COGNITIVE INFLUENCES ON THE CROSSED-HANDS DEFICIT

COGNITIVE INFLUENCES ON THE CROSSED HANDS DEFICIT:

AN INVESTIGATION OF THE DYNAMIC NATURE OF TACTILE PROCESSING

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LAY ABSTRACT

Our ability to localize tactile stimuli is critical to successfully interact with our environment: if we feel something crawling on us, we need to eliminate this unwanted visitor as quickly and accurately as possible. A large body of evidence suggests that tactile localization requires perceptual signals beyond the somatotopic information about where on your skin you feel the tactile stimulus. Just think about how much easier it is to swat at a bug on your arm when you can see it as well as feel it. In this thesis I provide novel empirical evidence that cognitive factors also influence our ability to engage in tactile localization, including visual imagery and attention. I then propose an update to existing theory that can account for the influence of these cognitive factors, alongside the traditional approach to the integration of perceptual signals such as vision.

ABSTRACT

Theories of tactile localization ability are based largely on the study of crossing effects, in which crossing the hands leads to a significant impairment in performance. This work has resulted in a rich literature that establishes tactile localization as inherently multisensory in nature. However, new work suggests that the studies used to date have made incorrect assumptions about the processes underlying performance (Maij et al., 2020) and the perceptual information that is considered (Badde et al., 2019). This thesis proposes the addition of a new parameter to existing theory that allows for these new results to be incorporated into the existing literature—specifically, the influence of cognitive factors on performance. The Introduction provides an overview of the current state of the literature, as well as the novel findings that seem to contradict it. I then propose a framework that highlights the malleability of tactile localization. The empirical work focuses on previously unexplored cognitive influences on tactile localization performance. In Chapter 2 I demonstrate that visual imagery influences performance, and importantly, that individual differences in visual imagery ability influence imagery's effect on performance. In Chapter 3 I demonstrate that an individual's attentional set influences performance, and that results previously thought to be due to changes in perceptual signal are likely due to changes in attentional focus. In Chapter 4 I highlight the biases in theory and measurement practice that have limited our understanding of tactile localization more broadly. The General Discussion then provides a detailed discussion about how to incorporate the findings of this thesis with existing literature, which requires a paradigm shift to how we view tactile localization.

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DECLARATION OF ACADEMIC ACHIEVEMENT

The Introduction of this thesis was conceptualized and written by Lisa Lorentz, with edits from Dr. Sandra Monteiro.

Chapter 2 is an empirical article by Lisa Lorentz, and Drs. Kaian Unwalla and David I. Shore submitted to *Multisensory Research* for publication. Experiments 1 and 2 were conceptualized and designed by Lisa Lorentz and David I. Shore, programmed by Kaian Unwalla, and conducted and analysed by Lisa Lorentz. The writing of this manuscript was completed by Lisa Lorentz and David I. Shore, with input from Kaian Unwalla.

Chapter 3 is an empirical article in manuscript form for publication. Experiment 1 was conceptualized, designed, programmed, conducted, and analysed by Lisa Lorentz with guidance from David I. Shore. Experiments 2A & 2B were conceptualized, designed, programmed, and conducted by Kaian Unwalla and David I. Shore. The re-analyses of Experiments 2A & 2B were conceptualized and analyzed by Lisa Lorentz with guidance from Sandra Monteiro. The writing of this manuscript was completed by Lisa Lorentz and David I. Shore, with input from Kaian Unwalla.

Chapter 4 is a state-of-the-art/critical review in manuscript form for publication. The narrative was conceptualized by Lisa Lorentz with guidance from Sandra Monteiro. The writing of this manuscript was completed by Lisa Lorentz and Sandra Monteiro.

The General Discussion of this thesis was conceptualized and written by Lisa Lorentz, with edits from Sandra Monteiro.

Chapter 1

General Introduction

You feel a bug on your arm and you want to swat it away. To do so, you locate the bug based on where you feel it on your skin. But this isn't enough information. You also need to know where your arm is in space so that you can swat at the bug's precise location. This cliched example of tactile localization is used by most people who study it because this scenario clearly highlights the inherently multisensory nature of touch.

Touch is a unique sense for two reasons. First, the sense organ is large, with the mechanical processing of touch able to occur essentially anywhere on the body's surface. Second, this sense organ's location isn't static, with our limbs being able to inhabit a variety of locations about our trunk. These two features mean that tactile localization cannot occur in a unisensory fashion. Whereas visual location can be calculated based solely on retinal coordinates, and auditory location can be determined based on differential timing of sound waves between the two ears, tactile localization requires information about where body parts are in space, which cannot be calculated based on somatotopic information alone.

These features of touch have led to a two-decades long investigation of the processes underlying tactile localization (for seminal work see Shore, Spry, & Spence, 2002 and Yamamoto & Kitazawa, 2001; but also see Drew, 1896 for a very early investigation). It seemed that recently the field had mostly reached a consensus about the processes at play (Badde & Heed, 2016; Badde, Heed, & Röder, 2014; Shore, Spry, &

Spence, 2002; but see Takahashi et al., 2013; Yamamoto & Kitazawa, 2001), with complex mathematical modelling supporting theoretical assumptions based in behavioural observation (Badde & Heed, 2016; Unwalla et al., submitted). However, novel work has begun to question the fundamental assumptions underlying all of the information collected to date and consequently demands a critical reworking of existing theory (Badde et al, 2019; Maij et al., 2020).

The dominant theory of tactile localization (integration theory; Badde & Heed, 2016; Badde, Heed & Röder, 2014; Heed et al., 2015; Shore, Spry, & Spence, 2002) suggests that signals from multiple sensory modalities are integrated when localizing tactile stimuli. For our bug example, think about how much easier it is to swat the bug if you can see it, as well as feel it. Much of the work on tactile localization supports the important role of visual information about space during tactile localization (Azañón & Soto-Faraco, 2007, Cadieux & Shore, 2013; Gallace & Spence, 2005; Kóbor et al., Lorentz et al., submitted; 2006; Röder et al., 2004), but recent work by Badde et al. (2019) questions whether the information provided about external space by vision actually influences tactile localization. Maij et al. (2020) goes further to suggest that the task used in almost all studies of tactile localization doesn't actually index tactile localization ability at all.

These new findings by Badde et al. (2019) and Maij et al. (2020) have placed the study of tactile localization at a cross-roads. This new work suggests a fundamental re-evaluation of the work collected to date due to assumptions about the sensory information at play (Badde et al, 2019) or the nature of the task being used (Maij et al., 2020). So how do we look forward from here? Do we leave behind two decades of research and continue to look for evidence in favour of these new models? Do we defend the theories of years past? In the present work I suggest that the future of our understanding of tactile localization requires a paradigm shift. We cannot simply decide to abandon old work or to staunchly defend it. We must instead critically evaluate the assumptions and biases that have influenced our work so far and explore how these factors have influenced our theories. This will require going so far as to critically re-evaluate what it is that we are actually measuring in studies of tactile localization.

In Chapters 2 and 3 I provide evidence of previously unexplored influences on tactile localization that go beyond typical perceptual studies to investigate cognitive influences on tactile perception. In Chapter 4 I provide a framework for how the findings of Chapters 2 and 3 fit into our understanding of tactile localization. I will present the argument that in order to appreciate the co-existence of previous findings with new (seemingly) contradictory findings (Badde et al., 2019; Maij et al., 2020), as well as the novel cognitive influences discussed in the present work (Chapter 2; Chapter 3), we need to critically re-evaluate the assumptions that have influenced all work completed to date and their impacts on our understanding of observed patterns of data and resulting theory.

How Tactile Localization is Studied and Understood

Measuring Tactile Localization. To understand the recent shift in tactile localization research, we must first look at how tactile localization is typically observed and measured. Tactile localization is almost exclusively studied using the tactile temporal order judgment (TOJ) task, in which participants are presented with two successive vibrations, one to each hand, and are asked to respond with the hand that vibrated first (see Heed & Azañón, 2014 for an excellent review of how this temporal task indexes spatial processing). Behavioural results are plotted as a proportion of "right hand first" responses, and usually result in a S-shaped psychometric curve (but see Yamamoto & Kitazawa, 2001). Results are then evaluated using traditional measures such as probit slope and just noticeable difference scores (see Heed & Azañón, 2016 for a review), or a newer measure specific to tactile localization, the proportion correct difference (PCD) score (Cadieux et al., 2010).

When the hands are in their uncrossed canonical posture performance is near ceiling on this task, leaving researchers without much to explore. However, simply asking participants to cross their hands over the body midline leads to a significant detriment to performance. This "crossing effect", often referred to as the crossed-hands deficit (CHD), has served as the basis for our understanding of tactile localization and has essentially become synonymous with it. It is assumed that understanding why tactile localization is "tricked" or error-prone in the crossed posture allows us to understand how typical uncrossed tactile localization occurs.

Theories of the CHD. The integration theory of the CHD (Badde & Heed, 2016; Badde, Heed & Röder, 2014; Heed et al., 2015; Shore, Spry, & Spence, 2002) posits that although information from many senses contributes to tactile localization, they can be categorized into one of two broad categories: internal reference frame information and external reference frame information. Information from the internal reference frame localizes the tactile stimulus in bodily coordinates. This includes somatotopic, or bodily-map information, as well as information about the limb's canonical location (Badde et al., 2019). Information in the external reference frame localizes the tactile stimulus in the space surrounding the body and is informed by vision (Azañón & Soto-Faraco, 2007; Cadieux & Shore, 2013; Gallace & Spence, 2005; Kóbor et al., 2006; Röder et al., 2004; but see Badde et al., 2019) and by vestibular information (Unwalla et al., submitted).

When the hands are uncrossed the information in these two reference frames is congruent, and therefore, integrating internal and external reference frame information results in a reliable tactile location estimate. However, when the hands are crossed the information in these two reference frames conflicts, and, thus, integrating these sources of information will lead to an unreliable tactile location estimate, and consequently to error-prone responding. Essentially, the mechanism that evolved to increase precision of tactile localization in our typical uncrossed posture is negatively impacted when the hands are in the uncommon crossed posture.

The integration theory has been largely informed by tactile TOJ studies in which conflicting visual information from the external reference frame is removed (Cadieux & Shore, 2013; Kóbor et al., 2006; Röder et al., 2004) or replaced with congruent visual information when the hands are crossed (Azañón & Soto-Faraco, 2007; Lorentz et al., submitted). Both manipulations lead to a reduction in the magnitude of the CHD, presumably by decreasing conflict between information from the two reference frames during calculation of the location estimate. However, two new studies using unconventional tactile TOJ tasks provide evidence to suggest that this previous work is fundamentally flawed.

Using an atypical hand and foot tactile TOJ task, Badde et al. (2019) found evidence to suggest that visual information about external space is not incorporated into estimates of tactile location. In this task participants received two vibrations, one to a hand and one to a foot, while the hands, feet, or both, were either crossed or uncrossed. Errors in this task were not made based on the side of space that was stimulated, but were instead influenced by the side of space where the stimulated limb typically exists (i.e., canonical posture). The visual information about general spatial location did not seem to influence performance in this task.

