides a direct opportunity to examine whether visual calibration contributes to the development of tactile motion processing mechanisms.

Addressing these questions requires precise and controlled methods to quantify tactile motion perception. However, many previous approaches have relied on manually delivered stimulation or tactile devices originally developed for assistive or display purposes. These systems often provide limited control over motion parameters and offer little flexibility for systematic experimental manipulation (Gori et al., 2016; Pawluk et al., 2015; Vidal-Verdu & Hafez, 2007). These constraints make it difficult to directly link behavioural performance to the computational mechanisms underlying tactile motion perception. Experimental platforms that allow systematic manipulation of motion parameters and precise measurement of perceptual sensitivity are therefore essential to characterize the computational principles governing tactile motion processing and to determine how these mechanisms are shaped by visual experience.

1.5 Aims and structure of the thesis

The overarching aim of this thesis is to characterize how visual and tactile motion signals are integrated and how sensory experience contributes to shaping the computational mechanisms underlying this process. Motion perception provides a particularly powerful model system for addressing this question, because it relies on well-defined computational operations that must transform ambiguous local sensory signals into coherent global motion estimates. While these mechanisms have been extensively studied within individual modalities, less is known about how motion

signals interact across modalities and how sensory experience contributes to shaping these processes.

To address these issues, this thesis adopts a progressive experimental approach, moving from multisensory interaction to modality-specific processing and finally to the role of visual experience in shaping tactile motion perception.

Chapter 2 investigates visuo–tactile motion integration using the RoMAT robotic platform (Gori et al., 2021), which enables precise and independent control of visual and tactile motion signals. By measuring perceptual responses under unisensory and multisensory conditions, this chapter examines how motion information from vision and touch is combined and whether their interaction reflects shared computational principles. Establishing how visual and tactile signals influence each other provides a critical foundation for interpreting tactile motion perception and for identifying the computational constraints governing multisensory motion processing.

Chapter 3 addresses a key methodological challenge that arises when studying tactile perception independently of vision. Many conventional response methods rely on visually guided reporting, which can introduce cross-modal transformations and limit the ability to measure tactile perception in a modality-consistent manner. To overcome this limitation, this chapter introduces and validates the TaK device (Vitale et al., 2025), a tactile-only response system that enables precise measurement of perceived motion orientation without requiring visual mediation. The validation of this tool in both sighted and visually impaired participants establishes a reliable method for quantifying tactile perception across individuals with different sensory backgrounds.

Building on this methodological foundation, Chapter 4 investigates tactile motion direction sensitivity in sighted, early-blind, and late-blind individuals. By comparing perceptual thresholds across groups and motion orientations, this chapter examines whether tactile motion processing depends on visual experience and whether the absence of vision alters perceptual sensitivity or directional anisotropies. This approach provides insight into whether tactile motion perception develops independently within the somatosensory system or is shaped by cross-sensory calibration during development.

Taken together, these studies provide a comprehensive investigation of tactile motion perception across multiple levels of analysis. By combining multisensory experiments,

methodological development, and comparisons across different visual experiences, this thesis aims to clarify both the computational mechanisms underlying visuo–tactile motion perception and the role of sensory experience in shaping tactile motion processing.

CHAPTER 2

Visuo–Tactile Motion Integration and Shared Computational Mechanisms

2.1 Background: Visuo-Tactile Motion Integration

Motion processing shows remarkable analogies between vision and touch (Casado-Palacios et al., 2023; Gori et al., 2011; Moscatelli et al., 2015; Y. C. Pei et al., 2008). In both sensory systems, the direction and orientation of a moving stimulus are encoded through spatiotemporal patterns of activation across the sensory surface - the retina in vision and the skin in touch. These similarities, together with converging behavioural and neurophysiological evidence, support the idea that motion perception relies on canonical computational mechanisms that operate across sensory modalities rather than being specific to a single sensory system (Pack & Bensmaia, 2015).

In both vision and touch, motion processing begins with local signals encoded by neurons with relatively small receptive fields. However, the perception of object motion requires the integration of these local motion signals into a coherent global representation. Stimuli such as gratings and plaid patterns are particularly useful to investigate this process because they allow dissociation between local motion components and global motion percept. Classic examples in vision include the barber-pole illusion, in which stripes physically moving horizontally are perceived as moving vertically due to the influence of the global stimulus configuration (Fisher & Zanker, 2001). Importantly, tactile analogues of such phenomena have also been observed (Bicchi et al., 2008; Y. C. Pei et al., 2008), indicating that similar integration mechanisms operate in the somatosensory system.

These behavioural similarities are supported by neurophysiological evidence. In the visual system, direction-selective responses emerge early in the processing hierarchy, starting from retinal ganglion cells and neurons in the primary visual cortex (V1) (Andersen, 1997). However, neurons in V1 show limited selectivity for stimuli containing multiple motion components, such as plaid patterns (Snowden et al., 1992). This ambiguity is resolved at later stages of processing, particularly in the middle

temporal area (MT, corresponding to hMT/V5+ in humans), where neurons integrate local motion signals and respond selectively to the global motion of the stimulus (Movshon & Newsome, 1996; Rust et al., 2006). Similarly, in the somatosensory system, neurons in Brodmann's Area 1 respond selectively to tactile plaid stimuli, providing direct evidence of motion integration mechanisms in touch (Y.-C. Pei et al., 2011). Moreover, sequential activation across neighbouring regions of the somatosensory cortex can generate the percept of continuous motion across the skin, further supporting the role of distributed neural activity in tactile motion perception (Valle et al., 2025).

Consistent with these neural findings, behavioural studies have shown that both visual and tactile motion perception rely on the integration of multiple motion components. When observers see (Adelson & Movshon, 1982) or feel (Y. C. Pei et al., 2008) plaid stimuli, they typically perceive motion in a direction resulting from the combination of the individual components. However, this integration process is not fixed but depends on the relative strength and reliability of the sensory signals. For example, altering the contrast of one of the visual components biases the perceived motion toward the component with higher contrast (Weiss et al., 2002), indicating that motion perception reflects a weighted integration of sensory information.

To explain how global motion is derived from local motion signals, several computational models have been proposed. In vision, the main classes of models include the Intersection of Constraints (IOC), the Vector Average (VA), and Feature Tracking (FT) models. These models differ in their assumptions about how ambiguous motion signals are combined. In particular, the vector average model proposes that motion direction is computed through a weighted combination of component motion signals, and this framework has been successfully applied to both visual and tactile motion perception (Adelson & Movshon, 1982; Y.-C. Pei et al., 2011). Similar integration principles have been observed in touch when motion signals are presented across multiple fingers (Takamuku et al., 2024). Bayesian approaches have further extended these models by incorporating sensory uncertainty and prior expectations, providing a unified framework for understanding motion perception across sensory modalities (Freeman et al., 2010; Moscatelli et al., 2015, 2019; Weiss et al., 2002).

While most of these studies have investigated motion processing within individual sensory modalities, everyday perception often involves the simultaneous availability of visual and tactile motion information. Evidence from cross-modal studies suggests that these signals interact and influence each other. For example, tactile motion can bias visual motion perception when visual information is degraded (Y.-C. Pei et al., 2013), and incongruent visual and tactile motion cues can lead to systematic perceptual errors (Craig, 2006). These findings indicate that motion perception reflects the integration of multisensory information rather than independent processing within each modality.

Building on this theoretical framework, the present study investigates visuo-tactile motion integration using the RoMAT device, a robotic platform designed to deliver controlled visual and tactile motion stimuli. By presenting visual and tactile motion signals either independently or simultaneously, this approach allows investigation of how motion information from different sensory modalities is combined and how each modality contributes to the final percept.

Establishing how visual and tactile motion signals interact represents a critical step for understanding the mechanisms underlying tactile motion perception and provides the foundation for the subsequent chapters of this thesis, which investigate tactile motion perception in the absence of vision.

2.2 Methods

2.2.1 The RoMAT device

The tactile stimuli used in this study were delivered using RoMAT (Robot for Multisensory Analysis and Testing), a robotic platform specifically developed to investigate motion perception and multisensory processing through controlled visual and tactile stimulation (Gori et al., 2021).

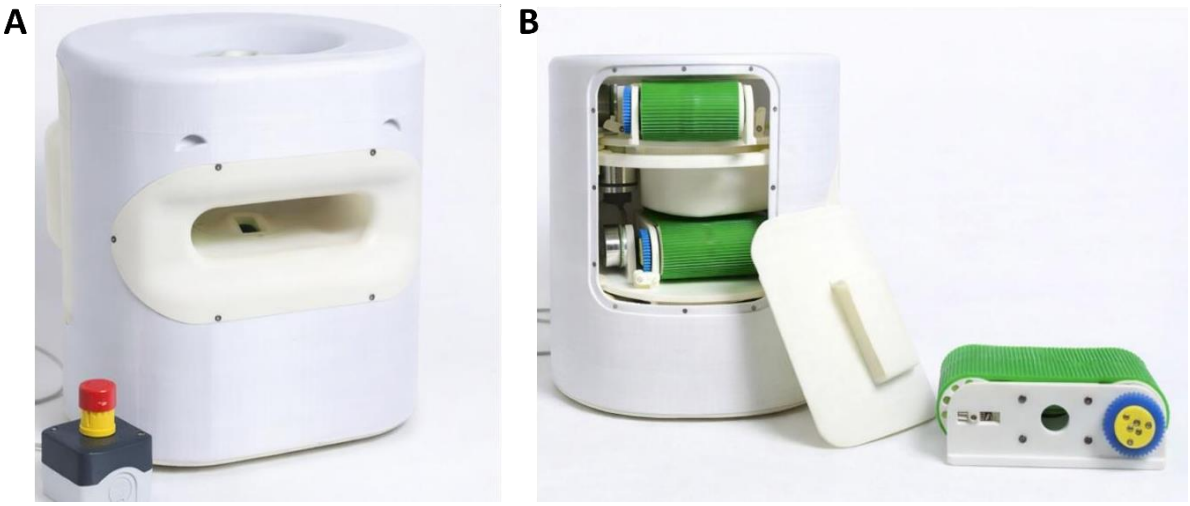

Figure 2.1 External view of RoMAT. (A) The front opening allows finger placement for tactile stimulation. The emergency stop button ensures safe operation. **(B)** Internal view of the romat device showing the two tactile stimulation modules and the removable stimulus cartridge. The interchangeable cartridge, shown removed in the foreground, contains the ridged belt that moves across the fingertip to deliver controlled tactile motion stimulation.

RoMAT consists of two vertically stacked rotating modules, each equipped with a motorized wheel capable of presenting motion stimuli with precise control over orientation and velocity. Each module includes a stimulus belt mounted on a rotating plate, driven by independent motors that control both the rotational orientation of the plate and the movement of the belt itself. By combining rotatable plates with interchangeable patterned belts, the system allows controlled manipulation of both motion direction and spatial pattern information. The tactile stimulus is delivered through a belt with raised ridges that moves across the participant's fingertip, producing controlled motion cues through passive stimulation. To ensure consistent stimulation and prevent active exploration, the system includes a cover with a finger-shaped aperture that constrains finger position and contact area.

The device is controlled by an electronic system that coordinates multiple motors through a dedicated control unit, allowing precise regulation of stimulus timing, speed, and orientation. The modular design also enables rapid replacement of stimulus belts, allowing different tactile patterns to be presented depending on the experimental requirements. This architecture enables the precise and repeatable delivery of motion stimuli and makes RoMAT particularly suitable for psychophysical experiments investigating motion perception.

2.2.2 Electronic architecture and motor control

The RoMAT device is equipped with four brushless DC motors controlling its degrees of freedom: two motors regulate the rotational orientation of the upper and lower plates, while two additional motors drive the movement of the stimulus belts. This configuration allows independent and precise control of both motion direction and motion speed for visual and tactile stimulation. The motors are controlled through a dedicated electronic architecture composed of an Ethernet Motor Supervisor (EMS4) board and two Field-Oriented Control driver boards (2FOC). The EMS4 module provides communication between the device and the control computer via an Ethernet connection, allowing the experimenter to remotely configure and execute experimental protocols. Communication between the EMS4 and motor driver boards is implemented through Controller Area Network (CAN) interfaces.

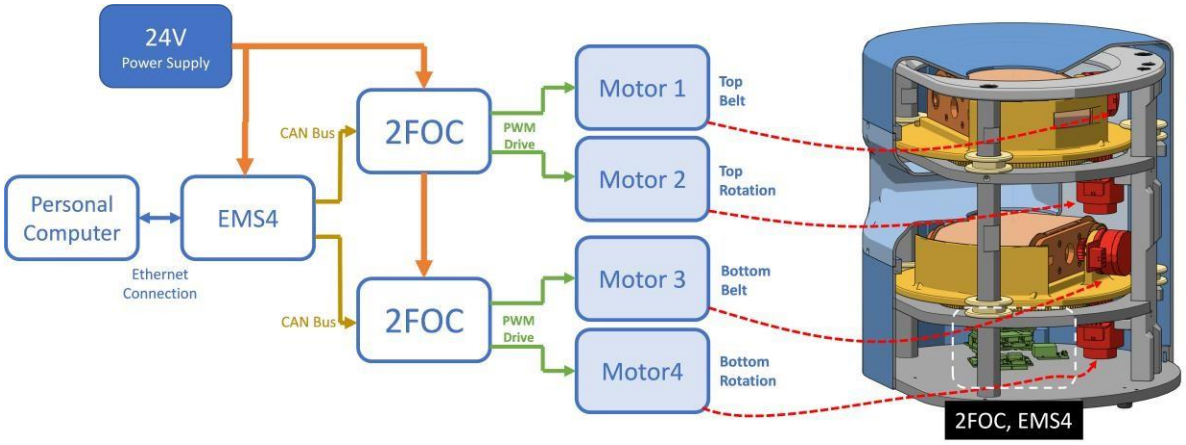

Figure 2.2. Electronic architecture of the RoMAT device. Block diagram illustrating the control system used to regulate the four brushless motors responsible for belt motion and plate rotation. The Ethernet Motor Supervisor (EMS4) communicates with the control computer and coordinates two Field-Oriented Control (2FOC) motor driver boards via CAN bus interfaces. Each driver board independently controls belt movement and plate rotation, enabling precise and synchronized delivery of visual and tactile motion stimuli. *Adapted from Gori et al. (2021).*

Each 2FOC board controls two motors and implements Field-Oriented Control algorithms, generating Pulse Width Modulation signals and running nested current and speed Proportional–Integral–Derivative control loops to ensure precise and stable

motor operation. The motors responsible for belt motion receive speed commands directly from the control computer, whereas the motors controlling plate rotation are regulated through minimum-jerk trajectories generated by the EMS4 module, ensuring smooth and accurate positioning. This electronic architecture enables precise synchronization between visual and tactile stimuli, independent control of motion parameters, and highly reproducible stimulus delivery, which are essential requirements for psychophysical investigation of motion perception.

2.2.3 Participants

Twenty naïve participants (mean age 25.8 years, SD = 3.9) took part in our behavioural studies. All participants were right-handed with normal or corrected-to-normal vision and reported no medical conditions that could have impacted the experimental findings. Written informed consent was obtained from all individuals involved in the research. The research protocol was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy) and conducted in line with the Declaration of Helsinki.

2.2.4 Experimental Setup and Procedures

During the experiment, participants were seated comfortably in front of the RoMAT device, positioned at approximately chest height (*see Figure 2.3*). The upper module of the device was visible and provided visual motion stimulation, whereas the lower module, accessible through a lateral opening, delivered tactile stimulation to the right index fingertip. The presence of a cover with a finger-shaped aperture ensured stable finger positioning and prevented active exploration, allowing controlled passive tactile stimulation. Following stimulus presentation, participants reported the perceived motion direction using a response interface consisting of a knob (Griffin PowerMate USB Programmable Controller) and a graphical display presented on a monitor positioned in front of them. By rotating the knob, participants adjusted the orientation of a visual arrow displayed on the screen until it matched the perceived motion direction. Once participants were satisfied with the selected orientation, they verbally informed the experimenter, who recorded the response via keyboard input.

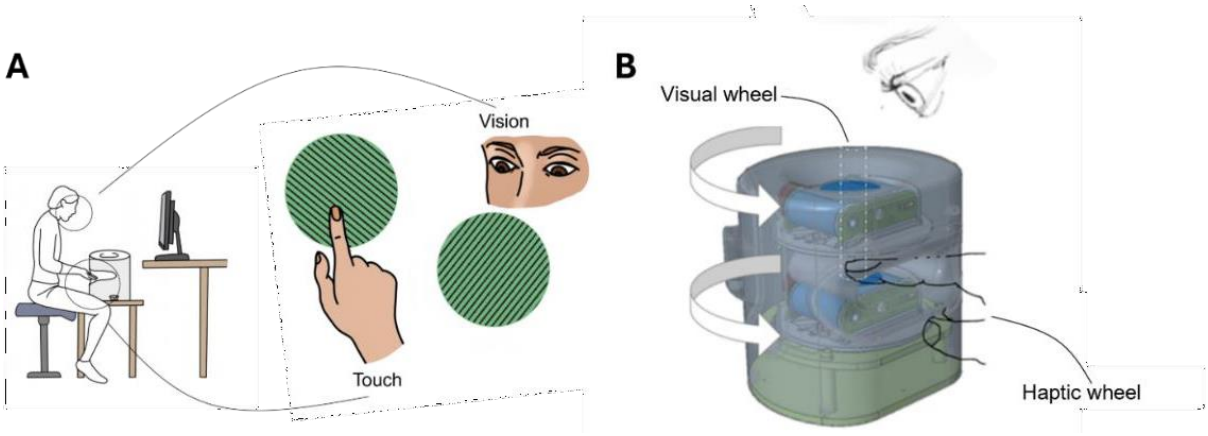

Figure 2.3. Experimental setup and participant interaction with the RoMAT device. (A) Schematic representation of a participant seated in front of the device during the visuo-tactile condition, illustrating simultaneous visual and tactile stimulation. **(B)** Internal view of the RoMAT device showing the visual stimulation module (upper wheel) and the tactile stimulation module (lower wheel), and their respective interaction interfaces. *Adapted from Gori et al. (2021).*

Both visual and tactile stimuli consisted of ridged belts moving across the respective sensory surfaces. The two modules were spatially aligned along the vertical axis and separated by approximately 20 cm, ensuring spatial correspondence between visual and tactile stimulation. Motion direction was controlled by rotating the stimulus plates while maintaining a constant belt speed of 3 cm/s.