Separate work using a different atypical tactile TOJ task found evidence to suggest that the standard tactile TOJ task does not actually index tactile localization performance. Maij et al. (2020) examined errors from a task in which the participants received two successive vibrations while hands were in a crossed or uncrossed posture and they moved the hands toward the body to either end in the same posture that they began in, or to end in the opposite posture. Participants were asked to point to the location of the first tactile stimulus with the hand that was vibrated first. Importantly, crossing the hands did not affect errors in pointing to the stimulus location (i.e., tactile localization); instead, crossing the hands influenced hand assignment (i.e., identifying which hand vibrated first).

Taken together these two studies question two fundamental assumptions of integration theory and the studies used to inform it. Badde et al. (2019) suggest that visual information about external space does not inform a spatial external reference frame that contributes to tactile TOJ performance, and Maij et al. (2020) suggest that all of the work done using tactile TOJ tasks hasn't studied tactile localization at all and has instead been examining hand assignment during tactile stimulation.

Although these studies open the door for a necessary re-evaluation of the tactile localization data and theory examined to date, the idea that all work done to date is fundamentally flawed seems extreme. In the present work I instead suggest that these recent results (Badde et al., 2019; Maij et al., 2020) provide valuable insight into a critical assumption that is made in the CHD literature that has not been explicitly examined, and how the field can examine it to both incorporate these new results and to better understand previous work. Specifically, throughout this thesis I present evidence that tactile localization is not a static ability, but rather is a dynamic process that rapidly adapts to different task parameters and contexts, as well as different characteristics of the individual, such as attentional set. This paradigm shift allows for parsimony across the field and presents exciting avenues for future research.

New challenges for the CHD as a measure of tactile localization

Influences of Task Demands. To use the CHD as an index for tactile localization requires that uncrossed and crossed performance represent a baseline perceptual phenomenon. That is, all typically-developed individuals will respond to tactile stimuli in a systematic fashion when the hands are uncrossed and crossed, with this "systematic-fashion" representing basic tactile processing.

However, work in the CHD literature suggests against this and instead provides evidence that tactile TOJ performance is highly malleable depending on task parameters. Simply changing the required response from being externally based (i.e., which side of space vibrated first) to internally based (i.e., which hand vibrated first) systematically changes performance by changing whether the participant does or does not focus on conflicting external reference frame information respectively (Cadieux & Shore, 2013; Crollen et al., 2019; Unwalla et al., 2020). Similarly, changing the attentional focus of the participant by asking them to complete a simultaneous task decreases the likelihood that external reference frame information will be integrated (Badde & Heed, 2014). These response and attentional demand findings both systematically influence results through a reweighting of internal and external reference frame information (Badde & Heed, 2016; Unwalla et al., submitted). In other words, although baseline performance is malleable, task demands influence tactile TOJ responses in systematic ways, with performance shown to be consistent across time so long as the same set of task parameters are used (Unwalla, Kearney, & Shore, 2020).

This brings us back to the recent work by Badde et al. (2019) and Maij et al. (2020). They argue that external space does not contribute to tactile TOJ performance, and that tactile TOJ performance does not actually index tactile localization respectively. However, the results from which these conclusions are derived are from tasks that use drastically different procedures from typical CHD studies. Given the evidence that changes to task parameters drastically influence performance, we suggest that the results of Badde et al. (2019) and Maij et al. (2020) inform how tactile localization is carried out in those specific tasks, rather than question the fundamental appropriateness of the assumptions underlying the TOJ task and integration theory more broadly.

It is not that previous work is flawed. Instead, I suggest that the parameters used in Badde et al. (2019) and Maij et al. (2020)'s tasks differentially tapped the dynamic processes underlying tactile localization, leading to their unique results. For example, it is not unlikely that introducing the feet as effectors in the tactile TOJ task (Badde et al., 2019) change the relative weighting of internal and external reference frame information for the hands, as well as for the feet. But to answer this question, we would need to first explore whether the feet have their own relative weights, and these weights interact with the hands' weights. Similarly, requiring participants to move their hands (Maij et al., 2020) changes the task goal from a typical tactile TOJ task (i.e., which hand vibrated first), to perception for action (i.e., point to the location in space that was stimulated). This change in goal likely changes the way perceptual information is used. In other words, I propose an approach that accounts for the flexible manner in which reliably present perceptual information is differentially weighted depending on task demands, rather than questioning the use or disuse of entire categories of information across the board. However, doing so will first require examination of the influences of multiple effectors and movement, as mentioned above.

Viewing the results of these tasks in these ways provide parsimony and allows for all of the data considered to date to be understood using the same—albeit an expanded version of—existing theory. However, doing so requires a fundamental change to our understanding of tactile localization and the CHD. We must see the processes underlying performance on the tactile TOJ task as malleable and adaptable to the current situation, but following systematic rules based on task parameters. Tactile perception is not a static perceptual phenomenon; rather it is predictably influenced by context and task parameters (Cadieux & Shore, 2013; Crollen et al., 2019; Unwalla et al., 2020). In Chapter 4 I examine the internalized and sometimes unconscious biases that must be critically examined for this paradigm shift in our understanding of the CHD to allow for this parsimony to be found.

Influences of Individual Differences and Attention. But this paradigm shift for our understanding of tactile localization and the CHD does not end at a critical evaluation of the influences of task demands. In Chapters 2 and 3 I provide evidence that tactile TOJ performance can also be influenced by parameters within the perceiver's control. In Chapter 2 I explore the influence of visual imagery and in Chapter 3 I explore the influences of attention. Just like task demands, these individual traits and internally generated signals influence performance in systematic ways. But the inherently personal nature of these internally generated signals means that current and baseline levels can differ between individuals at any point in time and even across the same individual at different points in time. This positions the influences of individual differences in abilities and dispositions as prime candidates to explain the extreme variability observed in tactile TOJ performance for years (Cadieux et al., 2010; Figure 2), but that has evaded explanation thus far (Craig & Belser, 2006; Kóbor et al., 2006). In Chapter 2 I provide evidence that individual differences in the ability to engage in visual imagery influence the magnitude of imagery's influence on tactile TOJ performance.

Although the role of visual imagery in tactile localization was not studied in previous work (but see Sathian & Zangaladze, 2001 for the role of visual imagery in tactile perception of grating orientation), the role of attention within the crossed tactile TOJ task has been examined (Badde & Heed, 2014). However, the goal of this attention study was much different than that of Chapter 3 of the present work. Badde and Heed (2014) found that dividing attention by completing a secondary task concurrently with the tactile TOJ task influences performance by decreasing the probability that reference frame integration will occur (Badde & Heed, 2014). This result was used to suggest that integration of the reference frames is not automatic, and instead requires attention. In Chapter 3 of the present work I push this idea further by providing evidence that an individual's attentional set is critical for their performance on the tactile TOJ task, with different attentional sets (i.e., focused or relaxed) able to either prioritize or decrease reliance on conflicting information from the external reference frame. This more nuanced approach suggests that attention does not simply determine whether integration occurs, but rather influences the relative weighting of information from the two reference frames. Importantly, Chapter 3 provides evidence that results previously thought to be due to a change in perceptual signal are instead due to changes in the allocation of attention.

The results of Chapters 2 and 3 therefore have important implications for our understanding of tactile localization. Taken together with existing task demand results

(Badde & Heed, 2014; Cadieux & Shore 2013; Crollen et al., 2019; Unwalla et al., submitted), the visual imagery (Chapter 2) and attentional set (Chapter 3) results suggest that tactile localization is highly malleable. More specifically, an individual's tactile localization performance will differ depending on the internal state of the participant and the current task demands.

Potential for Parsimony in a Field at a Cross-Roads

Although it appeared we had mostly reached a consensus about the processes underlying tactile localization, new work by Badde et al. (2019) and Maij (2020) demands a critical re-evaluation of theory. But rather than interpreting these results as cause for concern about all of the work done to date, I propose that they instead support a much-needed re-evaluation of how we have studied tactile localization and highlight the potential biases in our theory. I propose that by simply changing our view of tactile localization as a static perceptual ability to seeing it as a dynamic ability that adapts to different contexts allows for these new results to help us better understand existing results and provide exciting avenues for future research.

Given the inherently dynamic nature of touch, with the tactile sense organ able to move relatively freely throughout space, it makes sense that tactile localization would be a dynamic process. It is not surprising that we adapted to incorporate information that will best inform our location estimate (see Stein & Meredith, 1993 for an overview of multisensory integration; see Ernst & Bulthoff for an overview of the underlying math)—it's just that in the unusual crossed posture adapted in CHD experiments we are intentionally exploiting a weakness of this system. The task demand results (Cadieux & Shore, 2013; Crollen et al., 2019; Unwalla et al., 2020) and visual imagery (Chapter 2) and attention results (Chapter 3; Badde & Heed, 2014) support this view. But to interpret the results in this way requires a shift from the way we currently view tactile localization. It is not simply a static ability, but rather a dynamic process that fundamentally changes depending on the current task context, as well as the current internal disposition of the individual being tested.

The Role of Attention. Suggesting that tactile localization is a dynamic process seems to be at odds with parsimony—a static ability requires fewer free parameters than a dynamic ability. However, viewing attention as a key factor in tactile localization performance may be the key to parsimony (see Spence, 2002 for a review of the role of selective attention in tactile processing more broadly).

In Chapter 3 I provide convergent evidence with existing work that suggests that attention can influence tactile TOJ performance (Badde & Heed, 2014). But I also provide evidence that findings currently thought to be a consequence of perceptual changes (Unwalla et al., submitted) are actually due to shifts in attention. In Chapter 3 I also discuss how influences of attention act as the mechanism by which task demands influence performance: changing the way a participant responds or adding an additional task likely changes the allocation of attention to information from different reference frames, consequently influencing performance. This attentional explanation has potential for further explanatory power to account for how tactile TOJ performance changes with training (Azañón et al., 2015; Craig & Belser, 2006). It is unlikely that the perceptual system changes at the acute timescale in which tactile TOJ performance improves over time (Azañón et al., 2015), but attention is notorious for rapid changes in deployment.

Taken together, these suggestions propose that careful considerations of attention may be a key to parsimony in the field. Task demands and internally generated signals influence tactile TOJ performance via attention in systematic ways, leading to the stable influence on performance over time. Individual differences in skill (Chapter 2) or attentional disposition (Chapter 3) can account for the variability observed across individuals, even under consistent task demands. However, our current task designs and statistics aren't conducive to measuring these influences of attention. In Chapter 4 I examine the statistical and theoretical biases that have led to our neglect in understanding these influences—influences that are likely the key to parsimony in the field and our path forward.

Conclusion

Our understanding of tactile localization has progressed dramatically in the past few decades, but we have recently reached an important turning point. How do we proceed with new evidence that seems to contradict old evidence, but at the same time cannot account for all of the existing results?