Participants performed three experimental conditions in which motion was presented either visually (V), tactilely (T), or simultaneously in both modalities (VT). In the visual-only condition, only the upper wheel moved, delivering visual stimulation while the tactile module remained stationary. In the tactile-only condition, only the lower wheel moved, providing tactile stimulation without visual motion. In the visuo-tactile condition, both wheels moved synchronously, delivering simultaneous visual and tactile motion cues. In each trial, the motion direction of the wheels in the horizontal plane was randomly selected from three possible orientations: −22°, 0°, and +22°. The horizontal direction (0°) corresponded to motion orthogonal to the participant's line of sight, whereas the two oblique directions represented angular deviations from this axis. Each stimulus was presented for a duration of 3 seconds.

In the unisensory conditions, each direction was repeated 15 times, resulting in a total of 45 trials for each modality. In the multisensory condition, both congruent and incongruent combinations of visual and tactile motion directions were presented. Congruent trials corresponded to cases in which both wheels moved in the same

direction, whereas incongruent trials involved different motion directions between modalities. All nine possible combinations of visual and tactile orientations were presented (*see Figure 2.4*), with each combination repeated 15 times, yielding a total of 135 multisensory trials.

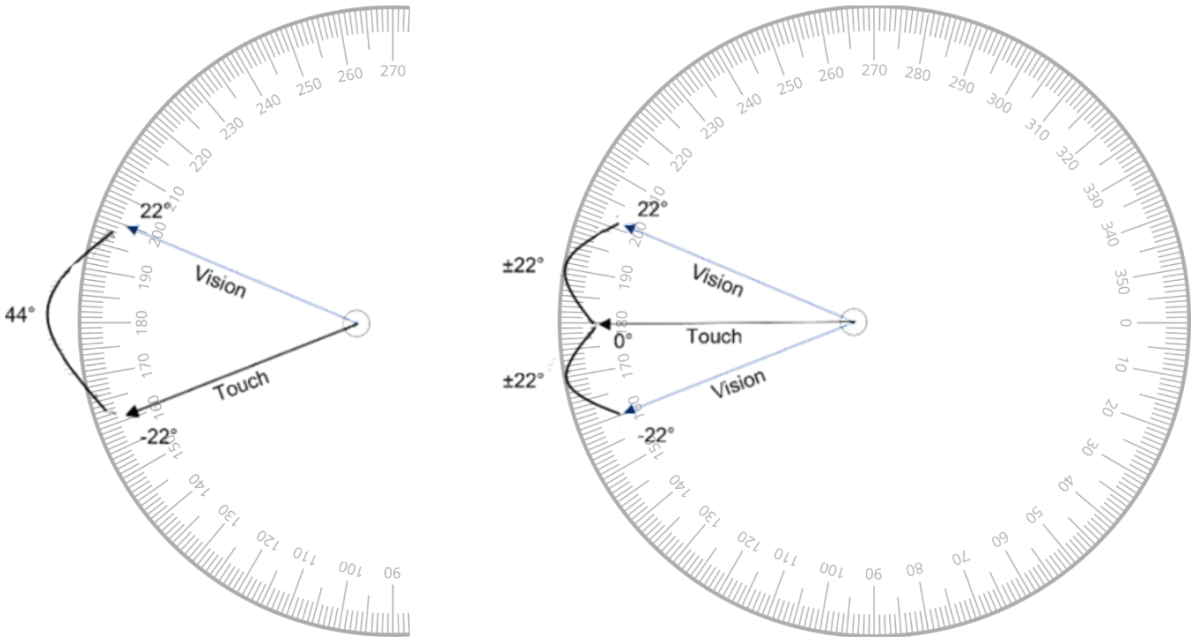

Figure 2.4 Visuo-tactile motion direction combinations in the multisensory condition. Schematic representation of the angular relationships between visual and tactile motion directions. Blue arrows represent visual motion, while black arrows represent tactile motion. The figure illustrates both congruent and incongruent combinations used in the experiment, including the largest angular discrepancy (±44°) and intermediate discrepancies (±22°).

In the visual-only condition, participants reported the direction of the visual stimulus, whereas in the tactile-only condition they reported the direction of the tactile stimulus. In the visuo-tactile condition, participants were instructed to report the direction of the tactile stimulus while also attending to the visual stimulus.

Participants used their right hand both to perceive tactile stimulation and to provide responses. The sequence of trials was pseudo-randomized using custom scripts implemented in R (version 4.3.0). Participants were allowed to take breaks approximately every 45 trials to minimize fatigue. The entire experimental session lasted approximately 1.5 hours.

2.3 Data analysis

All data preprocessing and statistical analyses were conducted using R (version 4.3.0). Linear mixed-effects models were fitted using the *lme4* package (Bates et al., 2015).

Prior to statistical analysis, outliers were identified and removed to reduce the influence of extreme observations. This procedure was performed in two steps. First, responses falling outside ±2.5 standard deviations from each participant's mean response were excluded. Second, for each combination of sensory condition and stimulus direction, the mean and standard deviation of responses were calculated, and observations falling outside ±2.5 standard deviations from the corresponding condition mean were excluded. Overall, this procedure removed 2.53% of trials. This approach allowed us to retain the large majority of valid responses while minimizing the impact of anomalous values, which likely reflected occasional response inaccuracies, lapses of attention, or imprecise knob adjustments rather than stable perceptual estimates. Importantly, the exclusion procedure did not qualitatively alter the overall pattern of results.

2.3.1 Unisensory conditions

To quantify perceptual biases in the visual-only and tactile-only conditions, two separate linear mixed-effects models were fitted. The model was specified as follows:

$$\hat{D}_{i,j} = \beta_0 + \beta_1 D_k + u_i \quad (1)$$

where $\hat{D}_{i,j}$ represents the motion direction reproduced by participant i in trial j, D_k represents the physical motion direction of the stimulus, β_0 is the intercept representing the baseline response, and β_1 represents the fixed effect of stimulus direction. The term $u_i$represents the random intercept for participant i, accounting for inter-individual variability.

Residual diagnostics were evaluated using the *DHARMa* package (Hartig, 2022; Hartig, 2026), and 95% confidence intervals for model parameters were estimated using parametric bootstrapping with 1000 replicates.

2.3.2 Multisensory condition

To investigate how visual and tactile signals jointly influenced perceptual responses, linear mixed-effects models were fitted to data from the visuo-tactile condition.

The primary model was specified as follows:

$$\hat{D}_{i,j} = \beta_0 + \beta_1 V_{i,j} + \beta_2 T_{i,j} + \beta_3 (V_{i,j} \times T_{i,j}) + u_i \quad (2)$$

where $\hat{D}_{i,j}$ represents the motion direction reported by participant i in trial j, $V_{i,j}$ and $T_{i,j}$ represent the visual and tactile stimulus directions, respectively, and β_1, β_2, and β_3 represent the fixed effects of visual input, tactile input, and their interaction. The random effect term u_i accounts for individual differences between participants.

The intercept represents the expected response when both visual and tactile motion directions are equal to 0°.

To further examine differences between specific combinations of visual and tactile directions, an additional linear mixed-effects model was fitted in which visual and tactile stimulus directions were treated as categorical variables. Estimated marginal means were computed using the *emmeans* package (Lenth, 2018), allowing pairwise comparisons between experimental conditions while controlling for other model factors.

Moreover, a post-hoc power analysis was conducted using the *simr* package (Green & MacLeod, 2016) to evaluate the sensitivity of the multisensory model. The fitted model was extended to a simulated sample of 20 participants, and statistical power was estimated through 100 simulations for each effect. This analysis provided an estimate of the probability of detecting the main effect of visual input and the visuo-tactile interaction given the current sample size and model structure.

2.4 Results

In the visual-only (V) condition, responses showed a clear and systematic distortion (Eq. 1). The mixed-effects model revealed a markedly inflated slope (b = 1.56, SE =

0.02, t(862) = 101.79, p < .001, 95% CI [1.53, 1.59]), indicating that perceived directions increased more than proportionally with the physical stimulus. To characterise this distortion, we computed the signed bias (bias = perceived angle − physical angle) separately for each visual direction (-22°, 0°, +22°). This is illustrated in *Figure 2.5-A*. Visual perception displayed a strongly asymmetric pattern: participants underestimated −22° (mean bias = −12.4°), were nearly veridical at 0° (−0.6°), and markedly overestimated +22° (+12.1°). Thus, visual perception was clearly non-veridical and subject to a magnitude-dependent expansion. In the tactile-only (T) condition, responses were also biased, though to a lesser extent. The slope of the mixed-effects model was again greater than 1 (b = 1.23, SE = 0.03, t(851) = 47.52, p < .001, 95% CI [1.18, 1.28]), indicating positive overestimation. Tactile bias was smaller and more symmetric: −2.6° at −22°, +1.0° at 0°, and +7.3° at +22°.

We also examined the precision of the two sensory modalities by analysing the variance of participants' responses (*Figure 2.5-B*). Response variance was computed separately for each stimulus direction and then averaged across directions within each modality, thereby isolating variable error from systematic directional biases. Visual estimates were less variable than tactile ones, indicating higher perceptual precision in the visual modality.

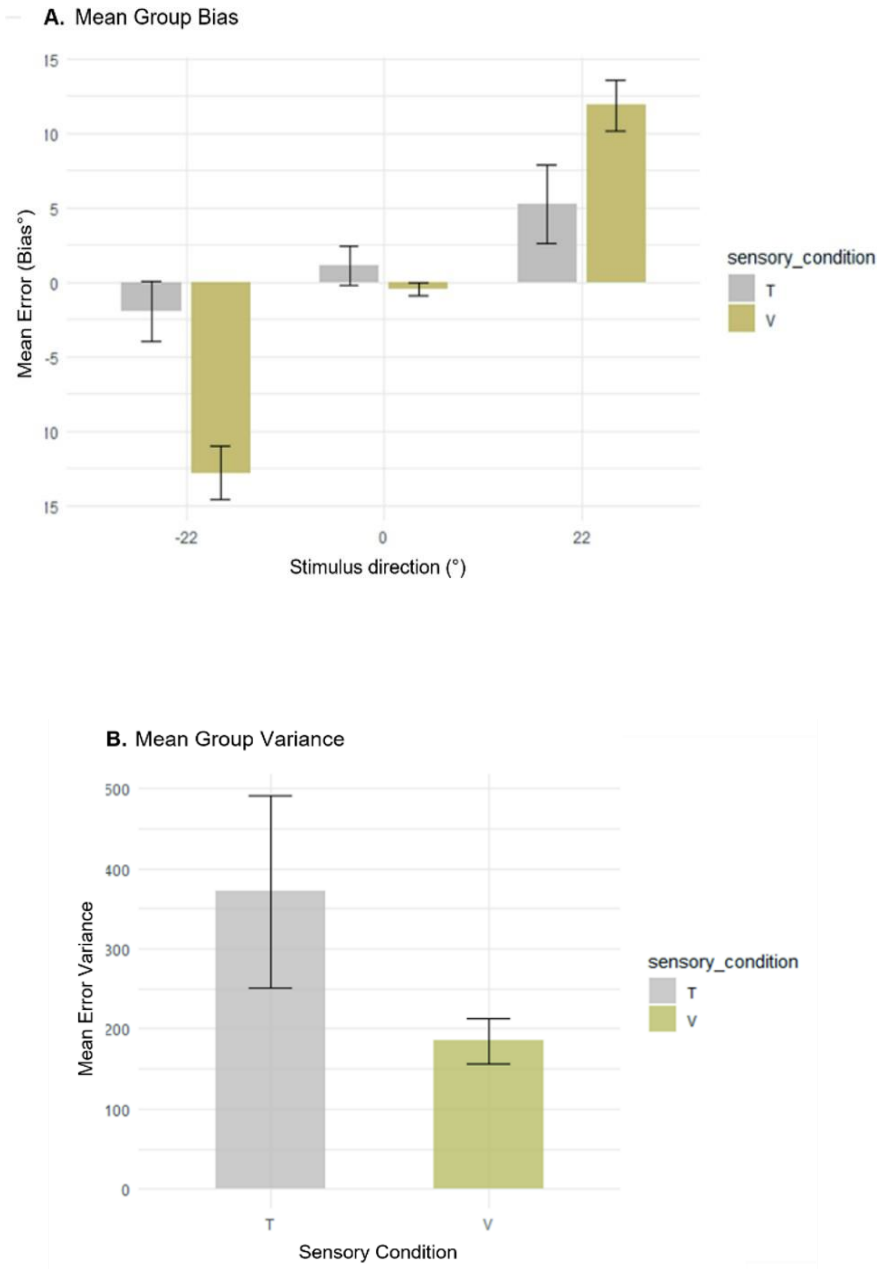

Figure 2.5 Bias and Response variability in unisensory conditions. (A) Mean perceptual bias in the unisensory visual (V) and tactile (T) conditions as a function of stimulus direction (−22°, 0°, +22°). Bias was computed as the difference between the reported and the physical motion direction. **(B)** Mean response variance in the unisensory conditions, averaged across stimulus directions, shown separately for visual and tactile trials. Error bars indicate the standard error of the mean (SEM) across participants.

2.4.1 Response distributions reveal unimodal percepts and inter-individual variability

First, we visually inspected the distribution of participants' responses for each combination of visual and tactile stimuli in VT condition. This descriptive analysis allowed us to qualitatively assess whether the response distributions were unimodal and whether participants' reported directions aligned with one of the sensory cues (winner-take-all strategy) or fell between them, as would be expected under multisensory integration or combination.

Figure 2.6 illustrates the response distributions of a representative participant. Distributions for all participants and all visual–tactile combinations are provided in the Supplementary Materials (Appendix A). At the individual level, responses exhibited clear unimodal distributions, suggesting that participants adopted consistent perceptual strategies rather than switching between modalities. At the same time, the mean and variability of these distributions differed considerably across observers, revealing pronounced inter-individual heterogeneity. This pattern supports the use of a hierarchical linear mixed-effects model: by treating each participant as a separate cluster and incorporating random intercepts, the model appropriately captures the participant-specific biases and differences in precision that characterise our data (see below).

On average, perceived directions fell closer to the tactile input while being systematically shifted toward the visual cue, consistent with partial integration characterized by tactile dominance with visual contamination.

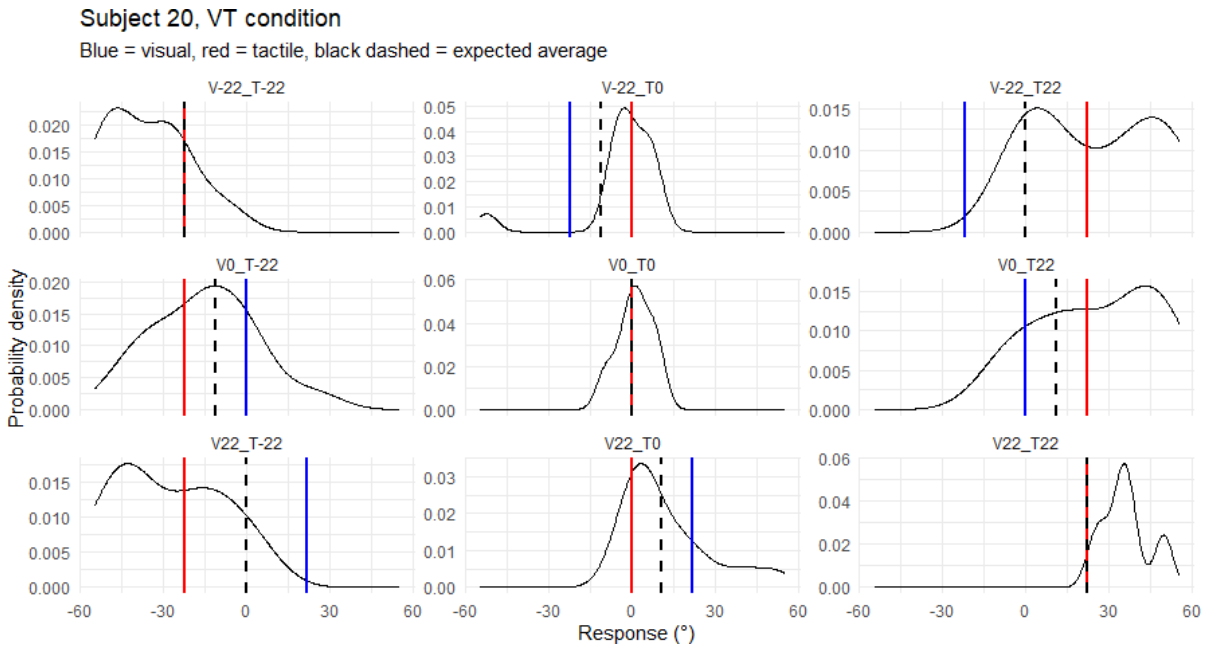

Figure 2.6 Response distributions for Subject 20 across the nine visuo–tactile combinations. The density curves show that Subject 20 adopts a stable and clearly unimodal perceptual strategy in all conditions. In congruent conditions (e.g., V0° & T0°), responses are tightly clustered around the common motion direction, while in conditions with cue conflict (e.g., V−22° & T22°, V22° & T−22°), response distributions consistently fall between the visual (blue line) and tactile (red line) motion directions but are shifted closer to the tactile value, while still showing a systematic bias toward the visual input. This pattern reflects partial integration of the two cues, characterized by tactile dominance with visual contamination, consistent with the average behavior observed at the group level.

Subject 20 displayed unimodal and stable response profiles across conditions. In congruent pairings (e.g., V0° & T0°), responses were tightly clustered around the shared motion direction, whereas in conflicting conditions (e.g., V−22° & T22°, V22° & T−22°), responses consistently fell between the two cues, closer to the tactile value but systematically biased toward the visual motion direction. This profile reflects the general trend observed across the sample.

2.4.2 Effects of visual and tactile motion directions in the Multisensory Condition

We employed a linear mixed-effects model (LMM) to assess how the tactile and visual wheels' direction influenced participants' responses in the multisensory (VT) condition. A first model included the two predictors (tactile and visual wheels' motion direction) as continuous variables, as well as their interaction term, and a random intercept for each participant to account for individual variability (Eq. 2). The model revealed a high

variance of the random intercept (u = 27.5), indicating notable individual differences across participants, and a residual variance of 287.2. The intercept estimate was 2.23 (p = 0.08) meaning that—when both the tactile and visual wheels' directions were set to 0°—perceived direction was not significantly different from zero. Both the tactile (β_2 = 0.94, SE = 0.018, p < .001) and visual (β_1 = 0.43, SE = 0.018, p < .001) cues exerted significant main effects on perceived direction. The interaction between the two predictors was also significant (β_3 = –0.005, SE = 0.001, p < .001), indicating that the contribution of each sensory modality to the final response varied systematically with the direction of the wheel in the other modality.

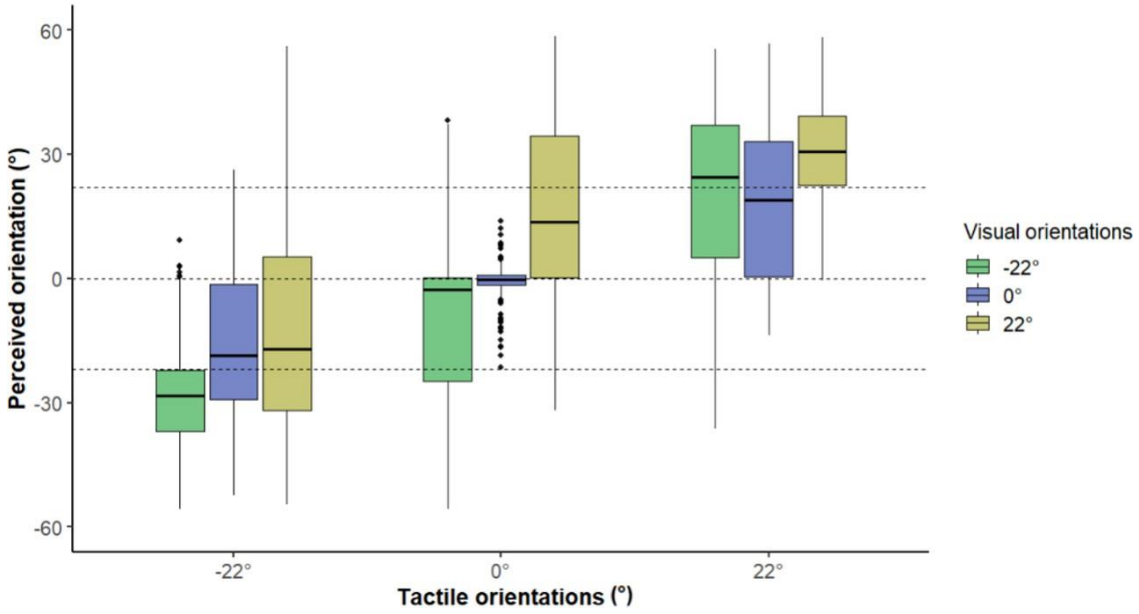

Figure 2.7 Mean responses in the multisensory condition. Boxplots represent the distribution of participants' responses (y-axis) for each tactile wheel direction(x-axis). Colours indicate the visual wheel directions (green = −22°, blue = 0°, yellow = +22°). Each boxplot shows the median, first and third quartiles, and outliers. Dashed horizontal lines mark the reference direction of the tactile and visual stimuli (−22°, 0°, +22°). Responses systematically varied with both tactile and visual inputs, consistent with an interaction between modalities.

It is important to note that the variance of the responses obtained through the knob may include a small motor component (e.g., related to manual adjustment or visual feedback during the response). However, this motor variance is expected to be constant across all sensory conditions (V, T, and VT), as the response procedure was identical in every trial. Therefore, while it may slightly inflate absolute variance values, it does not differentially affect the estimation of relative sensory reliability Model diagnostics supported the adequacy of the model. Visual inspection of the residual

histogram and Q–Q plot indicated that the residuals were approximately normally distributed. DHARMA-based tests showed no evidence of overdispersion (Dispersion test: p = 0.992) and no outliers (Outlier test: p = 0.742). Additionally, scaled residuals did not reveal any systematic deviation from homoscedasticity.

To further investigate these interactions, we fitted a second model in which both tactile and visual wheels' directions were treated as categorical variables (–22°, 0°, 22°). This allowed us to examine perceptual differences across specific combinations. Estimated marginal means (EMMs), computed using the emmeans package (Lenth, 2018), indicated significant differences between most combinations of tactile and visual wheels' directions. For instance, when the tactile wheel was oriented at –22°, responses were significantly higher when the visual wheel was at 22° compared to 0° or –22°. Conversely, when the tactile wheel was oriented at 22°, no significant differences emerged between visual directions of –22° and 0°.

Post-hoc pairwise comparisons using Tukey-adjusted emmeans revealed that all pairwise contrasts were statistically significant (p < .001) except for one case: when the tactile wheel moved in the +22° direction, the difference between the visual directions of –22° and 0° was not significant (p = .19). Full results of post-hoc comparisons are reported in Table 2.1.

Tactile orientation: -22°

Contrast	*estimate*	*SE*	*t.ratio*	*p.value*
visual -22°; 0°	-11.16	1.34	-8.316	<.0001
visual -22°; 22°	-19.88	1.34	-14.868	<.0001
visual 0°; 22°	-8.73	1.33	-6.555	<.0001
Tactile orientation: 0°				
Contrast	*estimate*	*SE*	*t.ratio*	*p.value*
visual -22°; 0°	-9.72	1.35	-7.222	<.0001
visual -22°; 22°	-26.56	1.33	-19.912	<.0001
visual 0°; 22°	-16.84	1.34	-12.569	<.0001
Tactile orientation: 22°				
Contrast	*estimate*	*SE*	*t.ratio*	*p.value*
visual -22°- 0°	2.72	1.33	2.036	0.1039
visual -22°-22°	-9.52	1.34	-7.121	<.0001
visual 0°-22°	-12.24	1.33	-9.207	<.0001

Table 2.1 Post-hoc contrast analyses. Post-hoc analyses evaluating the effect of visual stimulus orientation on the estimation of tactile orientation by participants. The analyses were stratified by each level of tactile orientation (-22°, 0°, and 22°). For each tactile condition, we compared the mean estimates across the different visual orientations. The estimated mean differences, their standard errors (SE), t-ratios, and corresponding p-values are reported.

This pattern confirms that participants' responses systematically varied across most combinations of visual and tactile positions, demonstrating a robust interaction between modalities.

2.4.3 Power Analysis

To evaluate whether the sample size was sufficient to detect the effects observed in the multisensory model, we conducted a simulation-based power analysis using the *simr* package (Green & MacLeod, 2016). Starting from the fitted LMM, we generated an extended dataset with 20 participants, matching the actual sample size. For the main visual predictor (visual_orientation), the estimated effect size in the simulated model was
0.43. The simulation yielded a power of >95% (95% CI: 96.38–100%) based on 100 simulations, indicating excellent sensitivity to detect visual effects at α = .05. We then assessed power for the interaction term (tactile_orientation × visual_orientation), whose estimated effect size was small (–0.005). Despite the modest magnitude, the simulation produced a power of 99% (95% CI: 94.55–99.97%). This result indicates that, given the number of trials in the experiment, the design had more than adequate power to detect the interaction effect.

2.5 Discussion

This chapter investigated the interplay between visual and tactile motion when two cues are presented simultaneously, using controlled grating stimuli delivered through the RoMAT device (Gori et al., 2021). Using RoMAT, we presented participants with two independently controlled wheels, one visual and one tactile, whose motion directions could be either congruent or incongruent. Participants were required to report the perceived direction of motion under unisensory (visual-only and tactile-only) and multisensory stimulation, allowing us to first characterize modality-specific perceptual biases and then assess visuo–tactile interactions.

Unisensory visual and tactile judgments both showed systematic distortions, with visual responses exhibiting larger biases but higher precision than tactile ones. These modality-specific patterns provided an essential baseline for interpreting multisensory behaviour and highlight that the two modalities differ not only in accuracy but also in reliability, a factor known to shape multisensory weighting.

In multisensory trials, perceived motion direction remained anchored to the tactile signal but was consistently biased toward the visual input. This pattern indicates that tactile information provided the primary reference for motion direction, while visual cues exerted a reliable modulatory influence. Such tactile anchoring is consistent with previous findings showing asymmetric crossmodal interactions depending on task demands and response instructions (Craig, 2006; Y.-C. Pei et al., 2013). Importantly, the persistence of visual influence despite explicit instructions to report tactile motion suggests that visuo–tactile interactions reflect automatic perceptual mechanisms rather than purely strategic or decisional processes.

The significant interaction between visual and tactile motion directions further indicates that the contribution of one modality depends on the configuration of the other. This aligns with the broader literature on motion integration within single modalities, where the combination of local motion components depends on their relative orientation, speed, and ambiguity (Adelson & Movshon, 1982; Y.-C. Pei et al., 2011; Rust et al., 2006). Our results extend this principle across sensory modalities: visuo–tactile motion integration appears to be governed by structured computational constraints analogous to those observed in unimodal global motion processing, rather than reflecting simple sensory dominance. One notable aspect of our study is the high degree of inter-individual variability. Participants differed both in their tactile reference bias and in the extent to which visual cues influenced their responses. Most participants displayed relatively stable response distributions, suggesting consistent individual weighting strategies rather than systematic perceptual switching between modalities. However, some participants showed greater variability and possible bimodal tendencies, potentially reflecting intermittent shifts in reliance between tactile and visual motion cues. Overall, this pattern remains compatible with models of multisensory integration based on stable but individually variable sensory weights (Ascher & Grzywacz, 2000; Ernst & Banks, 2002).

Taken together, these findings have several theoretical implications. First, they demonstrate that tactile motion can exert a dominant influence on perceptual judgments even in the presence of visual motion, particularly when the task is explicitly anchored to the tactile modality, while visual motion nonetheless continues to bias responses in a systematic manner. Second, the observed pattern of visuo–tactile interaction suggests that multisensory motion perception may inherit computational principles from unimodal motion processing, consistent with proposals of shared canonical motion computations across modalities (Pack & Bensmaia, 2015). Third, the systematic influence of visual motion on tactile perception indicates that tactile motion representations remain sensitive to visual input even when tactile information is task-relevant. This observation is consistent with the possibility that visual experience contributes to shaping or calibrating tactile motion representations during development.

Our data reveal a clear pull between visual and tactile motion signals; however, the computational rule underlying this interaction remains an open question. Work on gratings has long relied on vector-based frameworks - such as intersection-of-constraints (IOC) or vector averaging (VA) - to explain how multiple motion components are combined into a single global percept. By contrast, multisensory research has largely relied on Bayesian or MLE models, which assume that integration should produce a reliability-weighted estimate accompanied by a measurable increase in precision, typically reflected in a reduced JND. If participants combine visual and tactile signals as two noisy measurements of a common cause, such a precision gain should emerge. Otherwise, crossmodal motion may be processed more like a “multisensory plaid,” where the system merges component motions using geometric constraints rather than probabilistic weighting. Under this scenario, vector-based mechanisms would better capture behaviour and, crucially, would not require an improvement in precision.

A further methodological consideration concerns the interpretation of multisensory precision within the present experimental design. Classical Bayesian or maximum-likelihood estimation (MLE) models typically assume that different sensory modalities provide noisy but redundant estimates of the same underlying stimulus. Under these conditions, multisensory integration is expected to reduce response variance relative to unisensory estimates. In the present study, however, the critical visuo–tactile

conditions intentionally introduced directional conflicts between visual and tactile motion signals. Consequently, the two modalities did not provide fully congruent estimates of a common motion direction, but rather partially conflicting information.

Under such cue-conflict conditions, increased response variability may emerge even in the presence of multisensory interaction, reflecting conflict resolution processes, uncertainty regarding common source attribution, or inter-individual differences in sensory weighting strategies. Therefore, the absence of a clear reduction in variance in incongruent multisensory conditions should not necessarily be interpreted as evidence against sensory combination. Instead, the present paradigm is better suited to investigating systematic crossmodal biases and attraction effects than to testing optimal reliability-weighted integration in the strict Bayesian sense.

This tension between vector-based and probabilistic accounts exposes a conceptual gap in current theories of multisensory motion perception. While Bayesian frameworks anchor most models of multisensory integration, vector-based motion models have rarely been extended across modalities. The present findings suggest that visuo–tactile motion perception may not be fully captured by classical reliability-weighted cue combination alone. Resolving this issue will require experimental paradigms explicitly designed for model comparison, including manipulations of sensory reliability, broader sampling of motion directions, and direct assessment of changes in perceptual precision.

Finally, by demonstrating robust and systematic interactions between visual and tactile motion signals, this chapter establishes a critical foundation for the subsequent investigation of tactile motion perception in the absence of vision. If visual input contributes to shaping tactile motion representations, then examining tactile motion processing in individuals with different visual experience provides a powerful approach for determining which aspects of tactile motion computation depend on visual calibration and which emerge independently within the somatosensory system.

CHAPTER 3

Measuring Tactile Orientation Perception in Visually Impaired Individuals

3.1 Background: challenges in measuring tactile perception in blind populations

In the previous chapter, we investigated how visual and tactile motion signals interact using the RoMAT device, demonstrating that tactile and visual cues influence each other during motion perception. While these findings provide important insight into multisensory integration, they also raise a fundamental question: how is tactile motion perception measured when vision is absent or cannot be used to guide responses?

The ability to perceive and interact with the surrounding environment is fundamental for human adaptation. While vision typically provides the most precise spatial information, individuals with visual impairments rely heavily on non-visual sensory modalities, particularly touch and audition, to gather information about their surroundings and guide behaviour (Abboud et al., 2014; Bleau et al., 2022; Cappagli et al., 2019).

A large body of research has demonstrated that tactile processing can partially compensate for the absence of vision and, in some cases, may even be associated with cortical reorganization (Sadato et al., 2002; Wanet-Defalque et al., 1988). For example, studies on Braille reading have shown activation of occipital cortical areas in blind individuals, suggesting that neural resources typically dedicated to visual processing can be recruited for tactile perception (Siuda-Krzywicka et al., 2016). In contrast, in sighted individuals, Braille reading primarily activates somatosensory processing areas rather than visual cortex regions (Gaglianese et al., 2020). Given the crucial role of tactile information in visually impaired populations, considerable efforts have been devoted to developing technologies that exploit tactile abilities for spatial perception and interaction (Mulloy et al., 2014; Vidal-Verdu & Hafez, 2007). In particular, touch has proven to be an effective modality for identifying spatial position and object orientation (Bertonati et al., 2020; Facchini & Aglioti, 2003; Tivadar et al.,

2019). Through tactile exploration, visually impaired individuals can build spatial representations of the environment, anticipate obstacles, locate landmarks, and develop strategies that support independent navigation and movement (Cappagli & Gori, 2020). Despite this, reliable tools specifically designed to assess tactile perception of spatial features such as orientation and direction remain limited. Many experimental paradigms rely on visually guided response systems even when tactile stimuli are used, potentially introducing cross-modal biases and limiting the ecological validity of the measurement, especially when testing visually impaired populations. To address this limitation, we developed a tactile goniometer, the TaK (Tactile Knob), designed to investigate how individuals perceive object orientation and direction using tactile information alone. The TaK device consists of a 3D-printed structure housing electronic components, a circular board with an orientable arrow-shaped bar, and a digital angle measurement system, allowing precise and objective recording of orientation responses while minimizing human reporting errors. To evaluate the effectiveness of the TaK device, two experimental studies were conducted. In the first study, sighted participants reproduced perceived tactile orientations using either a commercial knob with visual feedback or the TaK device without visual feedback. In the second study, tactile perception performance was compared between sighted and visually impaired participants using the TaK device alone. Across both studies, tactile stimuli were delivered using the RoMAT robotic platform, which allows controlled presentation of moving tactile gratings (Gori et al., 2021). This experimental setup enabled a systematic assessment of the accuracy and reliability of the TaK device across populations.

The results showed no significant differences between visual and tactile knob performance in sighted participants, and no significant performance differences between sighted and visually impaired participants when using the tactile knob. Together, these findings demonstrate that the TaK device provides a reliable and inclusive method for assessing tactile spatial perception. By enabling modality-consistent measurement of tactile orientation, TaK fills an important methodological gap and supports the development of accessible experimental paradigms for studying tactile and multisensory spatial perception.

3.2 Methods

3.2.1 Development of the TaK device

The design of the TaK device (*Figure 3.1*) builds upon previous work developed within our research group, where a 3D-printed arrow mounted on a circular board was used to measure the perceived orientation of tactile stimuli (Cuturi & Gori, 2017, 2019). In those earlier implementations, orientation measurements were manually recorded by the experimenter, limiting precision to integer degree values (e.g., 56°, 57°) and preventing the acquisition of finer angular resolution (e.g., 56.1°). The primary advancement introduced in the TaK device is the integration of electronic angle measurement, allowing automatic recording of the arrow orientation. This improvement significantly reduces human reporting errors and increases measurement precision, enabling a more accurate characterization of tactile orientation perception. The development of TaK was guided by a set of qualitative design specifications addressing both perceptual and ergonomic requirements. In particular, the device was designed to ensure mechanical robustness and durability, allowing repeated experimental use without frequent maintenance. Surface roughness was optimized to guarantee a stable grip during manipulation, while the orientable control bar was shaped as an arrow to provide a clear tactile indication of direction without requiring visual feedback.