Chapters 2 and 3 of the present work provide novel behavioural evidence of factors that contribute to tactile localization that have been previously ignored. In Chapter 2 I examine how visual imagery influences performance on the tactile TOJ task, and how individual differences in visual imagery ability modulate its influence. In Chapter 3 I examine how the attentional set of the participant can influence performance on the tactile TOJ task, as well as provide evidence that existing results have been influenced by attention. In Chapter 4 I then provide a framework for thinking about tactile localization and the CHD that allows for the integration of the results of Chapters 2 and 3 with current thinking about the CHD, as well as ways to tackle new findings that suggest a critical re-evaluation of the field.

Although a paradigm shift and consideration of novel influences on tactile TOJ performance may seem to disrupt parsimony, in Chapter 4 I instead suggest that shifting our focus to consider these influences actually allows for cohesion across the field. However, this will require systematic unlearning of implicit theoretical biases, and a switch to viewing tactile localization as a dynamic set of processes, rather than a static process.

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Chapter 2

Imagine Your Crossed Hands as Uncrossed: Visual Imagery Impacts the Crossed-Hands Deficit

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Summary

Successful interaction with our environment requires accurate tactile localization. Although we seem to localize tactile stimuli effortlessly, the processes underlying this ability are complex, as evidenced by the crossed hands deficit. The deficit results from the conflict between an internal reference frame, based in somatotopic coordinates, and an external reference frame, based in external spatial coordinates. Previous evidence in favour of the integration model employed manipulations to the external reference frame (e.g., blindfolding participants), which reduced the deficit by reducing conflict between the two reference frames. The present study extends this finding by asking blindfolded participants to visually imagine their crossed arms as uncrossed. This imagery manipulation further decreased the magnitude of the crossed hands deficit by bringing information in the two reference frames into alignment. This imagery manipulation differentially affected males and females, which was consistent with the previously observed sex difference in this effect: females tend to show a larger crossed hands deficit than males and females were more impacted by the imagery manipulation. Results are discussed in terms of the integration model of the crossed hands deficit.

Keywords: Crossed hands deficit, visual imagery, visuotactile

Introduction

Although we experience the world as a collection of discrete events and coherent objects, the sensory inputs used to create these experiences are vast in both number and type. Consider the simple act of swatting an unwanted mosquito from your arm. To do so successfully, you must accurately localize where you feel the mosquito. This may seem like a simple feat informed solely by tactile information, but many other sources of information impact performance. Visual information has a particularly powerful effect on localization of tactile stimuli—just think about how much easier it is to swat the mosquito when you can see it, rather than just feel it. The independent pieces of tactile and visual information are combined by the human sensory system (see Ernst & Bültoff, 2004; Stein & Meredith, 1993 for comprehensive reviews). In the present experiments, we conceptually ask whether imagining the mosquito's location in your mind's eye enhances your ability to swat that mosquito.

Accurate tactile localization—to swat the mosquito—requires information provided by two separate reference frames (Badde & Heed, 2016; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001; see Heed & Azañón, 2014 for a review). The internal reference frame localizes touch based solely on the locus of tactile stimulation on the body. In contrast, the external reference frame localizes touch within the environmental context surrounding the body. When the limbs are in their expected position, such as when the left hand is in the left side of space, the external and internal reference frames provide consistent information. However, when the limbs are moved from their expected position, such as when the left hand is crossed over to the right side of space, information in the external reference frame conflicts with that in the internal reference frame. Under such circumstances, integration across the reference frames may fail completely, causing localization performance to suffer (Badde & Heed, 2016; Shore, Spry, & Spence, 2002). Probing this crossed hands deficit provides a fruitful avenue to understand these reference frames.

The tactile temporal order judgment (TOJ) task provides an excellent measure of this crossed hands deficit (Badde, Heed, & Röder, 2014; Badde, Heed, & Röder, 2016; Badde, Röder, & Heed, 2019; Cadieux et al., 2010; Cadieux & Shore, 2013; Craig & Belser, 2006; Kóbor et al., 2006; Röder, Rösler, & Spence, 2004; Shore, Spry, & Spence, 2002; Unwalla, Kearney, & Shore, 2020; Wada, Yamamoto, & Kitazawa, 2004; Yamamoto & Kitazawa, 2001; see Heed & Azañón, 2014 for a review). In this task, participants receive two vibrations separated by a short interval, one to each hand, and are instructed to identify which hand vibrated first. When the hands are uncrossed, participants perform near ceiling, presumably because information in the two reference frames is congruent. When participants are asked to cross their hands over the body midline, such that the right hand is in the left side of space and vice versa, participants' accuracy on the task significantly decreases—presumably because information in the two reference frames conflicts, making tactile localization slow and inaccurate. This task provides a reliable index of the crossed hands deficit (Unwalla, Kearney, & Shore, 2020) and can be used to extract the weights applied to the two reference frames (Badde, Heed, & Roder, 2016; Unwalla, Goldreich, & Shore, in press).

Although the internal reference frame is easily defined as a mapping of the skin surface, the external reference frame is more difficult to define. What is clear is that this external reference frame allows us to interact with the world around us. By combining signals from different senses, each of which capture information about the external world, one coherent representation can be generated and used for action. Given this purpose of the external reference frame, it is not surprising that vision contributes heavily to its construction. Evidence from a variety of perceptual studies demonstrates that vision provides reliable information about spatial attributes of the environment (Welch & Warren, 1986). Importantly, evidence from the crossed hands deficit literature seems to point to the same conclusion when investigating tactile localization and the crossed hands deficit more specifically (Azañón, Camacho, Morales, & Longo, 2018; Azañón & Soto-Faraco, 2007; Cadieux & Shore, 2013; Kóbor et al., 2006; Röder, Rösler, &, Spence, 2004; Crollen et al., 2019).

The impact of vision on the crossed-hands deficit can be observed by looking developmentally. Those born blind have no deficit; in contrast, late blind individuals obtain a normal crossed hands deficit (Röder, Rösler, &, Spence, 2004; Crollen et al., 2019). Interestingly, patients born blind (from congenital cataracts) who regain their sight early in life (from cataract removal) produce a crossed hands deficit, whereas individuals whose cataracts are not removed until very late in life perform like congenitally blind individuals (Azañón, Camacho, Morales, & Longo, 2018). Together, these studies suggest that experience with visual information in childhood has a formative effect on the construction of the external reference frame.

Importantly, typically developed adults also show significant influences of visual information on the crossed hands deficit. Blindfolding (Cadieux & Shore, 2013; Unwalla, Cadieux, & Shore, in press) or completing the task with the hands crossed behind the back (where participants have no visual representation of their hands in space; Kóbor et al., 2006), produces a smaller crossed hands deficit. Similarly, viewing rubber hands in an uncrossed posture while the hands are crossed decreases the magnitude of the crossed hands deficit (Azañón & Soto-Faraco, 2007). All of these data support the role of vision in establishing the external reference frame: a visual image of the world contributes to a precise and reliable external reference frame.

Even without visual input, most observers can create a mental image of the external world simply by imagining it. This visual imagery provides a structured perceptual phenomenon that impacts participant responding—a perceptual phenomenon that we might consider a weak form of visual perception (see Pearson et al., 2015 for a review). Several techniques support an identity relation between imagined representations and those produced from optical stimulation (see Lewis, O'Reilly, Khuu, & Pearson, 2013; Mohr et al., 2009; Winawer, Huk, & Boroditsky, 2009 for select examples, see Pearson et al., 2015 for a review), with similar brain areas activated during visual imagery and visual perception (see Pearson et al., 2015 for a review) and similar features encoded when imagining and perceiving (Thirion et al., 2006; Slotnick et al., 2005). Of specific interest to the present study, there is even evidence that visual imagery is required to engage in tactile perception of certain features (Sathian, & Zangaladze, 2001).

Given the relation between imagery and perception and the impact of visual perception on the crossed hands deficit, we predict that visual imagery may impact the crossed hands deficit—specifically, we may be able to use visual imagery instructions to reduce the deficit. It is also interesting to note that both visual imagery ability (Isaac & Marks, 1994; Kosslyn et al., 1984) and the crossed hands deficit (Cadieux et al., 2010; Unwalla et al., 2020) show large individual differences. It may be possible that imagery ability accounts for some of the individual differences in the crossed-hands deficit. The primary goal for the present work was to examine the question, can visual imagery reduce the crossed hands deficit? We also provide an initial examination of whether visual imagery ability can account for some of the individual differences seen in the crossed hands deficit.

Scope of the present study

The present study examined whether visual imagery influences the crossed hands deficit. Across two experiments, participants completed three blocks of trials in a tactile TOJ task while blindfolded. The first two blocks replicated previous crossed hands deficit studies: one block of trials with the hands uncrossed and a second block with the hands crossed. In the third block, participants were asked to visually imagine their crossed hands as uncrossed. Experiment two included a control group who did not engage in visual imagery in the third block to control for practice effects (see Craig & Belser, 2006; Azañón, Stenner, Cardini, & Haggard, 2015).

We derived two predictions. First, the magnitude of the crossed hands deficit would be significantly smaller when participants visually imagined their hands uncrossed. Second, individual differences in imagery ability would both affect the crossed hands deficit and modulate the impact of imagery on the deficit. Specifically, individuals with enhanced facets of imagery ability would demonstrate a larger baseline crossed hands deficit when blindfolded. Even without any imagery instructions, these participants may vividly (as measured by the Vividness of Visual Imagery Questionnaire (VVIQ) used in Experiment 1) or spontaneously (as indexed by the Spontaneous Use of Imagery Questionnaire (SUIS) used in Experiment 2) visually imagine their crossed hands as crossed, producing more conflict with the internal reference frame. However, these participants should, for the same reason, be better able to successfully imagine their crossed hands as uncrossed, and consequently should show a greater reduction in the deficit.

To address our second prediction, we used a variety of visual imagery measurements. We administered two commonly used imagery self-report measures: the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973, Experiment 1), which evaluates the vividness of participants' visual images, and the Spontaneous use of Visual Imagery Scale (SUIS; Kosslyn et al., 1998, Experiment 2), which evaluates the likelihood with which participants engage in visual images when they are not explicitly asked to do so. The goal of using these two self-report measures was to assess various potential indices of individual differences in visual imagery ability (see the General Discussion concerning limitations of these two measures).

However, we recognize the difficulty associated with measuring visual imagery ability using traditional self-report survey measures (see McAvinue & Robertson, 2007 for a review), as well as the multi-faceted nature of visual imagery that is not captured in any individual scale (Kosslyn et al., 1984). Consequently, we anticipated that individual differences in visual imagery ability as related to the current task would be difficult to assess using only these two self-report measures. To combat this, we introduced a novel measurement tool in Experiment 1. On a small subset of trials, we presented auditory probes on the left and right side of space and asked participants to respond with the hand imagined on the same side of space as the tone (recall, the participants are blindfolded). This allowed us to examine where participants perceived their hands, relative to an external stimulus.