Figure 3.1. External view of the TaK device. The device consists of a 3D-printed base supporting a rotating circular board with an arrow-shaped tactile bar used to reproduce perceived orientations.

An additional design goal was to ensure easy replicability of the device. The internal mechanical structure of the device is illustrated in *Figure 3.2.* Both mechanical and electronic components were selected to be low-cost and easily replaceable, and all custom parts were designed to be compatible with standard 3D printing technologies. The device components were manufactured using a Fortus 400 FDM printer with ABS M30 material, ensuring durability and structural stability while maintaining ease of assembly. The overall dimensions of the device were based on the size of an A4 sheet (30 × 21 × 6 cm), providing sufficient surface area for stable interaction while maintaining compactness. Rounded edges were introduced to improve ergonomic comfort during extended experimental sessions. The internal structure includes a base (30 × 21 × 4 cm) housing the electronic components, a rotating circular board with a radius of 15 cm, and an arrow-shaped bar measuring 15 × 1.5 × 1.5 cm (13 cm base length and 2 cm tip). To support discrete positioning when required, mechanical stops were implemented by introducing pairs of holes spaced every 45°. Each pair allows the arrow to be locked in position both clockwise and counterclockwise, increasing flexibility across experimental paradigms.

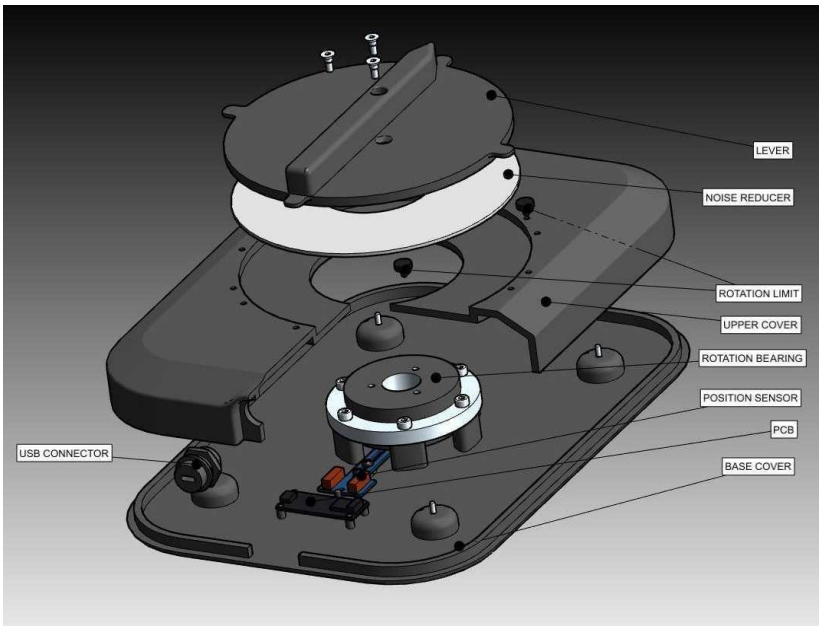

Figure 3.2. Isometric View of the Device. Exploded isometric view of the TaK device showing the main mechanical components, including the base cover, rotating board, shaft, and internal sensing components.

3.2.2 Electronic Design

The electronic architecture of TaK (*Figure 3.3*) is based on two main components: an MA710 magnetic angle sensor coupled with a diametrically magnetized 6 mm cylindrical magnet mounted on the rotating shaft, and an Arduino Nano microcontroller responsible for data acquisition and transmission. According to the manufacturer specifications, the MA710 magnetic encoder provides 12-bit angular resolution with low mechanical hysteresis and high repeatability, supporting stable and precise angle acquisition during repeated measurements. The Arduino Nano reads sensor data using the SimpleFOCLibrary (version 2.3.4), communicating with the encoder through an SPI interface. The device is connected to a computer via USB and is compatible with both Windows and Linux operating systems.

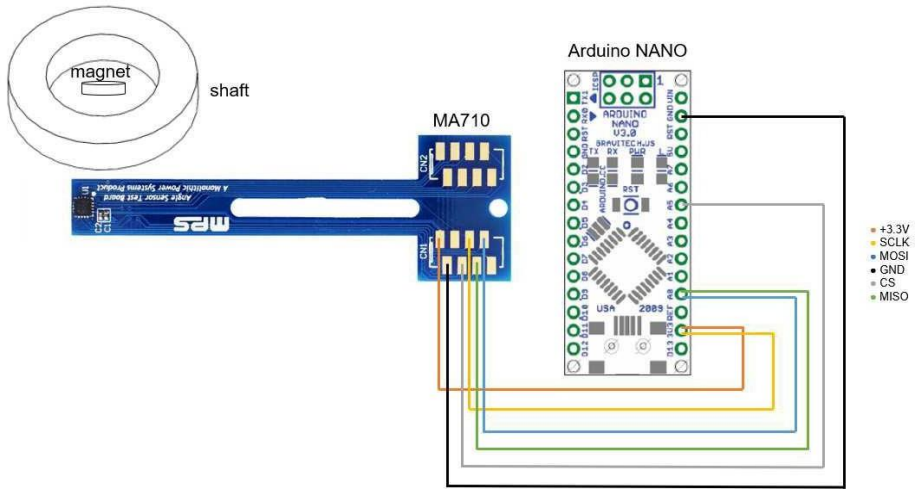

Figure 3.3. Electronic architecture of the TaK device. The MA710 magnetic angle sensor is interfaced with an Arduino Nano microcontroller via SPI communication for continuous angle acquisition.

During operation, the device continuously measures the orientation angle and transmits the data via UART serial communication. The transmitted data consist of ASCII strings terminated by CRLF characters, allowing straightforward integration with experimental acquisition software. The measured angle is expressed in absolute radians with a precision of two decimal places. The device can be used in both vertical and horizontal planes by redefining the reference zero position in the software.

3.3 Experimental validation of TaK device

To evaluate the effectiveness and usability of the TaK device, two experimental studies were conducted. The first experiment aimed to determine whether sighted participants could use the TaK device with performance comparable to that obtained using a commercial visually guided response knob. The second experiment aimed to assess whether visually impaired participants could use the TaK device with performance comparable to sighted individuals when relying exclusively on tactile feedback. The experimental procedures were approved by the local ethics committee (Comitato Etico, ASL3 Genovese, Italy) and were conducted in accordance with the principles of the Declaration of Helsinki.

3.3.1 Experimental setup and procedures

Both experiments were conducted using the RoMAT device (see Chapter 2, Section 2.2), an open-source robotic platform designed to deliver controlled tactile motion stimulation. For the present experiments, only the tactile module was used. The tactile stimulus consisted of a 3D-printed belt with ridges 1 mm in height and spaced 2 mm apart

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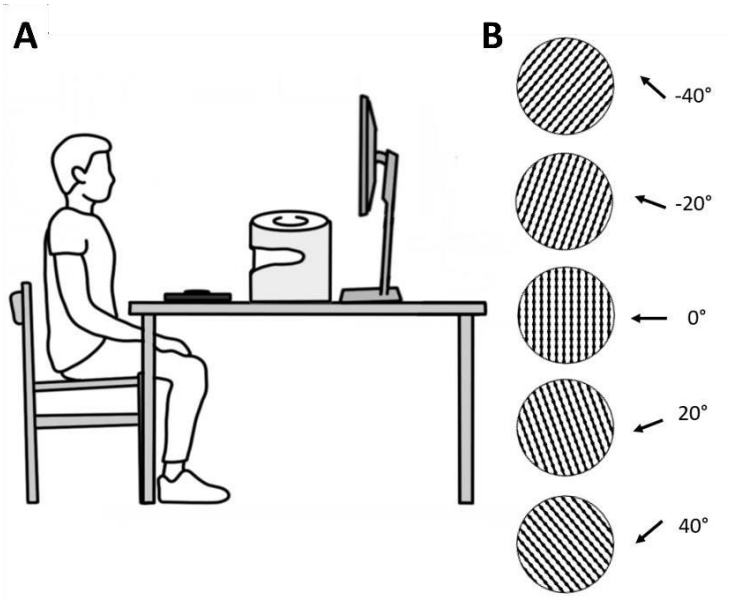

Figure 3.4 Experimental setup and orientations. **(A)** Participants sat in front of a table, with TaK in front of them and beside that, the RoMAT device. Also, we positioned a monitor behind RoMAT for the experimental condition with the visual knob. All the elements were aligned with participants' midline to avoid misperception of movement direction while responding with the knob. **(B)** Graphical depiction of grating orientation from -40° to 40°; the pattern stripes are always perpendicular to the direction of movement of the wheel.

During each trial, participants perceived the motion direction of the tactile wheel for 3 seconds (belt speed: 3 cm/s). Immediately afterward, using the same hand, participants reproduced the perceived orientation by adjusting a response knob, depending on the experimental condition. Trials followed each other continuously. Five motion orientations were tested (−40°, −20°, 0°, 20°, and 40°). The 0° condition corresponded to horizontal motion, while negative and positive angles represented top-left and top-right motion directions, respectively. The grating orientation was always perpendicular to the motion direction. Each orientation was repeated 15 times, resulting in 75 trials per condition.

3.3.2 Experiment 1: Sighted participants

In the first experiment, five right-handed sighted participants (2 males, 3 females; mean age = 28.4 ± 1.8 years) were recruited from the Italian Institute of Technology (IIT). The aim of this experiment was to compare performance obtained using the TaK device with that obtained using a standard visually guided response interface. To this end, participants reproduced the perceived tactile motion orientation under two

experimental conditions that differed in the response modality. In both conditions, participants first perceived the direction of motion delivered by the RoMAT tactile wheel. The tactile stimulus was explored passively for three seconds. Immediately afterward, participants reproduced the perceived orientation using a response knob.

In the Visual Knob condition (Vk), participants used a commercial rotary controller (Griffin PowerMate USB Programmable Controller) to adjust the orientation of a vector displayed on a monitor positioned behind the RoMAT device. In this case, participants initially explored the tactile stimulus with their eyes closed and subsequently opened their eyes to adjust the visual vector to match the perceived motion direction as accurately as possible.

In the Tactile Knob condition (Tk), participants were blindfolded throughout the entire session. After perceiving the tactile stimulus, they reproduced the perceived orientation using the TaK device, relying exclusively on tactile feedback. The order of the two conditions was counterbalanced across participants. The entire experimental session, including breaks, lasted approximately one hour.

3.3.3 Experiment 2: Visually Impaired participants

In the second experiment, five visually impaired participants (3 males, 2 females; mean age = 42.4± 4.9 years) were recruited. The group included four individuals with late-onset blindness and one individual with early-onset blindness. Detailed demographic and clinical information, including age, sex, blindness onset, and pathology, are reported in Table 2.1.

ID	Sex	Age	Blindness onset	Pathology
1	F	48	18 years	Accident, retinal loss
2	M	41	10 years	Accident
3	M	47	22 years	Retinitis pigmentosa
4	M	37	10 years	Retinal detachment and glaucoma
5	F	39	Since birth	Premature retinopathy

Table 3.1. Demographic and clinical characteristics of the visually impaired participants included in Experiment 2. The table reports participant ID, sex, age, age of blindness onset, and primary pathology.

Participants performed only the Tactile Knob condition (Tk). Prior to the experimental session, participants completed a familiarization phase to ensure correct use of the device. During this phase, participants were asked to adjust the TaK knob to predefined orientations (e.g., horizontal and vertical positions). After familiarization, participants performed the experimental task, reproducing the perceived orientation of the tactile stimulus using the TaK device, following the same procedure used in the tactile condition of Experiment 1. Because only one experimental condition was tested, the duration of the experiment was approximately 35 minutes per participant.

3.4 Data analysis

All statistical analyses were conducted using R (version 4.3.1; R Core Team and R Foundation for Statistical Computing, 2023). Prior to model estimation, the dataset was screened for outliers in order to reduce the influence of extreme responses on parameter estimation. For each participant and condition, trials in which the response exceeded ±2.5 standard deviations from the individual mean ($|z| > 2.5$) were classified as outliers and excluded from further analyses. Outlier removal was performed separately for each group (sighted and visually impaired) and for each response modality (tactile knob and visual knob). Overall, 33 trials out of 1125 observations were removed, corresponding to approximately 3% of the dataset. Specifically, 15 trials were excluded from the visually impaired group, 10 from sighted participants in the tactile condition, and 8 from sighted participants in the visual condition.

In Experiment 1, mean response bias was analysed using a linear mixed-effects model fitted with the *lmer* function from the lme4 package (Bates et al., 2015). Mixed-effects modelling was chosen to account for the hierarchical structure of the data, with repeated measurements nested within participants, and to properly model inter-individual variability. Orientation and response condition (visual knob versus tactile knob), together with their interaction, were included as fixed effects, while a random intercept was specified for each participant. This modelling approach allowed us to evaluate whether overall bias differed between response modalities, whether bias

varied across orientations, and whether the effect of orientation depended on the response modality used.

The model can be formally expressed as:

$$Y_{ij} = \beta_0 + \beta_1 \text{Orientation}_{ij} + \beta_2 \text{Condition}_{ij} + \beta_3 (\text{Orientation} \times \text{Condition})_{ij} + u_i + \varepsilon_{ij} \quad (3)$$

where Y_{ij} represent the mean response bias of participant $i$in trial j; $\beta_0$represents the fixed intercept; $\beta_1, \beta_2, \beta_3$ are the fixed-effect coefficients associated with orientation, condition, and their interaction, respectively; $u_i$denotes the participant-specific random intercept; and ε_{ij}represents the residual error term.

Given that the primary aim of Experiment 1 was to determine whether performance obtained with the TaK device was comparable to that obtained with a commercial visually guided response interface, equivalence testing was conducted in addition to traditional hypothesis testing. The Two One-Sided Tests (TOST) procedure was implemented using the TOSTER package in R (Lakens, 2017). Equivalence bounds were defined a priori at −0.5 and 0.5 in terms of Cohen's d, corresponding to small-to-moderate effect sizes. These bounds were subsequently converted into raw score units based on the standard errors of the relevant contrasts. Equivalence testing was performed separately for each orientation in order to determine whether the observed differences between response modalities fell within the predefined equivalence interval. This approach allowed us to formally assess statistical equivalence rather than merely relying on non-significant differences.

In Experiment 2, performance in the tactile condition was compared between sighted and visually impaired participants using a similar linear mixed-effects modelling framework. Orientation and group (sighted versus visually impaired) were included as fixed effects, together with their interaction, and a random intercept was specified for each participant. This model enabled the assessment of potential group differences in mean bias, orientation-dependent effects, and possible interactions between group and stimulus orientation.

The model can be formally expressed as:

$$Y_{ij} = \beta_0 + \beta_1 \text{Orientation}_{ij} + \beta_2 \text{Group}_{ij} + \beta_3 (\text{Orientation} \times \text{Group})_{ij} + u_i + \varepsilon_{ij} \quad (4)$$

where the notation follows Equation (3), with the only difference being that the fixed effect of condition is replaced by group.

3.5 Results

Descriptive statistics were first examined to summarize mean response bias and variability across orientations and response modalities (*see Figure 3.5*).

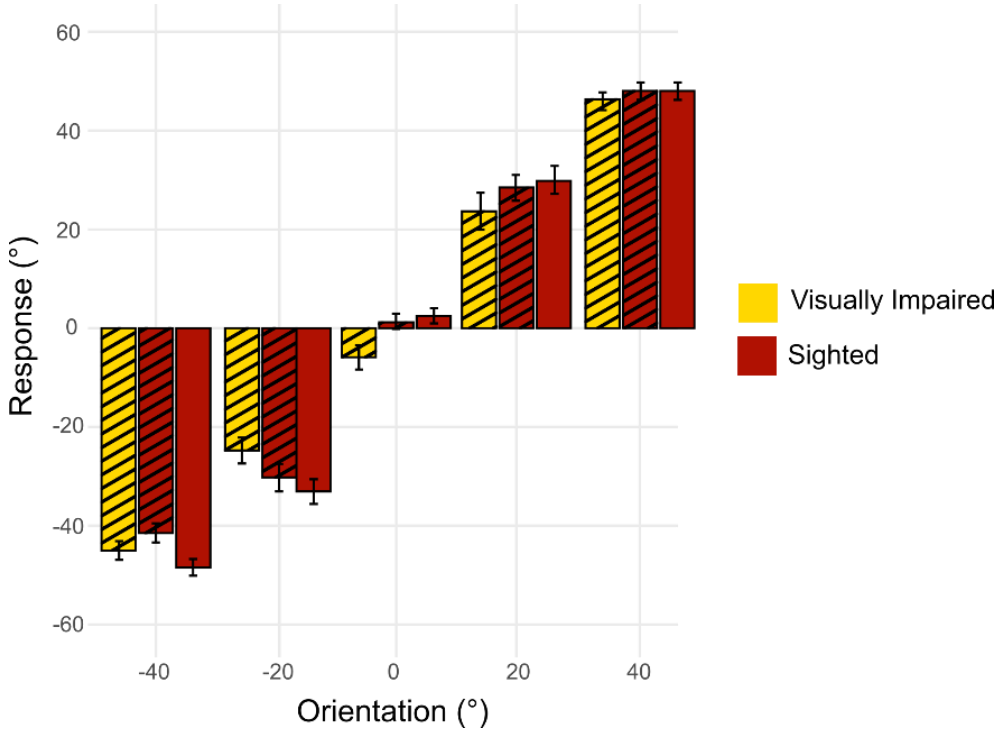

Figure. 3.5 Perceived orientation in tactile and visual conditions for sighted and visually impaired groups (mean±SE). In x-axis the different orientations, and in y-axis the responses of visually impaired (yellow) and sighted (red) participants for visual (full) and tactile (stripes) conditions.

3.5.1 Comparison Between Visual and Tactile Response in Sighted Participants

The linear mixed-effects model revealed no significant main effect of condition (Vk versus Tk), indicating that overall bias did not differ between the two response modalities (β = −4.70 ± 7.33, t = −0.64, p = 0.524). This result suggests that the TaK

device yields performance comparable to that obtained using a standard visually guided response interface. A significant main effect of orientation was observed (β = 3.83 ± 1.55, t = 2.47, p = 0.018), indicating that response bias varied systematically across stimulus orientations. Importantly, the interaction between orientation and response condition was not significant (β = 1.45 ± 2.20, t = 0.66, p = 0.514), suggesting that the orientation-dependent pattern of bias was consistent across both response modalities.

Because the primary goal of this experiment was to establish comparability rather than merely the absence of differences, equivalence testing was performed using the Two One-Sided Tests (TOST) procedure. Given the orientation-dependent variation in mean bias, equivalence was evaluated separately for each orientation. The results showed that equivalence was established for most orientations. Specifically, for orientations of -40° (p = 0.045), −20° (p = 0.007), 20° (p = 0.017), and 40° (p = 0.002), the equivalence tests were significant. However, for the orientation at 0°, the equivalence test was not significant (p = 0.053), showing a marginal trend toward significance. Taken together, these findings demonstrate that the TaK device produces response patterns comparable to those obtained with a commercial visual knob. Although response bias varied systematically with orientation, this relationship was consistent across response modalities, indicating that TaK provides a reliable tactile method for reproducing perceived spatial orientations.

3.5.2 Comparison Between Sighted and Visual Impaired Participants

To assess whether the TaK device could be reliably used by visually impaired participants, performance in the tactile condition was compared between sighted and blind individuals.

The linear mixed-effects model revealed no significant main effect of group (β = 1.22 ± 3.05, t = 0.40, p = 0.692), indicating that mean response bias did not differ between sighted and visually impaired participants. Likewise, the main effect of orientation was not significant (β = 0.06 ± 0.08, t = 0.77, p = 0.444), suggesting that bias did not vary systematically across orientations. The interaction between group and orientation was also not significant (β = 0.13 ± 0.11, t = 1.23, p = 0.224), indicating that the relationship between orientation and bias was consistent across the two groups. Taken together, these findings indicate that tactile orientation perception, as measured using the TaK

device, is comparable between sighted and visually impaired individuals. Furthermore, the absence of both group differences and orientation-dependent effects suggests that the device does not introduce systematic bias in either population.

3.6 Discussion

The present work introduced and validated the TaK device as a tactile-only tool for assessing spatial orientation perception. The results demonstrated that performance obtained using TaK was comparable to that obtained using a standard visually guided response interface, and that visually impaired participants performed similarly to sighted individuals when using the device. These findings support the validity of TaK as a reliable and inclusive tool for measuring tactile spatial perception.

The ability to accurately perceive spatial orientation through touch is particularly important for visually impaired individuals, who rely heavily on tactile and auditory information to interact with their environment and compensate for the absence of vision (Abboud et al., 2014; Bleau et al., 2022; Cappagli et al., 2019). Previous research has shown that tactile perception can partially substitute for visual input and may even be associated with functional reorganization of cortical areas typically involved in visual processing (Sadato et al., 2002; Wanet-Defalque et al., 1988). Furthermore, tactile processing plays a key role in enabling blind individuals to identify object orientation, build spatial representations, and support independent navigation (Bertonati et al., 2020; Cappagli & Gori, 2020; Facchini & Aglioti, 2003; Tivadar et al., 2019). In this context, the availability of reliable tools specifically designed to measure tactile perception independently of vision is essential.

A critical limitation of many previous approaches is that, even when tactile stimuli are used, perceptual responses are often reported through visually guided interfaces. This introduces an implicit cross-modal transformation, requiring participants to convert tactile percepts into visually referenced responses. Such transformations may introduce systematic biases and confound the interpretation of results, even in sighted individuals, because they require translating information between sensory reference frames. Previous work on haptic spatial processing has also shown that tactile orientation judgments can depend on the reference frame used to encode spatial information, including egocentric and allocentric coordinates (Kappers, 2007; Kappers et al., 2008; Postma et al., 2008). These findings further highlight the

importance of using modality-consistent response methods when investigating tactile spatial perception.

More critically, response methods relying on visually guided interfaces are not appropriate for studying tactile perception in blind individuals. These paradigms require participants to translate tactile percepts into visually defined reference frames that are not accessible in the absence of vision. As a result, they cannot provide a modality consistent measure of tactile perception and limit the ability to investigate tactile processing independently of visual experience. The TaK device overcomes this limitation by allowing both perception and response to occur entirely within the tactile modality. This modality-consistent design ensures that measured responses more directly reflect tactile perceptual representations, without relying on visually mediated reference frames.

Importantly, the comparable performance observed between sighted and visually impaired participants suggests that the TaK device can be effectively used across populations with different visual experience. By eliminating the need for visual response mediation, TaK enables a more direct assessment of tactile perceptual mechanisms while reducing potential confounds related to multisensory transformations. Nevertheless, these findings should be interpreted with caution given the limited sample size of the present validation studies. Although equivalence testing supported comparability between response modalities in sighted participants, larger samples will be necessary to establish the generalizability of these findings, particularly for visually impaired populations. Therefore, the primary aim of the present chapter was to provide a proof-of-concept validation of the TaK device as a modality-consistent tool for measuring tactile spatial perception across different populations.

This methodological advance is particularly relevant in light of the broader theoretical questions addressed in this thesis. As discussed in Chapter 1, visual experience is thought to play a critical role in calibrating tactile spatial representations during development (Burr & Gori, 2011). However, testing this hypothesis requires experimental paradigms that can isolate tactile perception from visually mediated response processes. The TaK device provides precisely this capability, allowing researchers to measure tactile perceptual performance without introducing visual reference frames that could obscure or compensate for underlying tactile differences.

Beyond its application in basic research, the device may also have potential implications for clinical and rehabilitative contexts. Because tactile perception plays a central role in spatial cognition and navigation in blind individuals (Cappagli & Gori, 2020; Giudice, 2018), tools such as TaK could be used to evaluate perceptual abilities, monitor rehabilitation progress, or support sensory training programs aimed at enhancing spatial awareness and sensory substitution skills.

Finally, the availability of a reliable tactile-only measurement tool provides the methodological foundation necessary to investigate tactile perceptual sensitivity in a modality-consistent manner. While the present chapter focused on validating the TaK device and demonstrating its applicability across populations, the next chapter builds directly on this foundation to investigate tactile motion discrimination thresholds in sighted and blind individuals. This approach enables a direct test of whether and how visual experience contributes to shaping tactile motion perception.

CHAPTER 4

Tactile Motion Direction Sensitivity and the Role of Visual Experience

4.1 Background: tactile motion perception and sensory plasticity

The previous chapter introduced and validated the TaK device, a tactile-only response system designed to measure orientation perception in a modality-consistent manner. The validation of this tool demonstrated that tactile spatial orientation can be reliably measured without relying on visually mediated response interfaces and that both sighted and visually impaired individuals can use the device with comparable performance. Establishing a reliable and accessible method for measuring tactile spatial perception represents a necessary step for investigating more fundamental perceptual properties, such as sensitivity to differences in motion direction.

One of the key measures used to quantify perceptual sensitivity is the just noticeable difference (JND), which represents the minimum difference between stimuli that can be reliably discriminated (Kingdom, 2016). While the previous chapter focused on validating the measurement method, the present chapter builds upon this methodological foundation to investigate tactile motion direction sensitivity itself.

The ability to perceive motion through touch plays a fundamental role in everyday interaction with the environment. Tactile motion cues provide essential information about the spatial properties of surfaces, including direction, velocity, and texture, thereby supporting object manipulation, environmental exploration, and navigation. When visual input is limited or absent, tactile motion becomes particularly important and can partially compensate for the lack of vision (Thinus-Blanc & Gaunet, 1997). This compensatory role reflects the ability of the somatosensory system to extract directional information from spatiotemporal patterns of mechanoreceptor activation, allowing individuals to reconstruct motion signals through touch alone (Ryan et al., 2021).

Importantly, tactile perception does not develop in isolation but in continuous interaction with visual experience. In sighted individuals, visual input contributes to the calibration of spatial representations, providing a reference framework that supports spatial processing across sensory modalities (Coelho et al., 2025). This raises a crucial question regarding how tactile motion perception develops when visual input is absent, and whether the absence of vision leads to enhanced, degraded, or qualitatively different perceptual abilities.

A substantial body of research has reported enhanced tactile acuity in visually impaired individuals, particularly in tasks involving static spatial judgments such as orientation discrimination or pattern recognition. Blind participants often show lower discrimination thresholds compared to sighted individuals (Boven et al., 2000; Goldreich & Kanics, 2003; Stevens et al., 1996). These findings have commonly been interpreted in terms of cross-modal plasticity, whereby neural resources typically dedicated to visual processing are reorganized to support tactile perception, as well as increased reliance on tactile input resulting from everyday experience.

However, enhanced tactile performance is not a universal consequence of visual deprivation. Evidence suggests that visual experience plays a critical role in shaping spatial representations, and that its absence during early development may lead to long-lasting differences in perceptual processing. For example, early-onset blind individuals have been shown to perform worse than both late-blind and sighted individuals in tasks requiring complex spatial processing and object recognition (Coelho et al., 2025). These findings suggest that early visual experience contributes to the calibration of spatial processing mechanisms and that the absence of such calibration may limit performance in certain perceptual domains. Consequently, blindness onset represents a key factor in understanding tactile perceptual abilities, as early and late visual deprivation may have distinct effects on sensory processing.

While most previous studies have focused on static tactile perception, less is known about dynamic tactile processing, particularly motion direction perception. Motion perception requires the integration of spatial and temporal information in order to extract directional signals (Adelson & Movshon, 1982; Y.-C. Pei & Bensmaia, 2014) and therefore relies on additional perceptual and neural mechanisms compared to static spatial judgments. Understanding tactile motion perception is particularly

important because motion cues play a central role in natural tactile exploration, such as when the hand moves across surfaces or when objects move relative to the skin.

In addition to the influence of visual experience, perceptual sensitivity may also depend on motion orientation. A well-known phenomenon, known as the oblique effect, describes the superior discrimination of cardinal orientations compared to oblique orientations. This effect was originally described in vision (Heeley et al., 1997) and reflects anisotropies in sensory processing favouring vertical and horizontal directions. Similar effects have also been observed in tactile perception, particularly in static orientation discrimination tasks (Gentaz et al., 2008). Importantly, studies in blind individuals suggest that the tactile oblique effect may arise independently of visual experience, potentially reflecting intrinsic somatosensory or biomechanical constraints rather than visually calibrated spatial representations (Gentaz et al., 2008).

Despite these findings, it remains unclear whether such directional anisotropies also affect tactile motion perception. Motion perception involves additional neural and perceptual mechanisms (Y.-C. Pei & Bensmaia, 2014), which may be influenced differently by visual experience. Therefore, it is still unknown whether blindness onset affects tactile motion direction sensitivity, and whether anisotropies such as the oblique effect extend to dynamic tactile perception.

Investigating these questions requires reliable and modality-appropriate measurement tools. In the previous chapter, we introduced and validated the TaK device, demonstrating that tactile orientation perception can be measured accurately using a tactile-only response system. This methodological advancement provides the necessary foundation for assessing perceptual sensitivity while minimizing cross-modal biases.

The present study builds upon the broader methodological framework established in the previous chapter to investigate tactile motion direction discrimination in sighted, early-onset blind, and late-onset blind individuals. Using the RoMAT robotic platform (Gori et al., 2021), participants performed a two-alternative forced-choice task to discriminate the direction of moving tactile gratings. By measuring JND across multiple reference orientations, this study aimed to determine whether tactile motion sensitivity depends on visual experience and blindness onset, and whether directional anisotropies influence tactile motion perception.

By extending the methodological and theoretical framework established in the previous chapters, this study directly addresses a fundamental question of this thesis: how visual experience shapes tactile motion perception.

4.2 Methods

4.2.1 Participants

A total of 42 participants were initially recruited for this study, including 23 visually impaired individuals and 19 sighted controls. Among the visually impaired participants, 9 had early-onset blindness (mean age = 43.6 ± 13.0 years) and 14 had late-onset blindness (mean age = 55.9 ± 12.9 years). Participants with congenital blindness (reported as ‘since birth’ or ‘before birth’) were classified as early-onset blind, whereas participants who acquired blindness later in life were classified as late-onset blind. Sighted participants had a mean age of 47.8 ± 14.4 years. Detailed demographic and clinical information for visually impaired participants is reported in Table 4.1. All participants met the inclusion criteria of having no history of neurological disorders. Prior to participation, all individuals received written and verbal information about the study and provided written informed consent. Two participants (one sighted and one early-onset blind) were excluded from the analysis because they did not complete the experimental protocol. The final sample therefore included 40 participants. The experimental procedures were approved by the local ethics committee (Comitato Etico, ASL3 Genovese, Italy) and were conducted in accordance with the principles of the Declaration of Helsinki.

ID	Sex	Age	Blindness onset	Pathology
20	M	33	Before birth	Leber's amaurosis
21	M	30	19 years	Brain surgery
22	F	35	Before birth	Premature retinopathy
23	F	48	18 years	Accident, retinal loss
24	F	60	40 years	Nystagmus and retinitis pigmentosa
25	F	61	7 years	Retinitis pigmentosa and nystagmus
26	F	60	46 years	Leber's congenital amaurosis
27	M	54	6 years	Congenital glaucoma
29	F	75	49 years	Degenerative maculopathy

30	F	73	67 years	Retinitis pigmentosa
31	F	26	Before birth	Premature retinopathy
32	F	66	Since birth	Microstalmic
33	M	59	Before birth	Premature retinopathy
34	M	58	45 years	Retinitis pigmentosa
35	M	41	10 years	Accident
36	F	59	35 years	Degenerative maculopathy and retinitis pigmentosa
38	M	74	35 years	Progressive ipovision
39	F	36	Since birth	Retinitis pigmentosa
41	M	47	22 years	Retinitis pigmentosa
42	M	62	14 years	Optic chiasm tumor
43	M	53	Before birth	Congenital optic nerve atrophy
44	M	37	10 years	Retinal detachment and glaucoma
45	F	39	Since birth	Premature retinopathy

Table 4.1. Demographic and clinical characteristics of visually impaired participants. The table reports participant ID, sex, age, blindness onset, and primary pathology.

4.2.2 Apparatus and Stimuli

Motion direction stimuli were delivered using the RoMAT device (Robot for Multisensory Analysis and Testing), an open-source robotic platform specifically developed to investigate visual and tactile motion perception under controlled experimental conditions (Gori et al., 2021). As described in Chapter 2, the device consists of two mechanically rotatable plates, each equipped with a motorized wheel. For the purpose of the present experiment, only the lower wheel, delivering tactile stimulation, was used.

The tactile stimulus was generated by a 3D-printed belt mounted on the wheel surface, characterized by parallel ridges 1 mm in height and spaced 2 mm apart. During stimulation, the belt moved across the participant's index fingertip at a constant velocity of 3 cm/s. To ensure consistent passive stimulation and prevent active exploratory movements, the wheel was covered by a protective plate with a finger-shaped aperture that constrained finger position and contact area (*Figure 4.1-A*). The perceived direction of motion corresponded to the direction orthogonal to the

orientation of the ridges, allowing precise control of motion direction through rotation of the stimulus plate (*Figure 4.1-B*).

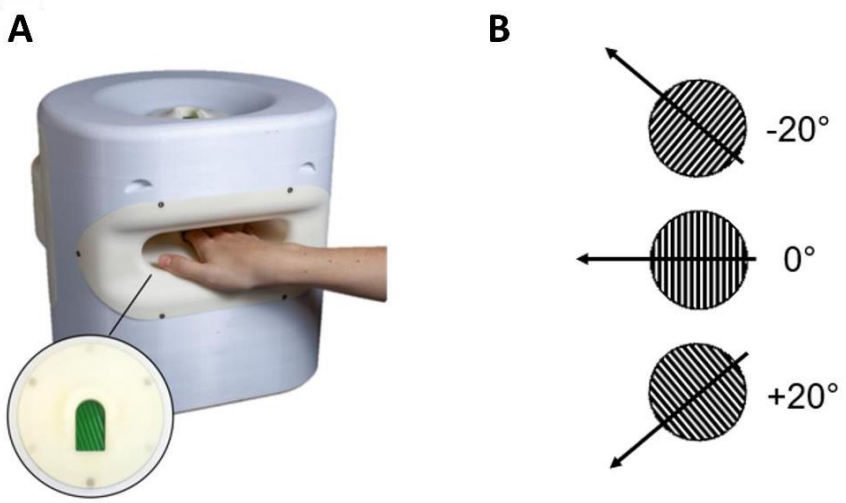

Figure 4.1 RoMAT device and orientation representation. **(A)** Participants positioned their hand in the lower wheel of the RoMAT device, aligning their index fingertip with the finger-shaped indentation. **(B)** Reference stimuli: horizontal one (0°) and diagonals (±20°). The movement perceived by participants was always perpendicular to the orientation of the stripes on the wheel

Each trial consisted of the sequential presentation of two tactile motion stimuli: a reference stimulus followed by a test stimulus. The reference stimulus was presented for 3 seconds, after which participants removed their finger from the device during a 5-second inter-stimulus interval. This pause was introduced to minimize tactile motion aftereffects and sensory adaptation (Wang & Alais, 2024). The test stimulus was then presented for 3 seconds using the same procedure.

Three reference orientations were used: −20°, 0°, and +20° (Table 4.2). These orientations were selected to sample motion perception across both cardinal and oblique directions.

For each reference orientation, nine test stimuli were presented, symmetrically distributed around the reference direction in steps of 5°. This resulted in test orientations spanning a total range of ±20° relative to each reference. For the distribution of the number of trials, see Table. 4.2

	Reference								
	-20	-15	-10	-5	**0**	5	10	15	20
	0	5	10	15	**20**	25	30	35	40
	-40	-35	-30	-25	**-20**	-15	-10	-5	0
Number of trials	*5*	*4*	*3*	*2*	*1*	*2*	*3*	*4*	*5*

Table 4.2 Range of test stimuli and test value. Each row illustrates the range of test stimuli presented around a central reference stimulus (shown in bold). The bottom row reports the number of repetitions for each test value: this number is highest (5) at the ends of the range and gradually decreases toward the center, reaching its minimum (1) when the test stimulus matches the reference.