Our index of the crossed-hands deficit was the proportion correct difference score (PCD; Cadieux et al., 2010). We expect smaller PCD scores when participants imagine their hands as uncrossed. Second, we expect people with high vividness or spontaneous use of imagery ability to have larger baseline PCD scores and be better able to use the imagery instructions to reduce this score. The larger baseline crossed hands deficit when blindfolded for people with enhanced imagery ability, as measured by the VVIQ, SUIS, or our novel auditory probe measure, stems from their vivid or spontaneous use of imagery to imagine their crossed hands as crossed (note that VVIQ and SUIS scores are correlated, suggesting that an individual who has vivid imagery may be more likely to spontaneously imagine and vice versa; Nelis et al., 2019), which produces greater conflict with the internal reference frame. However, these participants should be more successful in imagining their crossed hands as uncrossed for the same reasons, which should reduce the deficit. Although preliminary in nature, these explorations into potential effects of visual imagery on tactile localization performance present an exciting new framework within which to examine the crossed hands deficit.

Experiment 1

Method

Participants

Eighty undergraduate students (40 males, M_{Age}=19.1, SD_{Age}=1.61; 40 females, M_{Age}=18.6, SD_{Age}=1.17) from the McMaster University participant pool completed the experiment for course credit. The sample sizes for both experiments were chosen to balance the needs of our conservative expectation of a medium effect size, given the instructional nature of our manipulation, and the sample size required to detect a correlation between the visual imagery measures and crossed hands deficit performance.

All participants were right-handed, had normal or corrected-to-normal vision, and provided informed consent prior to participating. All research was approved by the McMaster Research Ethics Board and conformed to the tri-council policy on research with human participants (Canada).

Data from three participants were excluded from the following analyses who had no crossed hands deficit in block two (no imagery) of the experiment because we cannot measure a reduction in an effect that is not present. This left 77 participants (39 females; 38 males).

Apparatus & stimuli

Participants held two cubes, one in each hand, while sitting at a table 73.7 cm high. The vibrotactile stimuli were created within the cubes via an Oticon-A (100 Ohm) bone-conduction vibrator (driven by a 250 Hz amplified sinusoidal signal) mounted onto a response button. The cubes had a plexiglass top with a 2 cm hole to allow for direct contact between the vibrator and the thumb. One cube was held in each hand. All participants experienced the same amplitude of vibrotactile stimulus, which was deemed to be suprathreshold by the experimenters.

On each trial, participants received two 20 ms vibrotactile stimulations, one to each thumb. The vibrations were presented at one of eight randomly selected stimulus onset asynchronies (SOAs) of ±400 ms, ±200 ms, ±100 ms, and ±50 ms (where – signifies that the left hand was stimulated first, and + that the right hand was stimulated first). Each SOA was experienced equally often in each sub-block of trials, and consequently, across the entire experiment. The vibrotactile stimuli were controlled by a set of reed-relays connected to the parallel port of a Dell Dimension 8250 computer running MATLAB R2011b software (The MathWorks, Inc). For trials completed in the crossed posture, the hands were crossed right over left, with the right arm resting on an inclined plank to ensure that the hands did not touch.

White noise was presented over headphones at a volume that masked any auditory signals produced by the vibrations, but was also comfortable for the observer. Two speakers were placed 76 cm in front of the participant and 51 cm to the right and left of the midline of the participant. Auditory beeps were presented from the speakers at a volume judged subjectively by the experimenter to be audible over the white noise. Beep trials were presented in a pseudo-random order within each sub-block of 68 trials. One beep trial occurred in each quartile of each sub-block: specifically, a beep could occur up to 6 trials before or after trials 9, 25, 41 or 57.

We administered the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) using the reversed rating scale proposed by McKelvie (1995) and used in the VVIQ2 (Marks, 1995).

Design & procedure

Participants held the stimulus cubes in each hand with their hands placed 18 cm apart, resting on the table. They were blindfolded for the duration of the experiment and listened to white noise on headphones.

On each trial, either two consecutive vibrations were presented, one to each hand, or one auditory beep was presented from the left or right speaker. On vibration trials, participants responded by pressing the button in the hand that vibrated first. On beep trials, participants responded by pressing the button in the hand perceived on the same side of space as the location of the beep (i.e., regardless of hand posture, the auditory beep was to be coded in external space). Regardless of trial type, participants had three seconds to respond, after which the trial timed-out: both cubes would vibrate simultaneously three times and participants were instructed to press both buttons simultaneously to continue the experiment. Time-out trials were removed from all analyses and accounted for .002% of all trials.

Before beginning the experiment, participants completed 2 practice sets of 20 trials each (16 vibration trials and 4 beep trials). Participants' hands were uncrossed for the first set of practice trials. For the second practice block, the hands were crossed. Following the practice blocks, participants completed 4 experimental sub-blocks of 68 trials (64 vibration trials and 4 beep trials) with their hands uncrossed, followed by 4 sub-blocks with the hands crossed. Participants were given a short break between each block. No feedback about tactile TOJ or auditory probe performance was provided in either the practice or experimental blocks.

Following these 8 sub-blocks (4 uncrossed and 4 crossed), participants were instructed that they would complete 4 more sub-blocks of trials with their hands crossed, but were asked to visually imagine their hands uncrossed on every trial. They were instructed to respond to vibration trials exactly as before, but to now respond to the beep trials with the hand that they *felt* was on the same side of the table as the location of the beep. For example, if a beep came from the right side of space and their visual imagery successfully led them to feel that their right hand was in the right side of space (even though it was actually in the left side of space), the participant would press the button in their right hand. In contrast, if their visual imagery failed, they would feel that their left hand was in the right side of space (given that their hands were crossed, the left hand was actually in the right side of space), and would, thus, respond by pressing the button in their left hand.

To practice the imagery instructions, participants completed one set of practice trials (16 vibration trials, 4 beep trials) and then completed 4 sub-blocks of experimental trials (64 vibration trials, 4 beep trials), all with their hands crossed, while imagining their hands uncrossed. As before, no feedback was provided. After each experimental sub-block, participants were asked i) the percentage of trials on which they successfully imagined their hands crossed and ii) how vivid their imagery was in the previous block on a scale from 1 to 5, with 5 being as vivid as actual vision.

Lastly, participants completed the VVIQ (Marks, 1973) as a self-report measure of their imagery ability.

Results

We first conducted a multiple regression analysis that included our three measures of imagery ability (the percent of trials participants judged that they were successfully imagining, participants' vividness rating (1–5), and a median split of scores on the VVIQ, which resulted in high and low imagery groups) as predictors and average PCD scores as the outcome variable. The model that included all three measures did not account for any more variance than the model that only included VVIQ, $p=.228$. As such, only VVIQ was used in subsequent analyses.

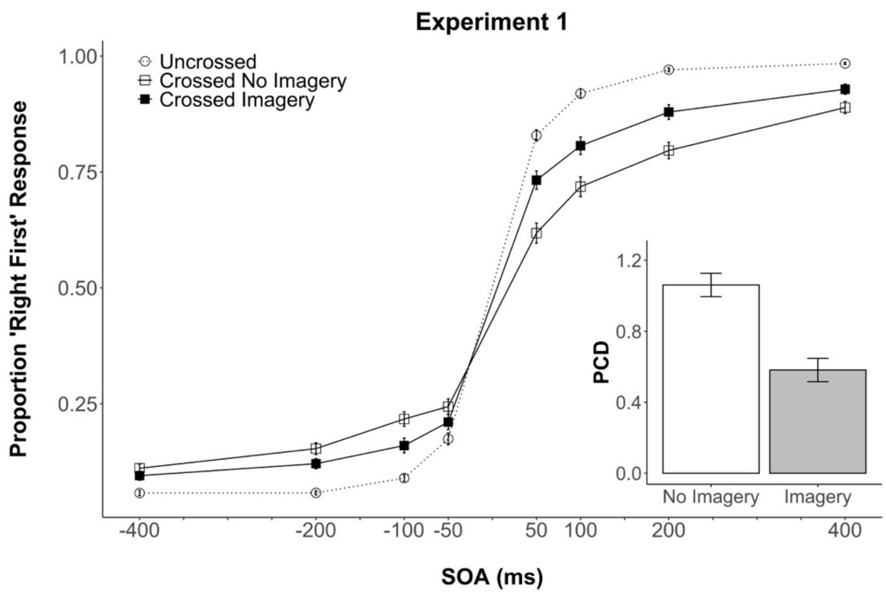

Figure 1. Proportion right first response and PCD collapsed across participants for Experiment 1 ($N=77$). Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Tactile TOJ performance

Two proportion correct difference (PCD) scores were calculated for each participant. PCD scores were calculated by computing proportion correct responses at each SOA and then summing the difference between crossed and uncrossed performance at all SOAs (see Cadieux et al., 2010). Uncrossed performance was compared to performance when the hands were crossed and participants did not engage in imagery for the no imagery PCD score, and compared to performance when the hands were crossed and participants were engaging in imagery for the imagery PCD score.

Resulting PCD scores were submitted to a 2x2x2 mixed factor ANOVA that treated imagery (no imagery/imagery) as a within-subjects factor, and sex (male/female) and VVIQ (low/high) as between-subjects factors. Hyuhn-Feldt corrected degrees of freedom and *p*-values are reported when appropriate throughout the present work[1].

PCD scores were higher when participants did not engage in imagery (1.06) than when participants imagined their crossed hands as uncrossed (0.58; $F(1,73)=28.18$, $p<.001$, $\eta p^2=.278$; see Fig. 1). This imagery effect was qualified by an interaction with sex, $F(1,73)=6.07$, $p=.016$, $\eta p^2=.084$. Imagery PCD scores were significantly smaller than no imagery PCD scores for both females, $t(38)=4.91$, $p<.001$, $d=.896$, and males, $t(37)=2.31$, $p=.027$, $d=.320$, but the difference between imagery and no imagery PCD scores was larger for females (difference = .72) than for males, (difference = .24; see Fig. 2). PCD scores were significantly different from zero in both the no imagery and imagery conditions ($t(76)=11.97$, $p<.001$, $d=1.36$, and $t(76)=6.62$, $p<.001$, $d=.76$ respectively, see Fig. 1).

[1]To address a potential concern of decreased power associated with median split analyses, we conducted an ANCOVA that treated VVIQ scores as a covariate, and treated imagery (no imagery/imagery) as a within-subjects factor, and sex (male/female) as a between-subjects factor. This analysis revealed no significant effect of the VVIQ covariate, $F=1.32$, $p=.254$, nor its interactions, all *p*s>.8.

There were no significant correlations between overall VVIQ score and PCD (all *p*s>.2).