To optimize the estimation of perceptual sensitivity, the number of repetitions varied as a function of the angular distance between reference and test stimuli. Specifically, stimuli closer to the reference orientation were presented fewer times, whereas stimuli farther from the reference were presented more frequently. This sampling strategy increased the statistical reliability of threshold estimation by providing greater sampling of stimulus pairs expected to be easier to discriminate, while maintaining sufficient sampling near the reference orientation where discrimination is more difficult.

Overall, each reference orientation was associated with 29 trials, resulting in a total of 87 trials per block. Each participant completed two experimental blocks, yielding a total of 174 trials per participant. The order of reference and test stimuli was pseudo-randomized within each block to prevent order effects and response prediction.

4.2.3 Experimental Procedure

Participants were seated in a quiet experimental room, with the RoMAT device positioned in front of them between their legs to allow comfortable access to the tactile stimulation module. Before the beginning of the experiment, participants received detailed verbal instructions explaining the experimental procedure and task requirements. Sighted participants were instructed to fixate a cross displayed in front of them throughout the experiment in order to prevent the use of external visual spatial references.

Each trial consisted of the sequential presentation of two tactile motion stimuli: a reference stimulus and a test stimulus. At the beginning of each stimulus presentation, participants were instructed to place their right index finger on the tactile wheel through the finger-shaped aperture. The tactile motion stimulus was delivered for 3 seconds, after which participants were instructed to remove their finger from the device. This was followed by a 5-second inter-stimulus interval, introduced to minimize sensory adaptation and tactile motion aftereffects.

After the pause, participants placed their finger on the wheel again to perceive the second stimulus, which was presented for the same duration and using the same procedure.

Following presentation of both stimuli, participants performed a two-alternative forced-choice (2AFC) discrimination task. Specifically, they were asked to verbally report which of the two stimuli was oriented more upward relative to the horizontal axis. In this context, “upward” referred to motion directions tilted toward the upper-left diagonal relative to horizontal, whereas “downward” referred to motion tilted toward the lower-right diagonal *(Figure 4.2-B*).

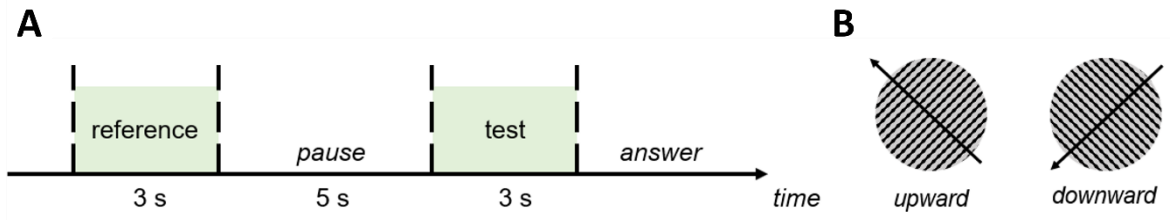

Figure 4.2 Experimental protocol. **(A)** Participants were instructed to place their index finger on the roller; Three seconds later, they were signaled to remove their hand. Following a 5-second pause, the procedure was repeated for the second stimulus. Afterward, participants were asked to determine which stimulus was oriented more upward. **(B)** In this task, “upward” referred to motion directions tilted toward the upper-left side relative to the horizontal axis, whereas “downward” referred to motion tilted toward the lower-right side..

Responses were recorded by the experimenter for offline analysis. Participants were instructed to prioritize accuracy over speed and were allowed to take short breaks at the end of each experimental block to minimize fatigue. The entire experimental session lasted approximately 1 hour and 30 minutes.

4.3 Data analysis

To quantify tactile motion direction sensitivity, the just noticeable difference (JND) was calculated for each participant and for each reference orientation (−20°, 0°, and +20°). The JND represents the minimum angular difference required to reliably discriminate between two motion directions and provides a standard measure of perceptual sensitivity. JND values were estimated by fitting a cumulative Gaussian function to the proportion of trials in which the participant judged the test stimulus as being oriented more upward than the reference stimulus, as a function of the angular difference between the two stimuli. The JND was defined as the difference between the 75% and 25% points of the fitted psychometric function, such that lower JND values indicate higher perceptual sensitivity. Psychometric fitting and JND extraction were performed in MATLAB (version R2022b; The MathWorks Inc., 2022).

To reduce the influence of extreme values, outliers were identified and removed at the participant level. Specifically, participants whose mean JND exceeded the threshold defined as the third quartile plus three times the interquartile range (Q3 + 3 × IQR) were excluded from further analyses (Tukey, 1977). This conservative criterion was adopted to identify potentially unreliable psychometric estimates that could reflect unstable threshold fitting or poor task engagement rather than genuine perceptual variability. The exclusion procedure was applied independently of participant group. Based on this criterion, two participants were excluded from all conditions: one sighted participant and one early-blind participant.

The distribution of JND values was assessed for normality using the Shapiro–Wilk test, confirming that the assumption of normality was met.

To evaluate the effects of visual experience and stimulus orientation on tactile motion sensitivity, JND values were analysed using a linear mixed-effects model. Group (sighted, early blind, late blind), reference orientation (−20°, 0°, +20°), and their interaction were included as fixed effects, while participant was included as a random intercept to account for inter-individual variability. The model was fitted using the lmer function from the lme4 package in R (version 4.4.2) (R Core Team, 2023).

The significance of fixed effects was assessed using analysis of variance (ANOVA) on the fitted model. When appropriate, post-hoc pairwise comparisons were conducted using estimated marginal means (Lenth, 2023) to further explore differences between

conditions. All statistical analyses were conducted in R, except for psychometric fitting, which was performed in MATLAB (The MathWorks Inc., 2022).

4.4 Results

To assess tactile motion direction sensitivity, perceptual thresholds were quantified by computing the just noticeable difference (JND) for each participant and each reference orientation. The JND reflects the minimum angular difference required to reliably discriminate between two motion directions, with lower values indicating higher perceptual sensitivity.

Mean JND values differed across participant groups and reference orientations. In sighted participants, mean JND values were 11.90 ± 2.64° for the −20° reference, 11.30 ± 4.91° for the 0° reference, and 11.10 ± 3.63° for the +20° reference. Early-onset blind participants showed mean JND values of 11.80 ± 4.23° at −20°, 8.60 ± 3.95° at 0°, and 12.40 ± 3.19° at +20°. Late-onset blind participants exhibited mean JND values of 9.97 ± 3.46° at −20°, 9.80 ± 3.13° at 0°, and 10.60 ± 5.41° at +20°.

Visual inspection of the psychometric functions confirmed these patterns (*Figure 4.3*). In particular, late-onset blind participants exhibited steeper psychometric curves compared to the other groups, reflecting lower discrimination thresholds and therefore higher sensitivity. In contrast, sighted and early-onset blind participants showed broader psychometric functions, indicating reduced discrimination precision relative to late blind individuals.

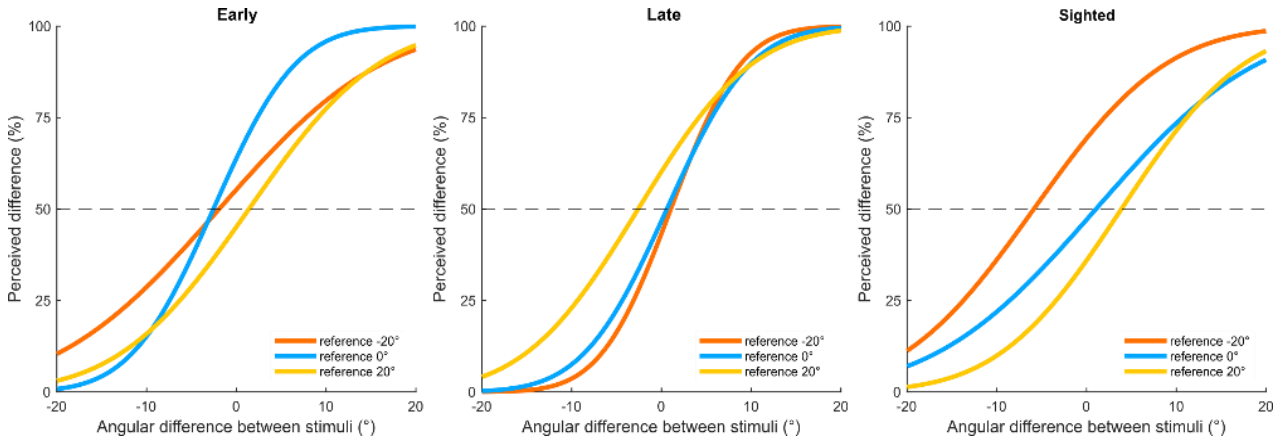

Figure 4.3. Representative psychometric functions for sighted, late-onset, and early-onset blind participants across the three reference orientations (-20°, 0° and 20°). The curves illustrate the group-specific discrimination patterns: late-onset blind participants show consistently sharper functions (indicating lower JNDs), whereas sighted and early-onset blind participants exhibit similar profiles

To formally assess the effects of visual experience and reference orientation on tactile motion sensitivity, JND values were analysed using a linear mixed-effects model including Group and Reference as fixed effects and Participant as a random intercept.

The analysis revealed a significant main effect of Reference orientation ($F(2, 68.84) = 3.60$, $p = 0.033$), indicating that tactile motion discrimination sensitivity varied as a function of stimulus orientation. Specifically, post-hoc comparisons showed that JND values were significantly lower for the horizontal reference (0°) compared to both oblique references. JND values at 0° were significantly lower than at −20° ($t(69.5) = 2.32$, $p = 0.023$) and +20° ($t(69.5) = -2.33$, $p = 0.023$), whereas no significant difference was observed between the two oblique orientations (−20° vs +20°; $t(70) = 0.007$, $p = 0.99$). This pattern indicates higher perceptual sensitivity for motion aligned with the horizontal axis compared to oblique directions.

In contrast, the main effect of Group was not statistically significant, indicating that overall tactile motion discrimination thresholds did not differ reliably between sighted, early blind, and late blind participants.

However, the interaction between Group and Reference showed a trend toward significance ($F(4, 68.92) = 2.13$, $p = 0.086$). Although this interaction did not reach conventional significance levels, the pattern of results suggests potential differences

in how reference orientation influenced tactile motion sensitivity across groups. *Figure 4.4* illustrates the distribution of JND values across groups and reference orientations .

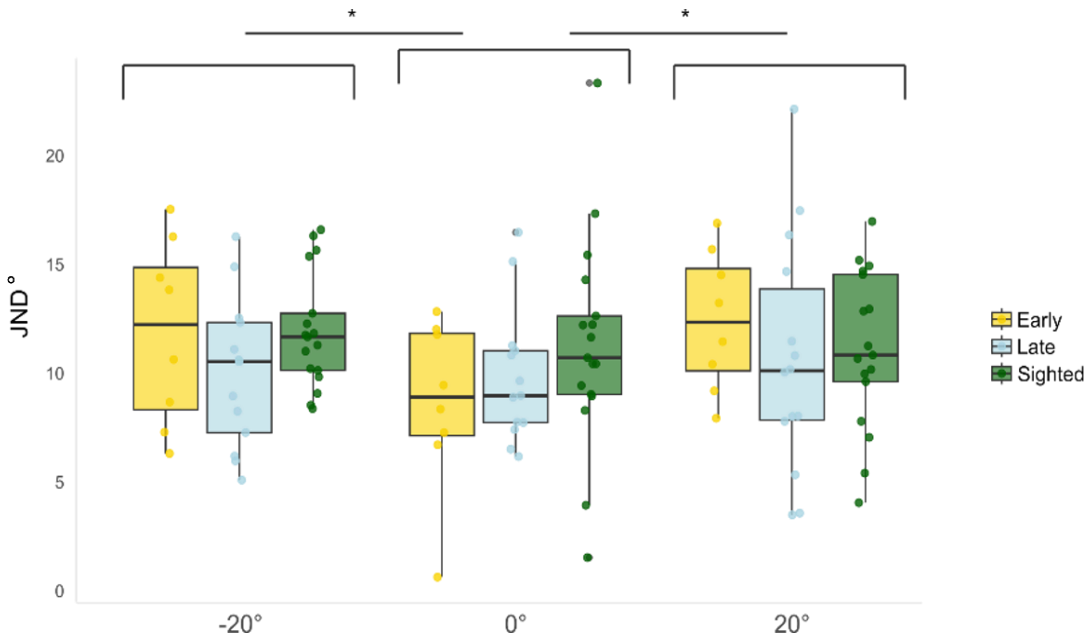

Figure 4.4. JND values for each group within each orientation. Distribution of Just Noticeable Difference (JND) values across motion orientations (−20°, 0°, 20°) for the three participant groups (sighted, late-blind, and early-blind). Boxplots represent the median and interquartile range, with whiskers indicating the range of the data. Individual dots correspond to participant-level estimates. Colours denote the different groups (yellow = sighted, light blue = late-blind, green = early-blind). Horizontal brackets indicate pairwise statistical comparisons between groups within each orientation.

Overall, these results indicate that tactile motion discrimination sensitivity is influenced by stimulus orientation, with higher sensitivity for cardinal orientations, while no clear overall advantage was observed as a function of visual experience.

4.5 Discussion

The present study investigated tactile motion direction sensitivity in sighted, early-onset blind, and late-onset blind individuals using controlled tactile stimulation delivered through the RoMAT robotic platform. By adopting a two-alternative forced-choice paradigm and quantifying perceptual thresholds through the just noticeable difference (JND), this experiment provided a direct measure of tactile motion discrimination sensitivity across groups differing in visual experience.

Contrary to our initial hypotheses, tactile motion discrimination thresholds did not differ significantly between sighted, early blind, and late blind participants. This finding indicates that, under the present experimental conditions, neither visual deprivation nor the timing of visual loss systematically altered tactile motion direction sensitivity. Although the interaction between participant group and reference orientation showed a trend toward significance, the absence of reliable group differences suggests that basic tactile motion sensitivity may be largely preserved even in the absence of visual experience.

This result is theoretically informative in light of the cross-sensory calibration framework discussed in Chapter 1. According to this framework, visual input plays a central role in calibrating spatial representations across sensory modalities during development (Burr & Gori, 2012; Gori et al., 2010). If tactile motion perception critically depended on visual calibration, early visual deprivation would be expected to produce measurable impairments in motion discrimination sensitivity. However, the absence of group differences observed here suggests that the computational mechanisms supporting tactile motion sensitivity may develop independently of visual input, or may rely primarily on somatosensory-specific signals rather than visually derived spatial reference frames. This interpretation refines the role of vision in tactile development, suggesting that visual calibration may be essential for some tactile spatial functions, such as orientation judgments (Gori et al., 2010), but not necessarily for the development of motion direction sensitivity.

Importantly, this conclusion complements the findings reported in Chapter 2. There, visual motion signals systematically biased tactile motion perception when both modalities were simultaneously available, demonstrating that vision can influence tactile motion processing. However, the present results show that tactile motion

sensitivity itself does not depend on visual experience for its development. Together, these findings suggest that visual input can modulate tactile motion perception when present, but may not be required to establish the fundamental computational mechanisms underlying tactile motion sensitivity. This dissociation supports the idea that tactile motion processing relies on modality-specific neural and computational mechanisms that remain functional even in the absence of vision, while still allowing flexible cross-modal interactions when visual information is available.

In contrast to the absence of group differences, the orientation of the reference stimulus exerted a clear and systematic influence on tactile motion discrimination sensitivity. Specifically, perceptual thresholds were significantly lower for the horizontal reference orientation (0°) compared to both oblique orientations (−20° and +20°), indicating higher sensitivity for motion aligned with the cardinal axis. This pattern constitutes a tactile analogue of the oblique effect, a well-established perceptual phenomenon originally described in vision, whereby discrimination performance is superior for cardinal orientations compared to oblique orientations (Appelle, 1972). Similar anisotropies have also been reported in tactile perception, particularly in tasks involving static orientation discrimination (Essock et al., 1997).

Importantly, the oblique effect observed in the present study extended to dynamic tactile motion perception, demonstrating that directional anisotropies are not limited to static spatial judgments but also affect the processing of moving tactile stimuli.

Furthermore, the fact that this effect was observed consistently across sighted, early blind, and late blind participants suggests that it does not depend on visual experience. Instead, these anisotropies likely reflect intrinsic properties of the somatosensory system, such as the spatial organization of mechanoreceptors, biomechanical constraints of the skin, or neural coding properties within somatosensory cortical areas. This interpretation is consistent with previous evidence suggesting that tactile orientation anisotropies can emerge independently of visual calibration and may reflect modality-specific computational constraints.

Together, these findings provide important insight into the relationship between tactile motion perception and visual experience. While vision is known to influence multisensory spatial processing and can modulate tactile motion perception when both modalities are available, the present results suggest that basic tactile motion discrimination sensitivity may rely on somatosensory-specific mechanisms that develop and operate independently of vision. This distinction between developmental independence and online multisensory interaction highlights the flexibility of multisensory systems, which can combine information across modalities without necessarily requiring cross-modal input for the establishment of fundamental perceptual computations.

Several limitations should be considered when interpreting these findings. First, the sample size was not fully balanced across groups, primarily due to the inherent difficulty of recruiting early-onset blind participants. This group also exhibited greater variability in perceptual thresholds, a pattern frequently observed in visually impaired populations. Increasing the sample size in future studies will be essential to improve statistical power and determine whether subtle group differences may emerge.

Second, the sampling strategy used for psychometric estimation introduces some methodological limitations. To reduce overall task duration and minimize fatigue, particularly in visually impaired participants, the number of repetitions varied across stimulus differences and was reduced near the point of subjective equality (PSE). Although this approach allowed efficient data collection, it may have reduced the stability of psychometric fitting around threshold, potentially increasing variability in PSE and JND estimation. Adaptive staircase procedures could in principle improve threshold sampling efficiency. However, we opted for a fixed pseudo-randomized design because adaptive methods tend to concentrate trials around highly similar

stimulus values. In tactile motion perception, this may increase serial dependence or short-term adaptation effects, whereby the perceived direction on a given trial is biased by the direction presented on preceding trials. The present design therefore reflects a trade-off between efficient threshold estimation and minimizing sequential dependencies between similar tactile motion stimuli. Future studies should directly compare fixed and adaptive procedures to further validate the reliability of tactile motion threshold estimation.

Third, the experimental paradigm employed here targeted a specific aspect of tactile motion perception, namely direction discrimination for grating stimuli presented under passive stimulation conditions. Tactile motion perception is a multifaceted process that may depend on additional factors such as stimulus speed, spatial frequency, active exploration, or contextual information. Future research should therefore investigate tactile motion sensitivity across a broader range of stimulus conditions and perceptual tasks in order to develop a more comprehensive understanding of how tactile motion processing is shaped by visual experience.

In conclusion, the present study demonstrates that tactile motion direction sensitivity is strongly influenced by stimulus orientation but is not reliably modulated by visual experience or blindness onset. These findings suggest that the fundamental computational mechanisms supporting tactile motion perception may emerge independently of visual calibration, while remaining capable of interacting with visual signals when available. This distinction provides new insight into the relationship between multisensory interaction and sensory development, and contributes to a more precise understanding of how tactile motion perception is established and maintained across different sensory conditions.

CHAPTER 5

General Discussion

5.1 Reframing the central question: how is tactile motion computed and shaped by vision?

A central theoretical framework motivating this thesis is the cross-sensory calibration hypothesis proposed by Burr and Gori (2012), according to which sensory modalities do not merely integrate information but actively calibrate one another during development. Within this framework, vision plays a central role in spatial processing: because it provides stable, high-resolution, and externally referenced spatial information, it is thought to guide the maturation of spatial representations in other modalities, particularly touch. Supporting evidence shows that early visual deprivation selectively impairs tactile orientation discrimination and spatial tasks requiring alignment with external reference frames (Gori et al., 2010; Burr & Gori, 2012), suggesting that vision contributes to establishing coherent spatial coding across sensory systems.

However, most empirical tests of cross-sensory calibration have focused on static spatial perception, such as size, orientation, or localization. Whether the same developmental dependency applies to motion perception remains largely unexplored. This represents an important theoretical gap. Motion perception requires integrating ambiguous local signals to reconstruct coherent direction, both in vision and in touch (Adelson & Movshon, 1982; Weiss et al., 2002; Pei et al., 2011). If visual experience is necessary to calibrate tactile spatial representations, early blindness should therefore disrupt not only static spatial judgments but also tactile motion computations that rely on directional coding in external space.

At the same time, motion perception has been described through computational frameworks emphasizing canonical integration rules within each modality. In vision, global motion emerges from constraint-based mechanisms such as the intersection-of-constraints or vector averaging (Adelson & Movshon, 1982; Rust et al., 2006). Converging evidence suggests that tactile motion perception relies on analogous

integration principles within the somatosensory cortex (Pei et al., 2011; Pack & Bensmaia, 2015). These parallels raise an alternative possibility: tactile motion perception may rely on modality-specific computational architectures that do not require visual calibration for their emergence.

This distinction between cross-sensory calibration and intrinsic computation frames the central question addressed in this thesis. The calibration hypothesis predicts that early visual deprivation should alter tactile motion processing if motion direction depends on visually anchored spatial coding. By contrast, if tactile motion perception arises from local spatiotemporal patterns of skin activation integrated within the somatosensory system, these computations may develop independently of visual input while still interacting with vision in adulthood. The present thesis addresses this question by examining visuo–tactile motion integration in sighted individuals and tactile motion perception across early-blind, late-blind, and sighted participants. This approach provides a direct test of whether visual calibration is necessary for the development of tactile motion computation. The findings presented here suggest that the role of vision may be functionally specific. While certain spatial computations depend strongly on visual experience during development, others may develop robustly even in the absence of vision while remaining sensitive to visual input when it is available.

5.2 Visuo–tactile motion integration and the structured architecture of multisensory processing

Chapter 2 revealed that when visual and tactile motion cues are simultaneously available, perceptual responses reflect neither strict modality dominance nor perceptual alternation between independent sensory estimates. Instead, participants exhibited stable percepts anchored to the tactile signal but systematically biased toward the visual input. Both modalities exerted significant main effects and their interaction depended on stimulus configuration: the contribution of one modality varied as a function of the directional properties of the other.

Within classical multisensory theory, such behaviour is typically interpreted through reliability-weighted cue combination models (Ernst & Banks, 2002; Ernst & Bülthoff, 2004), according to which sensory estimates are combined proportionally to their precision in order to minimize overall uncertainty. However, extensive empirical work

has shown that multisensory integration is not obligatory but conditional upon factors such as spatial and temporal congruency, task demands, and inferred causal structure (Helbig & Ernst, 2007; Körding et al., 2007; Shams & Beierholm, 2010; Rohe & Noppeney, 2015). Causal inference models propose that the brain first estimates whether sensory signals originate from a common source before integrating them, allowing graded fusion or segregation depending on contextual probability structure.

The present findings align with this flexible framework but reveal an additional property specific to motion perception. The tactile modality served as the perceptual anchor, likely reflecting task relevance and response instructions. However, visual motion exerted a robust and systematic bias even when it was task-irrelevant. This persistence suggests that visuo–tactile interaction occurs at a perceptual processing stage rather than at a post-perceptual decisional level, consistent with evidence that cross-modal influences can occur within early sensory cortices traditionally considered unimodal (Ghazanfar & Schroeder, 2006; Driver & Noesselt, 2008).

Importantly, the interaction between visual and tactile motion directions was not constant across stimulus configurations. Instead, the magnitude and direction of visual influence depended on the geometric relationship between the two motion signals. This configuration-dependent modulation closely parallels the integration of multiple motion components within a single modality. In vision, global motion perception emerges from combining local motion signals constrained by the aperture problem, and perceived direction depends on the relative orientation and reliability of these components (Adelson & Movshon, 1982; Rust et al., 2006; Weiss et al., 2002). Similarly, tactile motion perception relies on integrating sequential mechanoreceptor activation patterns into coherent directional representations within somatosensory cortex (Pei et al., 2011; Pack & Bensmaia, 2015). These parallels suggest that multisensory motion integration may operate on structured, geometry-sensitive motion representations rather than on abstract scalar estimates of direction. In this view, the perceptual system may not simply combine two independent directional judgments but instead integrate motion signals within a shared representational space shaped by canonical motion computations. This interpretation suggests that multisensory motion integration may follow principles analogous to those governing motion integration within individual modalities.

This perspective is consistent with neurophysiological evidence indicating that motion-selective regions such as area MT/V5 exhibit multisensory responses, including sensitivity to tactile motion stimulation (Hagen et al., 2002; Beauchamp et al., 2007). The existence of such convergent motion representations supports the possibility that cross-modal motion integration occurs within, or in interaction with, shared motion-processing circuits. This interpretation does not contradict probabilistic models of multisensory integration. Rather, it refines them. Reliability weighting may operate within representational constraints imposed by the computational architecture of motion processing. Optimal integration, in this sense, may not consist of averaging independent estimates but of combining structured motion representations under both probabilistic and geometric constraints.

Taken together, the findings of Chapter 2 suggest that visuo–tactile motion perception reflects a structured and hierarchical integration process. Sensory signals are not fused indiscriminately; instead, they interact within a computational architecture that preserves modality-specific motion coding while allowing flexible cross-modal influence. Understanding multisensory motion perception therefore requires integrating probabilistic frameworks with the domain-specific principles that govern motion computation within each sensory modality.

5.3 Developmental independence and online multisensory interaction

The findings of Chapter 4 provide an important complement to the visuo–tactile interactions observed in Chapter 2. While visual motion systematically biased tactile motion perception when both cues were available, tactile motion discrimination sensitivity did not differ significantly between sighted, early-blind, and late-blind participants. This pattern indicates that tactile motion perception can develop robustly even in the absence of visual experience, while remaining susceptible to visual influence when both signals are present.

Within the framework of cross-sensory calibration (Burr & Gori, 2012), these results suggest that the influence of visual experience may operate in a functionally selective manner. The calibration hypothesis proposes that certain sensory modalities provide reference signals that help stabilize or refine the representations of other modalities during development. Vision is thought to play a central role in calibrating spatial representations because it provides a stable and high-resolution mapping of external

space. However, the extent to which visual calibration is required may depend on the computational properties of the perceptual function involved. Spatial functions that require alignment with external reference frames are particularly likely to depend on visual calibration. Vision provides continuous information about the orientation of objects relative to the external environment, making it well suited to anchor these spatial representations during development. Consistent with this account, impairments in tactile orientation discrimination have been reported in congenitally blind individuals (Gori et al., 2010).

Tactile motion discrimination, however, may rely on partially different computational foundations. Unlike static orientation judgments, which require explicit alignment with external spatial axes, motion direction discrimination for moving gratings can be derived from local spatiotemporal patterns of activation across the skin. As a stimulus moves across the skin surface, successive mechanoreceptors are activated in sequence, generating spatiotemporal signals that contain directional information. The integration of these local signals into a coherent motion percept may therefore rely primarily on intrinsic somatosensory computations. Neurophysiological studies have shown that neurons in somatosensory cortex, particularly in area 1, respond selectively to the direction of global tactile motion, suggesting that motion direction is computed through the integration of local motion signals within the somatosensory system itself (Pei et al., 2011).

Within this framework, tactile motion perception may depend less on visually calibrated spatial reference frames than other tactile spatial functions. The somatosensory system may possess sufficient intrinsic structure to resolve directional ambiguity and encode motion through canonical integration rules. Visual experience, when available, may still refine or align these representations with external spatial coordinates, but the core computational mechanisms underlying tactile motion discrimination may emerge largely from somatosensory processing.

This interpretation is consistent with broader evidence from sensory development and plasticity. Multisensory systems exhibit both experience-dependent tuning and intrinsic organizational constraints (Wallace et al., 2004; Lewkowicz, 2000). Early sensory deprivation can therefore alter some cross-modal properties while leaving others relatively preserved. Moreover, neuroimaging studies have shown that motion-

selective cortical regions can respond to tactile motion stimulation even in the absence of vision (Hagen et al., 2002; Beauchamp et al., 2007), suggesting that motion representations may be organized around modality-general computational principles rather than exclusively visually derived spatial maps.

Importantly, the absence of group differences in tactile motion discrimination observed in Chapter 4 does not imply that vision plays no role when present. As demonstrated in Chapter 2, visual input clearly biased tactile motion perception when both signals were available. The present findings therefore support a layered architecture in which tactile motion computation develops largely within the somatosensory system while remaining embedded within a multisensory network capable of flexible cross-modal interaction.

This distinction between developmental independence and online integration has important theoretical implications. It suggests that multisensory interaction and cross-sensory calibration are related but distinct processes. A sensory system may acquire its core computational capacities without reliance on another modality, while still engaging in dynamic multisensory interaction when multiple signals are available. Recognizing this distinction helps clarify the role of vision in shaping tactile perception: not as a universal prerequisite for spatial computation, but as a modality that selectively calibrates specific functions while modulating others during ongoing perception.

5.5 Limitations and Future Directions

While the present work provides new insights into visuo–tactile motion perception and its dependence on sensory experience, several limitations should be considered when interpreting the findings and when designing future investigations.

A first limitation concerns the restricted range of motion parameters tested across experiments. In both the multisensory and tactile-only paradigms, motion direction was sampled from a relatively small set of orientations. This approach allowed for controlled comparisons and reliable estimation of perceptual biases, but it does not fully capture the broader space of motion signals that can occur in natural tactile interactions. Future studies could extend this approach by systematically manipulating additional parameters such as motion speed, spatial frequency of the gratings, or a

wider range of motion directions. Such manipulations would allow a more detailed characterization of how tactile motion signals are integrated and how cross-modal interactions vary across stimulus conditions.

A second limitation relates to the nature of the tactile stimulation used in the experiments. Motion stimuli were delivered through passive stimulation of the fingertip using moving gratings. Passive stimulation provides high experimental control and precise manipulation of motion parameters. However, natural tactile perception often involves active exploration, in which sensory signals are shaped by voluntary movements of the hand and fingers. Active touch engages additional sensorimotor mechanisms, including predictive processes and efference copy signals, which may influence motion perception. Future research could therefore investigate whether similar perceptual patterns emerge under conditions of active tactile exploration.

A third limitation concerns the sample size and composition of the visually impaired group. Recruiting participants with visual impairment is inherently challenging, and the present study included a relatively small number of early-blind and late-blind individuals. Although the results revealed consistent patterns across participants, larger samples would allow a more detailed characterization of individual variability and a more precise comparison between different forms of visual deprivation.

Finally, the experiments focused primarily on behavioural measures of perception, which provide important insight into the functional properties of the system but do not directly reveal the underlying neural mechanisms. Converging evidence from neurophysiological and neuroimaging studies suggests that motion-selective cortical regions may respond to both visual and tactile motion signals. Investigating visuo–tactile motion perception using neuroimaging or electrophysiological techniques could therefore provide important insight into the neural circuits supporting these interactions and into how sensory experience shapes their organization.

Despite these limitations, the present work provides a coherent framework for investigating motion perception across sensory modalities and across different sensory experiences. By combining multisensory experiments, methodological development, and comparisons between sighted and visually impaired individuals, this thesis establishes a foundation for future research aimed at understanding how motion signals are computed and integrated across the human sensory system.

5.4 Conclusions

Perception emerges from the interaction between sensory signals, internal computations, and experience. In everyday life, the brain must construct coherent percepts from information distributed across multiple sensory modalities. Understanding how these signals are processed within individual sensory systems and how they interact across modalities remains a central challenge for perceptual neuroscience.

Motion perception provides a particularly informative framework for addressing this problem. Because local motion signals are inherently ambiguous, perceiving motion requires structured integration processes that transform spatiotemporal sensory inputs into coherent directional estimates. While these computations have been extensively characterized within vision and, more recently, within touch, far less is known about how motion representations interact across modalities and how sensory experience contributes to shaping these interactions.

The findings of this thesis show that tactile motion perception relies on robust somatosensory computations capable of supporting motion discrimination even in the absence of visual experience. At the same time, tactile motion percepts remain sensitive to visual input when both modalities are available, revealing a dissociation between the developmental establishment of tactile motion processing and its online modulation by multisensory signals. This dissociation highlights an important distinction between the mechanisms that support the emergence of perceptual functions and those that govern their interaction during ongoing perception.

These findings refine the role of vision within the framework of cross-sensory calibration. Rather than acting as a universal prerequisite for spatial perception, visual experience appears to calibrate specific functions that require alignment with stable external reference frames, while other perceptual computations can develop from modality-specific signals alone. Motion perception exemplifies this functional specificity: tactile motion representations may emerge from intrinsic somatosensory structure while remaining embedded within a multisensory system that flexibly integrates visual information when available.

More broadly, this thesis underscores the importance of considering multisensory perception at multiple levels of description. Motion perception depends on computational principles that shape sensory representations within individual modalities, as well as on mechanisms that regulate how these representations interact across sensory systems. Integrating these perspectives is essential for understanding how coherent percepts arise from complex, distributed sensory signals.

By situating visuo–tactile motion perception at the intersection of sensory computation, multisensory interaction, and sensory experience, this work contributes to a more nuanced account of how the brain constructs dynamic representations of the external world. Such an approach provides a foundation for future research aimed at linking computational models, developmental processes, and multisensory integration within a unified theoretical framework.

Scientific Production

Journal Paper

Bertolasi, J., Esposito, D., Vitale, A., & Gori, M. (2025). Exploring the role of serial dependence in visual time perception. *Journal of Vision, 25*(8), Article 7. https://doi.org/10.1167/jov.25.8.7

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Poster

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Appendix A

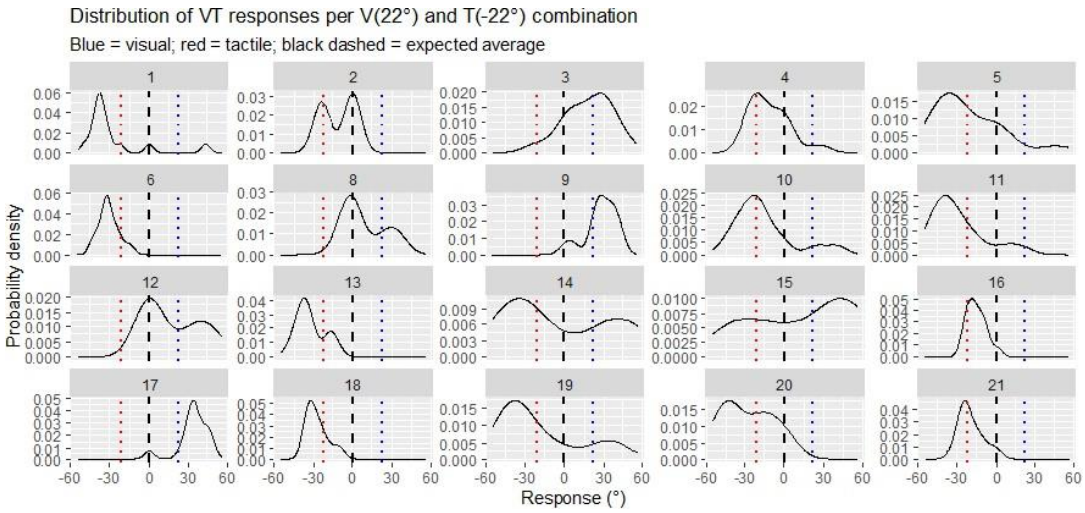

Figure S.1 Response distribution in the multisensory condition with visual and tactile directions (V = 22°, T = −22°). Probability density of participants' response distributions for the multisensory condition. Each figure represents a combination of visual- and tactile-wheel's direction. Every panel corresponds to one participant (N = 21). The solid blue and red vertical lines indicate the physical visual and tactile directions, respectively, while the black dashed line represents the arithmetic mean of the two cues (i.e., the expected integrated estimate). For ease of interpretation, data were aggregated across participants, and each condition is displayed separately to provide a clear visualisation of the resulting patterns.