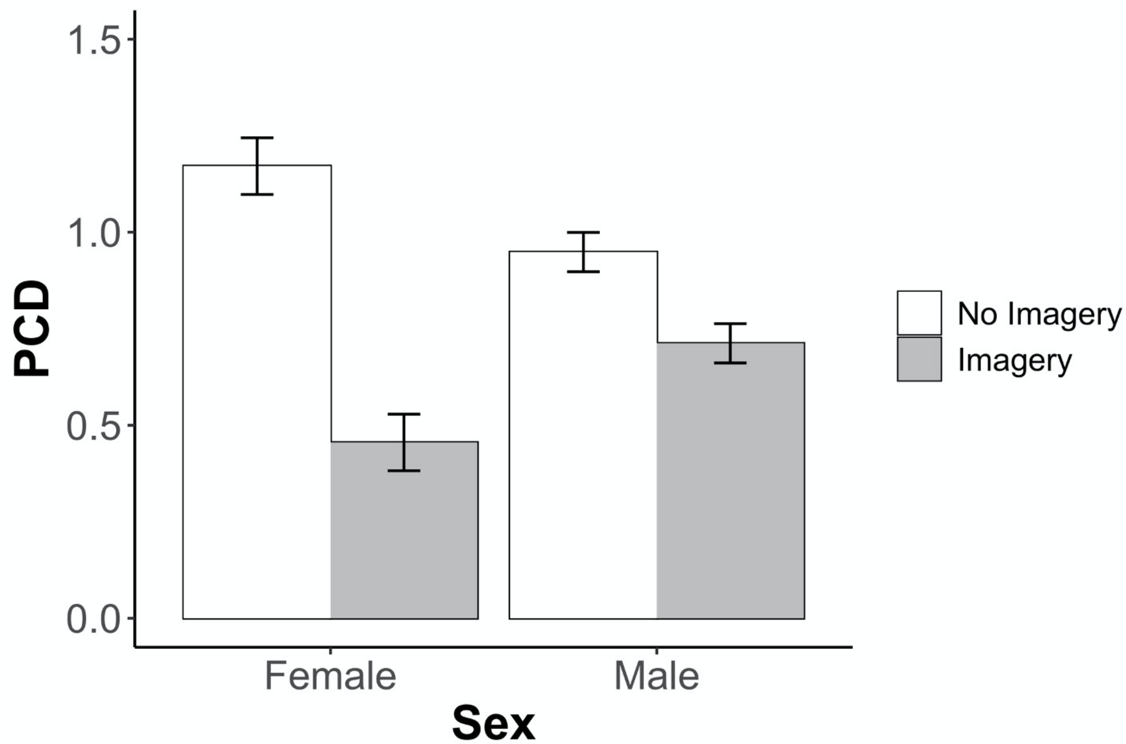

Figure 2. PCD scores from Experiment 1 separated by Sex and Imagery. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Auditory probe responses

Auditory probe localization score

We computed a score based on the relation between the side of space stimulated and imagined hand posture. Because there were no mental imagery instructions in the uncrossed and crossed no imagery blocks, responses were coded as 1 if the participant responded with the hand that was in the same side of space as the beep and a 0 if they responded with the hand on the opposite side. In the crossed imagery condition, this relation was reversed since they were instructed to imagine their hands as uncrossed. To be clear, for the purposes of computing this score we assumed that they correctly imagined their crossed hands as uncrossed. For example, a right hand response to a beep from the *right* speaker would be coded as 1 even though the hand was on the left side of space: the participant should be imagining the hand as being in the *right* side of space. For a summary of the auditory probe localization results see Table 1.

Expt 1: Auditory Probe Localization Results

Posture	*Score*	*RT*
Uncrossed	1.00 (0.02)	661 (95)
Crossed No Imagery	0.92 (0.15)	850 (162)
Crossed with Imagery	0.82 (0.26)	872 (214)

Table 1. Auditory probe localization score and auditory probe localization RT (in ms) collapsed across participants. Brackets indicate *SEM* with between-subjects variability removed (Morey, 2008).

Auditory probe localization scores were submitted to a 3x2x2 mixed factor ANOVA that treated posture (uncrossed/crossed no imagery/crossed imagery) as a within-subjects factor, and sex (male/female) and VVIQ (low/high) as between-subjects factors (see Table 1 for a summary of the results). Differences between the three blocks were compared with a t-test based on our *a priori* interest in this comparison.

Posture significantly impacted performance, $F(1.29, 94.46)=19.91$, $p<.001$, $\eta p^2=.214$, (Mauchly's W=.44, $p<.001$). The uncrossed posture produced higher scores than in the crossed posture with no imagery, $t(76)=4.38$, $p<.001$, $d=.693$, and crossed posture with imagery instructions, $t(76)=6.01$, $p<.001$, $d=.970$. Scores were lower in the crossed imagery posture than in the crossed no imagery posture, $t(76)=2.90$, $p=.005$, $d=.508$. No other main effects or interactions were significant, all *p*s>.2.

Relation between auditory probe localization and PCD scores

Auditory probe localization scores in the second block (crossed hands, no imagery) were not correlated with the PCD score from that block, $r=.161$, $p=.161$ (see left panel of Fig. 3). In contrast, auditory probe localization scores in the third block (crossed hands with imagery instruction) were negatively correlated with PCD score from that block, $r=-.409$, $p<.001$ (see right panel of Fig. 3). Removal of individuals whose auditory probe localization scores were more than ±2 standard deviations from the mean (3 individuals removed in no imagery, 6 in imagery) resulted in the same pattern of performance (no imagery, $r=.301$, $p=.009$; imagery, $r=-.351$, $p=.003$).

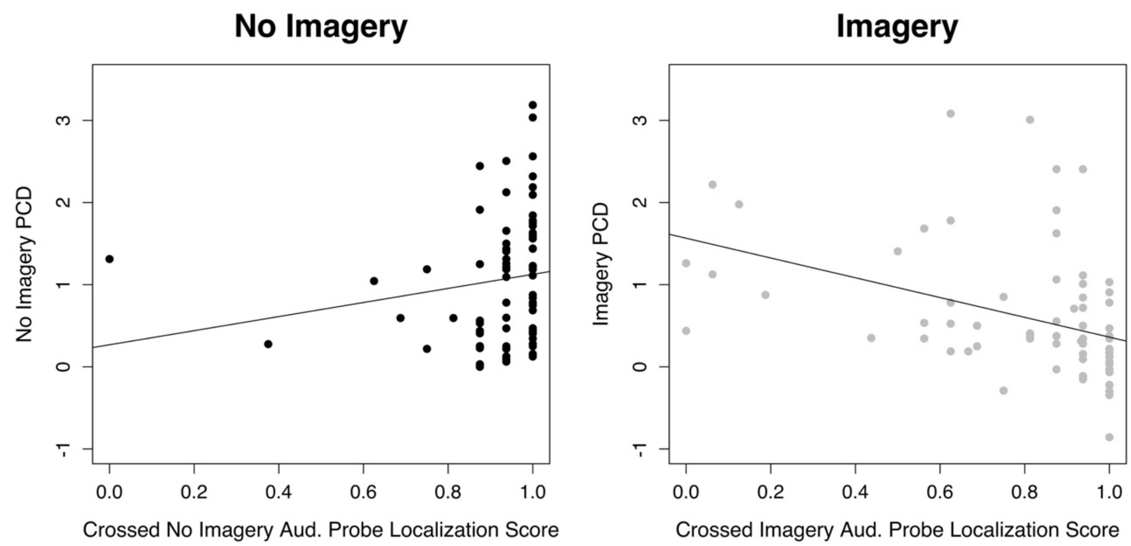

Figure 3. Relation between PCD scores and auditory probe localization scores in the No Imagery (left panel) and Imagery (right panel) conditions.

Reaction time

Average reaction times (RTs) were calculated for each participant for each posture (uncrossed/crossed no imagery/crossed imagery) by averaging response times for trials in which the response matched the desired mental image for the given posture (i.e., the trials that were coded as 1 in the performance analysis above). If no correct response was given for a cell, the associated participant was removed from the RT analyses, which resulted in the removal of 3 participants. See Table 1 for a summary of the auditory probe RT results.

Auditory probe RTs were submitted to a 3x2x2 mixed factor ANOVA that treated posture (uncrossed/crossed no imagery/crossed imagery) as a within-subjects factor, and sex (male/female) and VVIQ (low/high) as between-subjects factors. Hyuhn-Feldt corrected degrees of freedom and *p*-values are reported when appropriate. Differences between the three blocks were compared with a t-test based on our *a priori* interest in this comparison.

The effect of block was significant, $F(1.48,105.22)=52.36$, $p<.001$, $\eta p^2=.424$ (Mauchly's W=.63 $p<.001$). Responses were significantly faster in the uncrossed posture than in the crossed no imagery, $t(73)=12.9$, $p<.001$, $d=1.29$, and crossed imagery postures, $t(73)=8.78$, $p<.001$, $d=1.20$. Response times did not differ between the crossed no imagery and crossed imagery postures ($p=.463$). There was a trend, $F(1,71)=3.06$, $p=.08$, $d=.36$, toward females ($M_{RT=}.77$) being faster than males ($M_{RT=}.81$). No other main effects or interactions were significant, all *p*s>.1.

Discussion

Asking participants to imagine their crossed hands as uncrossed significantly decreased the magnitude of the crossed hands deficit. This result provides initial evidence that visual imagery can be used to bring information in the external reference frame back into alignment with information in the internal reference frame, reducing conflict and significantly decreasing the size of the crossed hands deficit.

Interestingly, females benefitted more from the visual imagery than males. In line with previous findings (Cadieux et al., 2010), females had a larger crossed hands deficit than males in the no imagery block. The larger deficit with greater variability for females was previously attributed to multiple ineffective strategies compared to males who appear to adopt one effective strategy (Cadieux et al., 2010). Females also demonstrated a smaller crossed hands deficit than males in the imagery block. This indicates that being given visual imagery instructions may have provided an effective strategy that benefited females more than males, because males already rely on an effective strategy (Cadieux et al., 2010).

VVIQ scores did not account for any patterns in PCD scores. However, previous work has noted the difficulty associated with measuring visual imagery using self-report measures (McAvinue & Robertson, 2007). In addition, the multi-faceted nature of visual imagery (Kosslyn et al., 1984) suggests that the aspect of visual imagery tapped by the VVIQ may not be not the visual imagery skill required to complete the present task (see General Discussion for a detailed discussion of the limitations of the VVIQ).

In contrast, there was a significant negative correlation between crossed imagery auditory probe localization scores and imagery PCD scores, suggesting that individuals who are better able to imagine their crossed hands as uncrossed (as indexed by responding to the location of the auditory probe as though their hands were actually uncrossed; i.e., the auditory probe localization score) have a smaller crossed hands deficit when asked to imagine their crossed hands as uncrossed. Interestingly, there was a numerical trend toward a positive correlation between crossed no imagery auditory probe localization scores and no imagery PCD, suggesting that those with better knowledge about where their hands are in space (as indexed by localization responses to the auditory probe in the no imagery condition) may have a larger crossed hands deficit, even when blindfolded. It is possible that this knowledge about where the hands are in space when blindfolded (which was required to accurately respond to the location of the auditory probe) was informed by visual imagery, but future work is required to answer this question. Importantly, reaction times to auditory probes did not differ between the crossed no imagery and crossed imagery postures, which suggests that participants responded to the probes based on their visual image. If participants had instead algorithmically determined the side of space that they knew the experimenter *hoped* they would respond with, reaction times would have been slower in the crossed imagery block of trials than in the crossed no imagery block.

It is important to note that although PCD scores are low overall for Experiment 1, this is because participants were blindfolded across all blocks. Blindfolding has been shown to decrease the magnitude of the crossed hands deficit, and the PCD scores observed in Experiment 1 are in line with previously published blindfolded PCD scores (PCD = ~1; Cadieux & Shore, 2013).