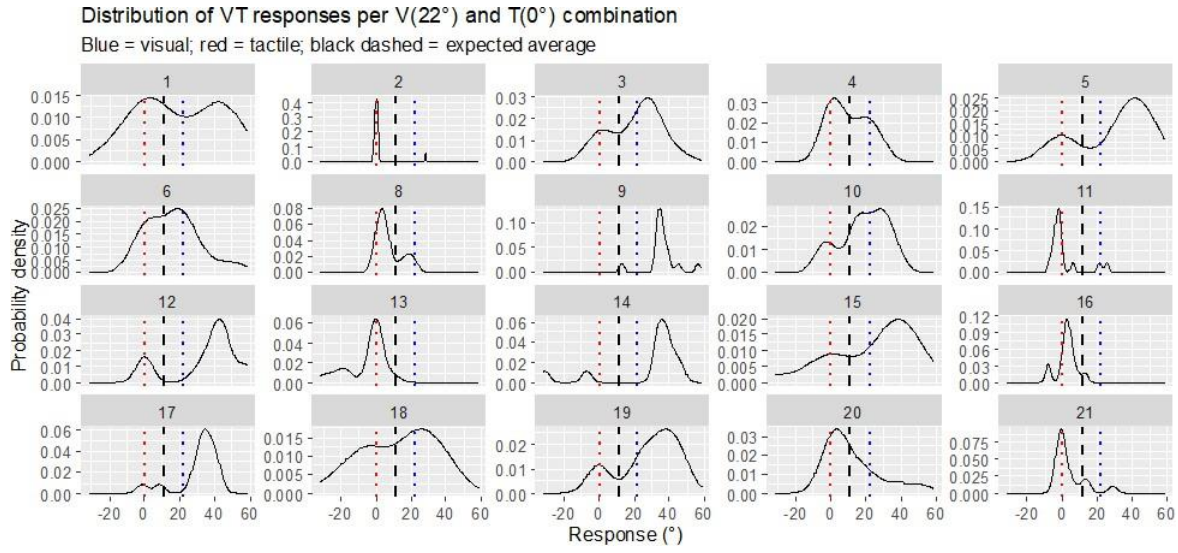

Figure S.2 Response distribution in the multisensory condition with visual and tactile directions (V = 22°, T = 0°).

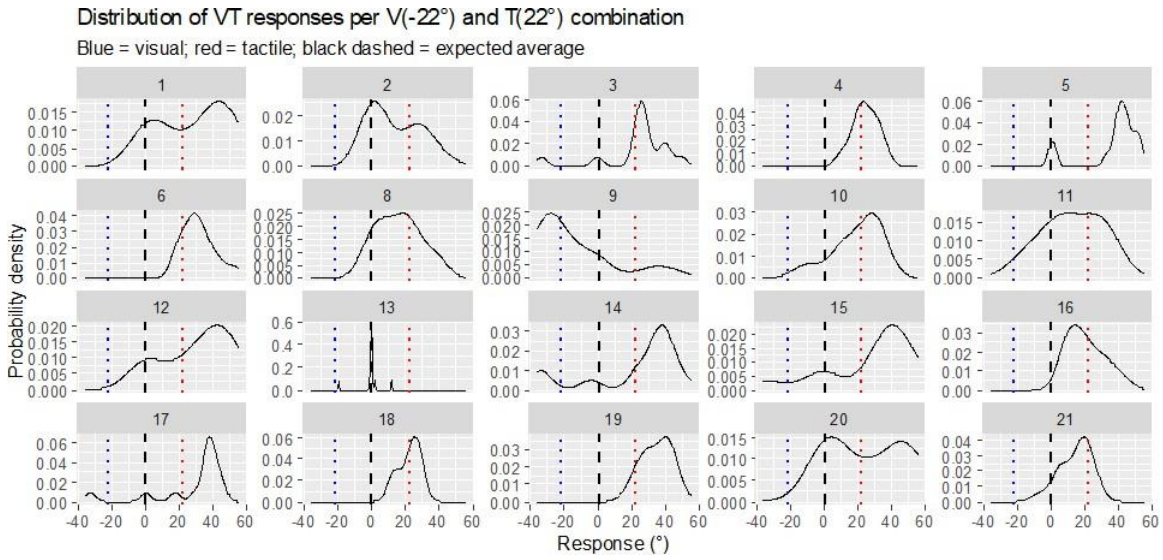

Figure S.3 Response distribution in the multisensory condition with visual and tactile directions (V = -22°, T = 22°).

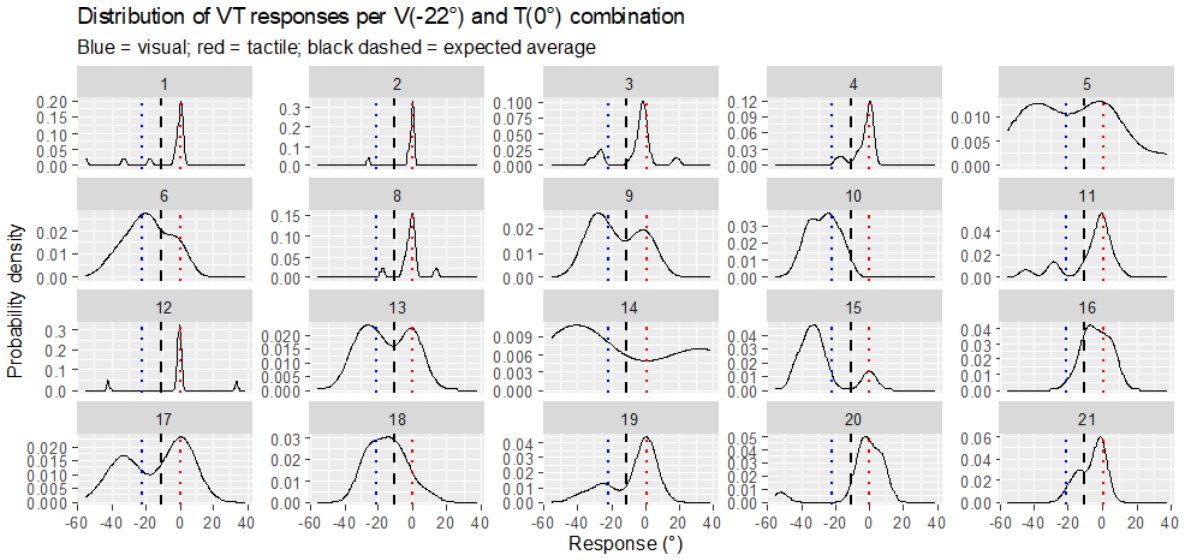

Figure S.4 Response distribution in the multisensory condition with visual and tactile directions (V = -22°, T = 0°).

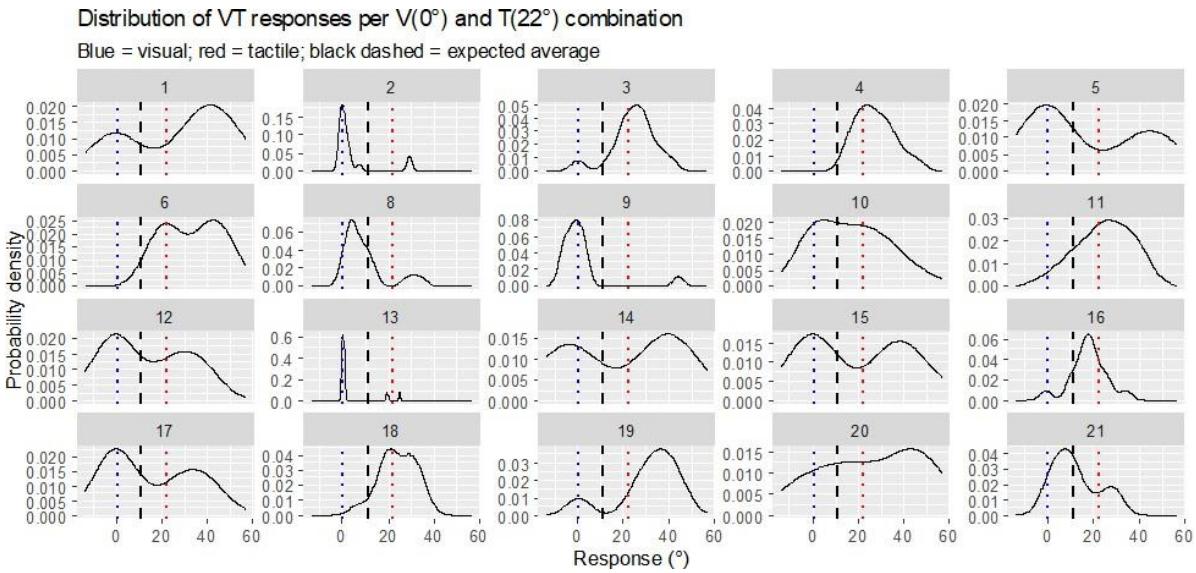

Figure S.5 Response distribution in the multisensory condition with visual and tactile directions (V = 0°, T = 22°).

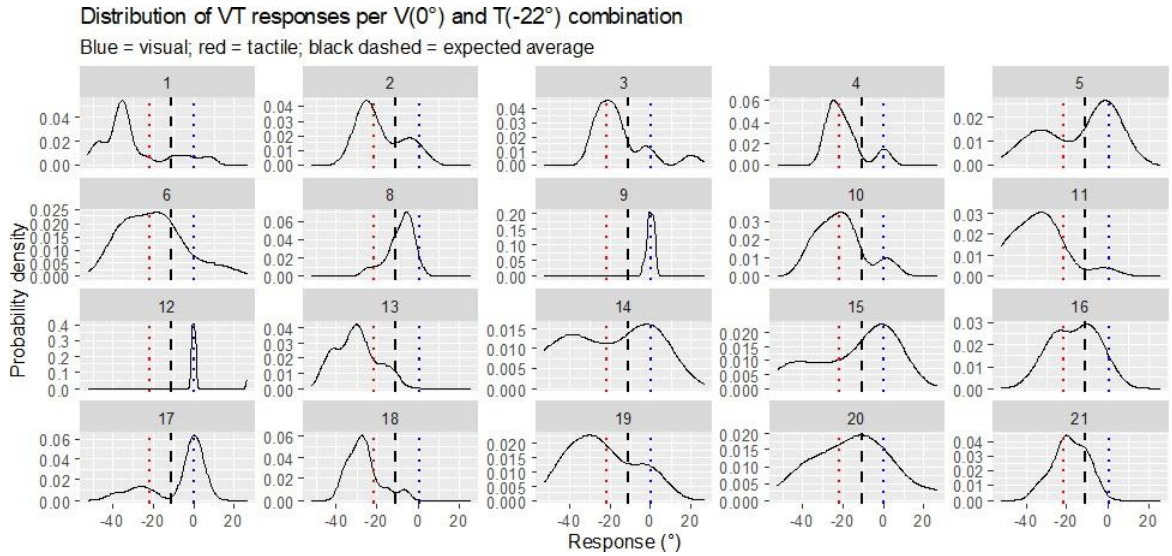

Figure S.6 Response distribution in the multisensory condition with visual and tactile directions (v = 0°, t = -22°).

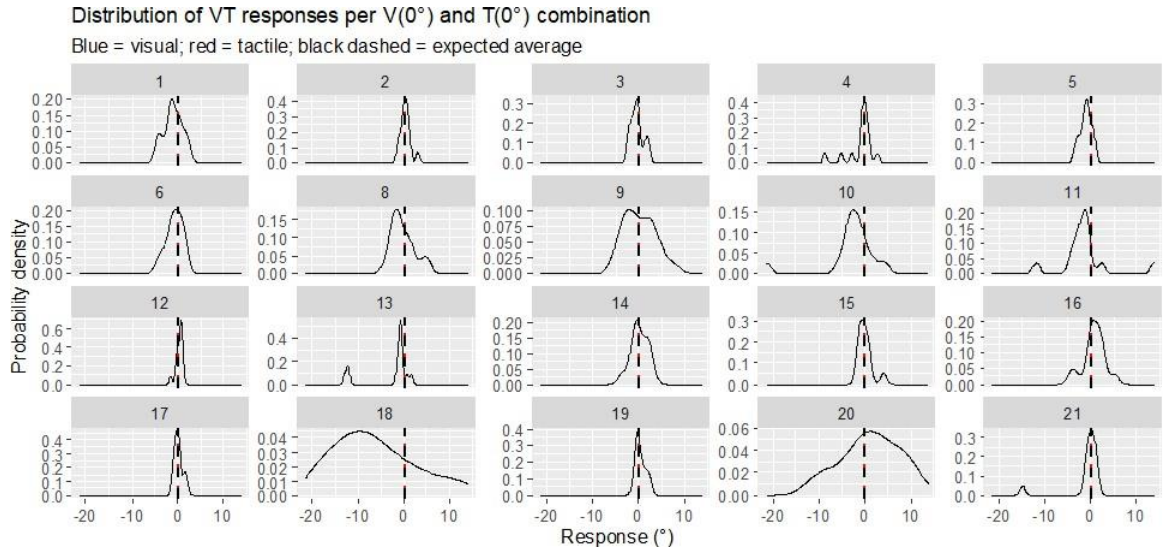

Figure S.7 Response distribution in the multisensory condition with visual and tactile directions (V = 0°, T = 0°).

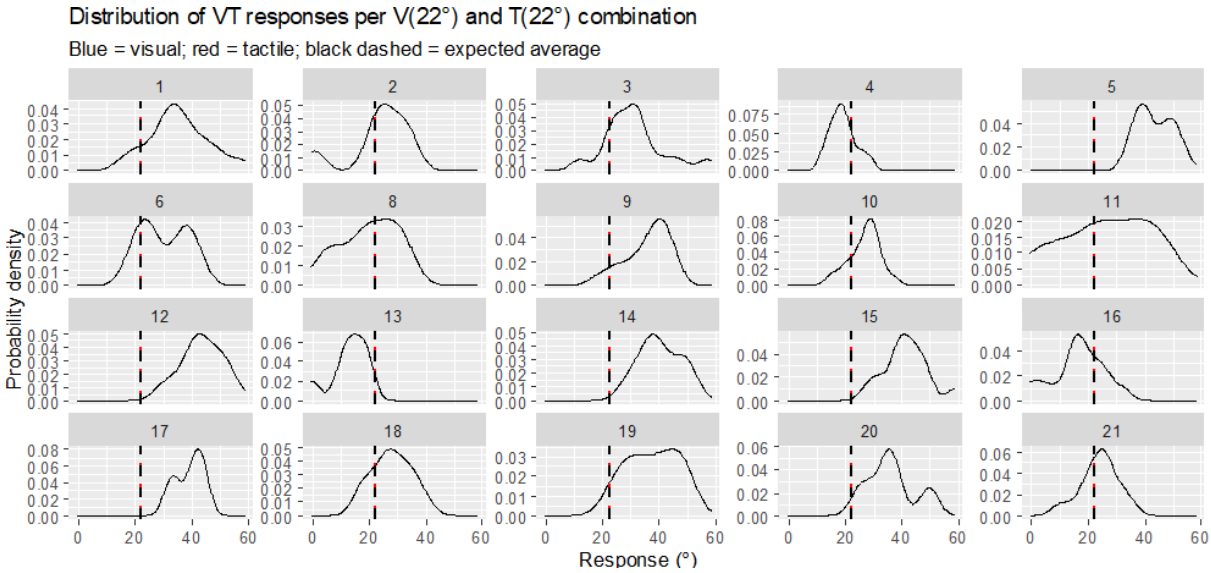

Figure S.8 Response distribution in the multisensory condition with visual and tactile directions (V = 22°, T = 22°).

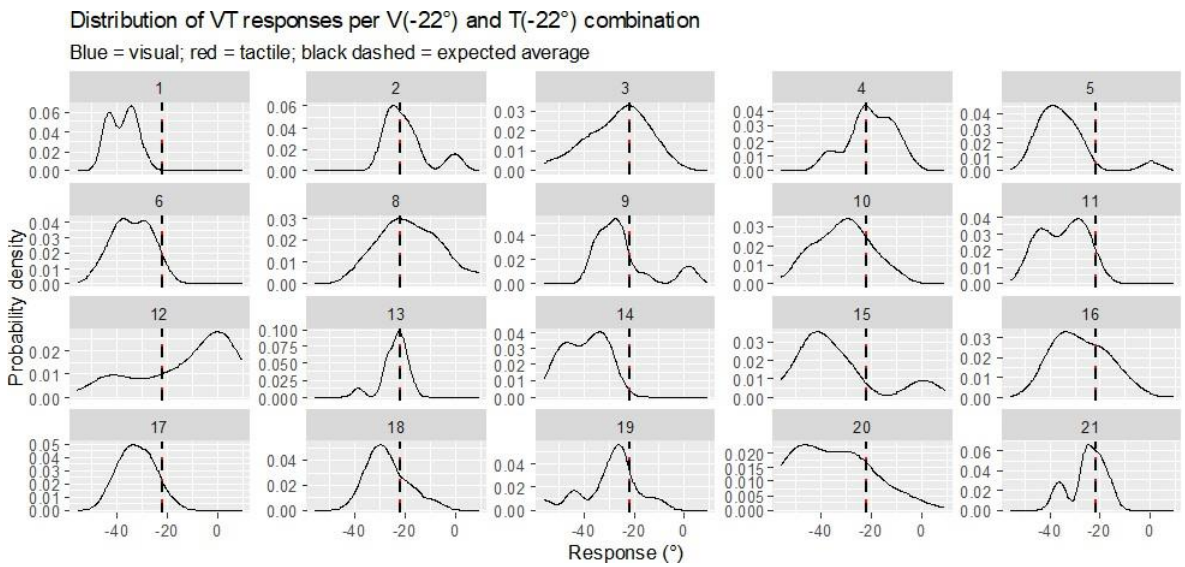

Figure S.9 Response distribution in the multisensory condition with visual and tactile directions (V =- 22°, T = -22°).