Experiment 2

Experiment 1 serves as initial evidence that visual imagery can influence the crossed hands deficit. In Experiment 2 we replicate the imagery manipulation of Experiment 1 and added a critical control group who were not given the imagery instructions. The possibility for a practice effect to influence our result in Experiment 1 was introduced by the order in which participants experienced the different imagery conditions. Participants always completed the crossed imagery blocks last to ensure that the uncrossed and crossed postures were not influenced by the imagery instructions.

Given that significant practice effects have been observed in the crossed hands deficit task (Azañón et al., 2015; Craig & Belser, 2006), the significantly smaller imagery PCD could possibly be accounted for by participants simply getting better at the task.

Rather than use the VVIQ, we administered the Spontaneous use of Imagery Scale (SUIS; Kosslyn et al., 1998). Given our prediction that individuals who spontaneously visually imagine their hands when blindfolded should produce a larger baseline crossed hands deficit, as well as the trend toward a positive correlation between crossed auditory probe localization scores and no imagery PCD in Experiment 1, we hoped this measure would better capture this aspect of visual imagery.

Method

Participants

One hundred undergraduate students (50 males) who met the same criteria as those in Experiment 1 completed the experiment for course credit. As in the analysis of Experiment 1, participants with a PCD score less than 0 in block two were removed from the analyses, resulting in the removal of 3 females and 1 male from the practice condition, and 4 females and 4 males from the imagery condition. We then equated sample size across the between subjects measures of condition and sex by including data in order of data collection (oldest to newest) until twenty subjects in each cell was reached. This resulted in removal of an additional 2 females and 4 males from the practice condition and 1 female and 1 male from the imagery condition, for a total of eighty participants (40 males), with 40 participants in both the imagery (20 males; M_{Age}=19.3, SD_{Age}=1.84) and practice group (20 males; M_{Age}=19.6, SD_{Age}=4.7).

Apparatus & stimuli

The apparatus was the same as Experiment 1; no auditory probes were presented in Experiment 2.

Design & procedure

The design and procedure were the same as Experiment 1 except for the following changes. We did not ask for percent imagine ratings or average vividness ratings after each block as these accounted for no variance in Experiment 1. No auditory probes were presented to reduce instructional load. This reduced the number of trials per block to 16 trials for the practice blocks and 64 trials for the experimental sub-blocks.

Instruction was manipulated between-subjects, with half of the participants given imagery instructions and the other half given practice instructions. Participants given imagery instructions completed the task as in Experiment 1. Participants given practice instructions first completed four blocks of uncrossed trials, followed by four blocks of crossed trials, as in Experiment 1. Participants then completed four additional blocks with their hands crossed, but did not receive instructions to engage in visual imagery. Instead they were told to continue completing the trials as they had in the previous four crossed hands blocks. Participants given practice instructions still completed a practice block of 16 trials before the final four blocks of crossed hands trials, but were simply told that the practice was to refresh their performance. This was done to ensure that participants in both instruction conditions completed the same number of trials.

The SUIS (Kosslyn et al., 1998) was administered after completion of all blocks.

Results

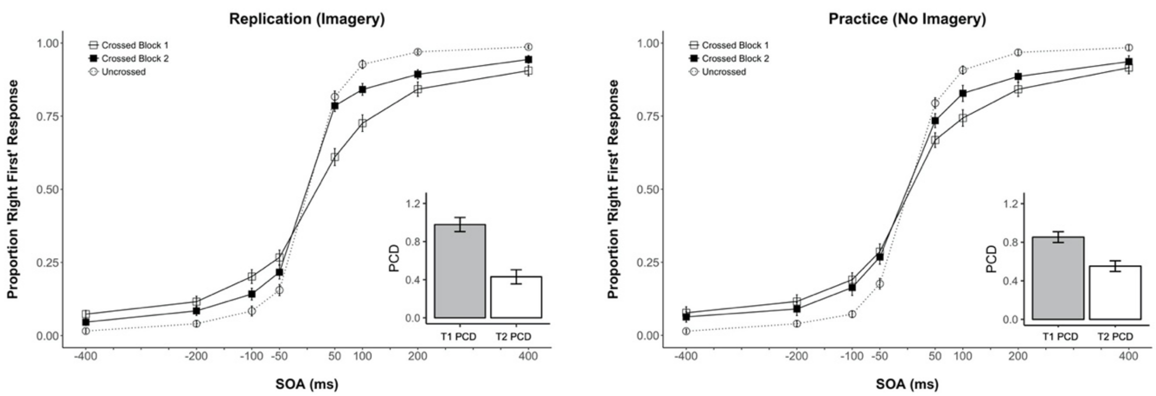

Figure 4. Proportion right first response and PCD collapsed across participants for the imagery (left) and practice (right) groups of Experiment 2 (*n*=40). Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Tactile TOJ performance

PCD score calculation

PCD scores were calculated the same as in Experiment 1. However, we refer to the two proportion correct difference (PCD) scores calculated for each participant as T1 PCD and T2 PCD (signifying time 1 and time 2 respectively). For the imagery group, T1 PCD scores reflect performance with no imagery instructions, and T2 PCD scores reflect performance with imagery instructions. For the practice group, T1 PCD scores reflect performance on the first block of crossed trials, and T2 PCD scores reflect on the second block of crossed trials.

Ensuring equivalent baseline performance

Baseline performance across the two groups (i.e., T1 PCD) was not significantly different, $t(78)=.68$, p = 0.499. This was confirmed with a bootstrap analysis with 9999 samples conducted with the wBoot package in R (Weiss, 2016): 95% confidence interval for between-groups difference in T1 PCD = (-0.2385, 0.4743), $p=.495$).

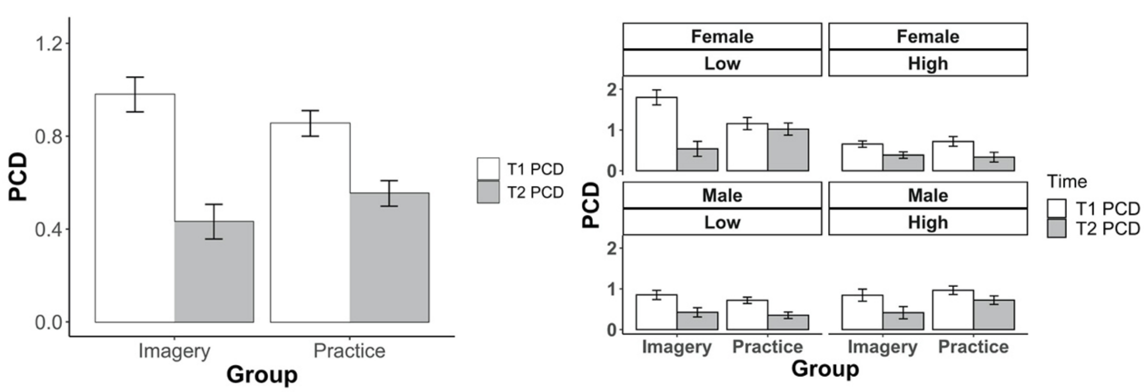

Figure 5. PCD scores for Experiment 2. Left Panel: PCD scores separated by group (Imagery/Practice) and time (T1 CHD/T2 CHD). Right Panel: PCD scores further

separated by Sex (Female/Male) and SUIS median split (High/Low). Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Results

PCD scores were submitted to a 2x2x2 mixed factor ANOVA that treated time (T1 PCD/T2 PCD) as a within-subjects factor, and group (imagery/practice), sex (male/female), and SUIS median split (low/high; calculated by performing a median split on SUIS scores across all participants) as between-subjects factors.

There was a significant four-way interaction between time, group, sex, and SUIS median split, $F(1,72)=7.63$, $p=.007$, $\eta p^2=.096$ (see right panel of Fig. 5). We discuss this result by breaking down the significant lower-order interactions in turn below, beginning with the two-way interaction between group and time, $F(1,72)=6.47$, $p=.013$, $\eta p^2=.082$, which was qualified by a three-way interaction with SUIS median split, $F(1,72)=5.11$, $p=.027$, $\eta p^2=.066$, which was further qualified by a the four-way interaction with sex interaction described above. We will discuss each of these lower order interactions in turn before finally discussing the four-way interaction.

To determine whether the result of Experiment 1 was merely a practice effect, we were most interested in the significant interaction between group and time (see left panel of Fig. 5). Although the effect of time was significant for both the practice group, $t(39)=3.86$, $p<.001$, $d=.361$, and the imagery group, $t(39)=5.20$, $p<.001$, $d=.763$, the reduction in PCD scores observed across time was larger in the imagery group (difference=.548) than in the practice group (difference=.301; see left panel of Fig. 5).

This group by time interaction was qualified by a three-way interaction involving SUIS median split. This three-way interaction was driven by the fact that the effect of time only differed between groups for individuals with low SUIS scores, $F(1,38)=5.80$, $p=.021$, $\eta p^2=.096$, not those with high SUIS scores, $p=.977$.

However, this was further qualified by a significant 4-way interaction involving sex (see right panel of Fig. 5). The three-way interaction between group, time, and SUIS median split discussed in the previous paragraph was only significant for females, $F(1,36)=10.81$, $p=.002$, $\eta p^2=.231$, but not for males, $p=.701$.

There were no significant correlations between overall SUIS score and PCD (all ps>.6).

Discussion

The results of Experiment 2 demonstrate that the effect of visual imagery observed in Experiment 1 cannot be explained as solely a practice effect. Although we observed a significant practice effect in Experiment 2 (with PCD scores lower in T2 PCD than in T1 PCD for the practice group), the difference between T1 PCD and T2 PCD performance in the imagery group was significantly larger than that observed in the practice group, indicating a benefit to performance beyond that afforded by practice.

The results of Experiment 2 highlight that the benefit of imagery occurs only in a specific subset of the population. In Experiment 1, the benefit of imagery was larger for females than for males; in Experiment 2 we found an even more nuanced effect of individual differences. Specifically, we found that only females with a low SUIS score demonstrated an imagery benefit beyond the benefit afforded by a simple practice effect.

In contrast, females with a high SUIS score, and males with either a low or high SUIS score did not demonstrate a significant reduction in PCD score in the imagery condition larger than that in the practice condition. To account for this pattern, we propose that females with low SUIS scores are the least likely out of all participants in the present work to have a pre-existing strategy to complete the TOJ task—first because females are less likely to have a set spatial task strategy (Cadieux et al., 2010), and second because they have a low SUIS score, which means that they are less likely to spontaneously engage in an imagery strategy (see General Discussion). However, it is important to note that cell size was quite small and not equal when separated by group, sex, and SUIS median split (*n*=~10), and, thus, future work must examine the reliability of this effect.

Experiment 2 provides additional evidence that individual differences influence the benefit of imagery on the crossed hands deficit, but it is important to further examine whether males and high SUIS females benefit from visually imagining the hands as uncrossed when an appropriate sample size is used to address this question. Nonetheless this result provides interesting support for the role of individual differences in the magnitude of the crossed hands deficit.

General Discussion

The goals of the present study were two-fold. First, we aimed to determine whether engaging in visual imagery could decrease the magnitude of the crossed hands deficit. Second, we provided an initial exploration of whether individual differences in imagery ability contribute to the baseline crossed hands deficit (i.e., no imagery crossed hands deficit).

Visually imagining crossed hands as uncrossed

The answer to our first question is clear: visually imagining crossed hands as uncrossed decreases the magnitude of the crossed hands deficit. This presumably occurs because visually imagining the hands as uncrossed brings visual (imagery) information in the external reference frame back in line with somatotopic information in the internal reference frame. This reduces the conflict between the two reference frames, and consequently, reduces the magnitude of the crossed hands deficit. This is similar to a previously reported result in which viewing uncrossed rubber hands decreased the magnitude of the crossed hands deficit (Azanon & Soto-Faraco, 2007). The novel result here is that the visual image of uncrossed hands was generated internally by the participant rather than externally by rubber hands.

Female participants demonstrated this benefit more than did male participants; in Experiment 2, there was no benefit for male participants. Previous work on sex differences in the crossed hands deficit may help to explain the sex differences observed here. Specifically, Cadieux et al. (2010) found that females tend to exhibit a larger crossed hands deficit than males. Females are also more likely to engage different strategies across spatial tasks (specifically the crossed hands tactile TOJ task and the rodand-frame task), whereas males seem to engage a consistent and effective strategy across spatial tasks.

Given that females tend to perform less accurately on spatial tasks and do not appear to have a set strategy (Cadieux et al., 2010), it makes sense that they would benefit when given an instruction that aids in successful tactile TOJ task performance (i.e., to visually imagine their crossed hands as uncrossed). In contrast, males tend to perform accurately on the task without any outside intervention, and also tend to have an effective strategy for completing the TOJ task. Thus, males may be less likely, or even less able, to engage in uncrossed visual imagery as this strategy differs from their established strategy, leading to a small (Experiment 1) or absent (Experiment 2) benefit of visual imagery.

Visual imagery ability and the crossed hands deficit

The answer to our second question of whether imagery ability influences the magnitude of the crossed hands deficit is less clear. There was no correlation between the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) and PCD scores in the no imagery and imagery conditions of Experiment 1. Similarly, there was no correlation between the Spontaneous Use of Imagery Scale (SUIS; Kosslyn et al., 1998) and PCD scores for T1 PCD or T2 PCD of Experiment 2. These results may suggest that a participant's imagery ability does not predict the magnitude of the crossed hands deficit. However, it is important to note that visual imagery is multi-faceted and that no one measure can index an individual's overall imagery ability (Kosslyn et al., 1984). In addition, given the many facets of visual imagery ability, it is likely that the VVIQ and SUIS used in the present work did not tap into the facet of visual imagery required to engage in the imagery manipulation here. However, our novel auditory probe localization measure, along with considerations of the effect of sex, present an interesting way to view the effect of visual imagery ability on our observed results.

Sex, visual imagery, and the crossed hands deficit

Females with a low SUIS score in Experiment 2 significantly benefitted from the visual imagery instructions beyond a benefit afforded by a practice effect, whereas females with high SUIS scores did not (males, regardless of SUIS, did not benefit from engaging in imagery beyond a practice effect). This finding suggests that a participant's imagery ability, as measured by SUIS score, does influence the crossed hands deficit magnitude, but only when considered along with their sex (however, it is important to note the small cell size that results from dividing the data in this manner).

This idea is made even more compelling when considered using the strategy logic outlined to explain the sex difference discussed above. Specifically, females tend to not have an internally generated strategy at the outset of the task (Cadieux et al., 2010), and low SUIS individuals are unlikely to engage in visual imagery if not prompted to do so. Thus, the reduction in crossed hands deficit magnitude with visual imagery for low SUIS females can be explained as the result of providing a strategy to a group who initially does not have one. In contrast, participants who already have an internally generated strategy (i.e., males), or are likely to engage in visual imagery unprompted (i.e., high

SUIS) are less likely to benefit from the instruction, given their disposition at the outset of the experiment.

Whether the true mechanism underlying this result is actually low SUIS or a confounding variable not measured in the present study is yet to be determined, and is an interesting avenue for future research. Examining this possibility also leads to an interesting question of why imagery ability, as measured by the VVIQ did not have a similar effect on performance as imagery ability, as measured by the SUIS. Given the difficulty associated with measuring visual imagery ability (McAvinue & Robertson, 2007) as well as the multi-faceted nature of visual imagery (Kosslyn et al., 1984), it will be important for future research to examine individual differences in visual imagery ability and their relation to the crossed hands deficit with a more exhaustive battery of visual imagery measures than the ones presented here.

Auditory probe localization and visual imagery

Our novel auditory probe localization task used in Experiment 1 provides preliminary insight in how visual imagery ability may influence the crossed hands deficit. Because participants were asked to respond with the hand that was in the same side of space as the beep, knowledge about where the hands are is necessary to complete the auditory probe task. Visual imagery of the hands would aid in knowing where the hands are, and in the imagery condition, participants were asked to do precisely that. Thus, the negative correlation between crossed imagery auditory probe localization scores and the imagery PCD (see the right panel of Fig. 3) suggests that auditory probe localization scores can be used to measure how effectively participants are engaging in imagery, and that this imagery ability influences the magnitude of the crossed hands deficit.

Although preliminary in nature, the trend toward a positive correlation between crossed no imagery auditory probe localization scores and the no imagery PCD (see the left panel of Fig. 3) is equally, if not more interesting. This effect highlights an individual difference that may contribute to the magnitude of the basic no-imagery crossed hands deficit. This finding suggests that individuals who have better knowledge about where their hands are in space have a larger crossed hands deficit, which is similar to our initial prediction that individuals who are better at visual imagery should have a larger baseline crossed hands deficit. This correlation is somewhat unsurprising, given that information from the external world about where your hands are in space leads to a larger crossed hands deficit (see Cadieux & Shore, 2013; Kóbor et al., 2006; Röder, Rösler, &, Spence, 2004), so having better access to external reference frame information in the form of knowledge about where the hands are should lead to a larger crossed hands deficit. However, the potential for spontaneous visual imagery of the hands to be contributing to this positive trend is an exciting avenue for future research that can be explored with more exhaustive battery of established visual imagery measures and their relation to our novel auditory probe measure.

Individual differences in visual imagery and body posture representations

In the previous section we examined how visual imagery ability, as indexed by auditory probe localization score, predicts the magnitude of the crossed hands deficit in the present work. An interesting addition to our interpretation of this relation is to consider the recent finding that body side (i.e., the side of the body associated with the stimulated hand) and canonical body posture (e.g., that the right hand typically resides on the right side of the body) influence the crossed hands deficit (Badde et al., 2019). More specifically, it may be that for individuals who have a stronger internal representation of canonical body posture, or who have a stronger bias to consider body side information during tactile localization, have a more difficult time overriding these representations to visually imagine their limbs in different postures. Thus, visual imagery ability in the tactile TOJ task may be directly related to the strength with which body side and canonical body posture are represented for that individual.

Viewing the results in this way may also explain why the traditional indices of visual imagery ability used in the present work (i.e., VVIQ; SUIS) did not correlate with crossed hands deficit magnitude. These measures index vividness and spontaneity of visual imagery ability respectively, rather than visual imagery ability constrained by the body side and canonical body posture representations that influence the TOJ task used here. In contrast, the auditory probe task was embedded within the same block of trials as the TOJ task. Thus, it is likely that performance on the auditory probe task was constrained in the same way as the TOJ task. This similarity likely allowed auditory probe localization scores to tap into the visual imagery ability that influenced performance on the TOJ task; the traditional measures of visual imagery ability lacked this connection and so failed to measure the relation. This is in line with work by Kosslyn and colleagues, which has suggested that imagery ability is comprised of multiple components, which can ostensibly differ depending on the task (Kosslyn et al., 1984).

Linking visual imagery ability in the TOJ task to the constraints imposed by body side and canonical body posture (Badde et al., 2019) presents an exciting avenue for future research. However, further work is needed to unravel the relation between those results and the findings reported here. Their work analysed phantom sensations that represented a small proportion of trials (less than 10%). In addition, the legs could be crossed or uncrossed, as well as the hands. Previous work has found that task demands influence integration of the external reference frame, and consequently influence responding (Cadieux & Shore, 2013; Unwalla, Goldreich, & Shore, in press; Crollen et al., 2019), and it is therefore unclear if the results found using the hand and foot task (Badde et al., 2019) translate to the typical crossed tactile TOJ task used here. Similarly, further work is needed to examine the effects of sex (Cadieux et al., 2010) and handedness (Wada, Yamamoto, & Kitazawa, 2004) on the generalizability of their results. Despite the clarification needed on these points, the results of Badde et al. (2019) present an exciting avenue for future examinations of individual differences in the crossed hands deficit.

Conclusion

The present study found that visually imagining uncrossed hands as crossed decreases the magnitude of the crossed hands deficit. This finding adds to a growing literature that supports conflict between internal and external reference frames as the locus of the crossed hands deficit. However, the present study is novel in its contribution of individual differences in the effectiveness of visual imagery as an effective intervention for the crossed hands deficit, as females are more likely to benefit than males, and participants with low spontaneous use of imagery are especially likely to benefit.

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Chapter 3

Attentional Set and Task Demands influence the Crossed-Hands Deficit

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Abstract

The crossing effect observed in tactile temporal order judgment tasks provides insight into the mental processes underlying tactile localization. By altering the reliability or availability of signals from modalities other than touch, we have seen that multiple sensory signals are integrated to create our estimate of tactile location. However, the impact of an individual's attentional set during this task has yet to be explored in depth. In the present work we manipulated participants' attentional set while they completed a tactile temporal order judgment task. In some blocks of trials participants focused their attention whereas in others they engaged with a relaxed attentional set. As predicted, the relaxed set produced a smaller crossed-hands deficit, but surprisingly, only when participants began the task in an uncrossed-hands posture. We attributed this effect of hand posture order to task difficulty: it was too difficult to try and control attentional set while also trying to do the TOJ task with the hands crossed. In a second experiment we tested and confirmed this order-effect prediction. The order in which participants engage with the crossed-hands posture influences how participants complete the task. Put differently, the present work provides evidence that attention can influence how the internal and external reference frames are integrated.

Introduction

Imagine feeling a bug crawl up your arm. Our natural instinct is to swat at the bug, and most of the time we do so successfully and with little effort. Although our conscious experience of localizing this bug seems effortless, there are complex processes that allow for this to happen. Tactile localization involves the integration of multiple sources of information beyond that provided by somatotopy alone, including visual and proprioceptive information (see Badde & Heed, 2016 for a review). This information is organized into two broad categories or reference frames. The internal reference frame localizes tactile stimuli in body-map coordinates and is informed largely by somatotopic information (see Badde, Röder, & Heed, 2019 for additional information sources). The external reference frame localizes tactile stimuli in external space and is informed largely by visual information (Azañón & Soto-Faraco, 2007; Cadieux & Shore, 2013; Kóbor et al., 2006; Lorentz et al., submitted; Röder et al. 2004; but see Badde et al., 2019; Maij et al., 2020). A simple anecdote can also demonstrate this integration phenomenon—consider how much easier is to accurately locate the bug when you can see it, as well as feel it.

Ample evidence supports an integration model when estimating stimulus location. Most evidence comes from experiments that vary the quality or availability of perceptual information in the external reference frame (Azañón & Soto-Faraco, 2007; Cadieux & Shore 2013; Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006; Röder, Rösler, & Spence, 2004; Unwalla, Cadieux & Shore, submitted; but see Badde, Heed, & Röder, 2014; Cadieux & Shore, 2013; Unwalla, Goldreich & Shore, submitted; for studies of attention). Changing the reliability of the information changes the weight applied to the external reference frame. However, few studies have examined the mechanism by which attention influences the applied weights.

The present study examines the influence of attention on tactile localization. We do so by asking participants to complete a tactile localization task in two different attentional sets: a broad attentional set, and a focused attentional set. The results of this study suggest that under certain conditions, attention can alter the extent to which available perceptual information from the external reference frame is considered in tactile localization estimates. We then examine data from existing studies (Unwalla, Goldreich, & Shore, submitted; Unwalla, Kearney, & Shore, 2020, Exp 2.6) and demonstrate that results currently thought to be based on changes to perceptual information may actually be due to the influence of attention on perception.

Taken together, the empirical evidence and re-analyses in the current paper suggest that attention may play a more important role in tactile localization than currently thought. We will discuss the implication of this in terms of current theories of tactile localization as well as the possibility for these results to open the door to individual differences analyses of tactile localization performance.

Tactile Localization and the Crossed-Hands Deficit (CHD)

Tactile localization is often studied using a crossing paradigm, in which participants perform tactile temporal order judgments (TOJs) with their hands uncrossed or crossed over the body midline (but see Maij et al., 2020). On each trial participants receive two vibrations, one to each hand, and are asked to identify the hand that vibrated first. When the hands are uncrossed, accuracy is high, even at short stimulus onset asynchronies (SOAs) between the two vibrations. However, simply asking participants to cross their hands over the body midline results in a significant impairment to performance (see Shore, Spry, & Spence, 2002 and Yamamoto & Kitazawa, 2001 for seminal work; see Heed & Azañón, 2016 for a review). This decrement in performance is referred to as the crossed-hands deficit (CHD).

The conflict (Shore, Spry, & Spence, 2002) and integration models (Badde & Heed, 2016; Badde, Heed, & Röder, 2016) of the CHD propose that the deficit results from the integration of information from the internal and external reference frames during formation of the tactile localization estimate. In the uncrossed posture these reference frames provide congruent information, meaning that combining information from the two reference frames increases the reliability of the tactile location estimate, which consequently aids performance. For example, a vibration to the right hand will also be localized in right external space. In contrast, when the hands are in the crossed posture, the reference frames provide conflicting information, and thus, integration of these two reference frames leads to errors in tactile localization. For example, a vibration to the right hand will be localized in left external space. The integration of information from the internal and external reference frames can explain the detriment to tactile localization observed when the hands are crossed compared to when they are uncrossed.

The CHD and External Reference Frame Information

The role of the external reference frame is highlighted by studies that manipulate the availability of relevant information. Removing visual information significantly decreases the magnitude of the CHD (Cadieux & Shore, 2013; Kóbor, Füredi, Kovács, Spence, & Vidnyánszky, 2006; Röder, Rösler, & Spence, 2004). The deficit is also reduced by asking participants to lie on their side, which presumably degrades the external reference frame by introducing uncertainty about orientation into the vestibular system (Unwalla, Cadieux, & Shore, submitted). We can also affect the representation of the external reference frame by supplementing visual information with congruent visual information, which also decreases the size of the CHD (Azañón, & Soto-Faraco, 2007; Lorentz, Unwalla & Shore, submitted).

Taken together, these studies demonstrate that changing the nature of available external reference frame information, either by removing it, or by replacing it with congruent information, influences tactile localization. These manipulations affect the quality or availability of perceptual information—in a Bayesian framework, the reliability of a cue is reduced or increased with predicable impact on the perceptual estimate of location (see Ernst & Bulthoff, 2004 for a review in the multisensory context). Critically, these changes are independent of the allocation of attention. At the same time, other studies highlight the importance of considering attention (Badde, Heed, & Röder, 2014) because performance can be affected without altering the quality or availability of perceptual information.

The CHD and Attention

Manipulations of task demands (Cadieux & Shore, 2013) provide one example where stimulation (i.e., quality of information) remains identical but performance changes based on attentional set (Cadieux & Shore, 2013; Crollen et al., 2019; Unwalla, Goldreich & Shore, submitted). In these studies, participants completed one block of trials in which they reported which side of the space was vibrated first whereas in another, they reported which hand was vibrated first. When taking an external perspective and considering the side of space the CHD was significantly larger, despite identical stimulation as in the internal perspective condition.

Focusing the task on the space around the body led participants to more heavily weigh information from the external reference frame. In contrast, focusing the task on the hand, and thus the physical body, might decrease the weight to information in the external reference frame, or alternatively increase the weight on information in the internal reference frame. Using on a probabilistic Bayesian model, the authors argued that the poorer performance in the external response demand condition resulted primarily from changes to the weight applied to the external reference frame, with a much smaller effect on the weight assigned to the internal reference frame (Unwalla, Goldreich, & Shore, submitted). These results highlighted the change in reference frame weights, but did not provide a specific mechanism to achieve the weight changes. Differential allocation of attention may provide a potential mechanism.

Additional support for the influence of attention on performance comes from dual-task experiments with the tactile temporal order judgment task (Badde, Heed, & Röder, 2014). Under divided attention, there was a reduced crossed-hands deficit, which the authors explained as a reduction in reference frame integration when completing two tasks. Alternatively, we propose that the working memory load pulled attention internally and shifted it away from the external reference frame. By shifting attention from one reference frame to the other, identical stimulation can produce differential performance.

Scope of the Present Study

In the present work we manipulated attention by varying the relative focus of participants (Olivers & Nieuwenhuis, 2005; Olivers & Nieuwenhuis, 2006; Smilek et al., 2006). For half of the experiment, participants were asked to engage in a focused set: concentrate on the stimuli as intently as possible. To promote this set, participants sat upright at a 90-degree angle with their head a chin-rest (Ptok et al., 2020). For the other half of the experiment, participants were asked to engage in a relaxed attentional set: let the stimuli wash over you. To promote this set, participants sat in a 135-degree leaned-back posture.

We predicted that when participants engaged in the focused attentional set, they would pay attention to information from both the internal and external reference frame, leading to both reference frames being weighted heavily in their tactile localization estimate. This would lead to improved performance in the uncrossed condition compared to the relaxed condition, as congruent location information would be highly weighted, but would lead to worse performance in the crossed condition, as conflicting location information would be considered.

In contrast, in the relaxed attentional condition we predicted that participants would pay less attention to information from the external reference frame. This prediction is based on the divided-attention results of Badde, Heed, & Röder (2014), as well as work in the cognition domain that has found that dividing attention and adopting a relaxed attentional set have similar influences on performance (Oliver & Nieuwenhuis, 2006). Low weighting of external reference frame information would hurt performance in the uncrossed condition, as participants would not be making use of the congruent visual information. In contrast, this would aid performance in the crossed condition, as conflicting visual information would not be integrated.

Experiment 1

Experiment 1 was a novel empirical study in which participants engaged in a focused and relaxed attentional set across separate blocks of trials in a tactile TOJ task.

Method

Participants. 48 female participants from the McMaster undergraduate participant pool completed the study and received course credit for their participation. All participants were right-handed, had normal or corrected-to-normal vision, and provided informed consent prior to participating. All research was approved by the McMaster Research Ethics Board and conformed to the tri-council policy on research with human participants (Canada).

This sample size was chosen to account for a conservative estimate of a medium-sized interaction (given that one manipulation of interest was an instructional manipulation), as well as to allow for proper counterbalancing of hand posture first and attention condition first.

Apparatus & stimuli. Participants were presented vibrotactile stimuli via an Oticon-A (100 Ohm) bone-conduction vibrator driven by a square wave signal. The bone conductors directly contacted the thumb through a 2 cm hole in the plexiglass top of the wooden cube that housed the conductors. All participants experienced the same amplitude of vibrotactile stimulus, which was deemed to be suprathreshold by the experimenters. White noise was played through over-ear headphones to mask any sounds emitted from the vibrating cubes.

On each trial, participants received two 20 ms vibrotactile stimulations, one to each hand. The vibrations were presented at randomly selected stimulus onset asynchronies (SOAs) of ±400 ms, ±200 ms, ±100 ms, and ±50 ms (where – signifies that the left hand was stimulated first, and + that the right hand was stimulated first). Each SOA was experienced equally often in each block of trials, and consequently, across the entire experiment. The vibrotactile stimuli were controlled by an Arduino card connected to the parallel port of a Macbook Pro laptop computer running PsychoPy software (Pierce et al., 2019).

Design & procedure. Participants held a cube-like button in each hand and white noise was played over headphones to mask auditory information provided by the cubes.

On each trial, two consecutive vibrations were presented, one to each hand. Participants responded with the hand that vibrated first by pressing the button in the corresponding hand. Participants had three seconds to respond following the offset of the second vibrotactile stimulus, after which time the cubes simultaneously vibrated three times to signal that the trial had timed out. To resume the experiment following a time-out trial, participants were instructed to press both buttons simultaneously. Time-out trials were removed from all analyses and accounted for .002% of all trials.

All participants completed the experiment in two different attentional conditions. In the focused attention condition, participants sat in a wooden chair with an adjustable back, with the back set at 90-degrees to the seat of the chair. The participant's hands rested 18 cm apart on a desk and their head sat in a chinrest affixed to the desk. Participants were read the following instructions at the start of the focused attention block, "In this part of the experiment you will complete the task while sitting upright in the chair and controlling your attention to concentrate on the task. You must ensure that your attention is focused on the task at all times. Concentrate and actively focus as much as you can on which hand vibrated first. It is critical that you adopt this very focused state for all trials".

In the relaxed attention condition participants sat in an adjustable-back chair with the back of the chair set at a 135-degree angle to the seat of the chair. The hands rested 18 cm apart on a table affixed to the chair, such that the arms remained at a 90-degree angle to the body, as in the focused attentional condition. Participants received the following instructions at the start of the relaxed attention block, "In this part of the experiment you will complete the task while leaning back in the chair and relaxing. Just simply let the vibrations wash over you while you are doing the task. Relax and trust your gut feelings or intuition about which hand vibrated first. Try to adopt this more diffuse, absent-minded, and passive state for all trials". In both attentional conditions, participants completed the task with the hands uncrossed and with the hand crossed over the body midline. Initial hand posture and attentional condition were counterbalanced across participants.

Before each attentional condition, participants completed 2 practice blocks of 16 trials each using the instructions for the upcoming block. All participants' hands were uncrossed for the first block of practice trials and crossed for the second block of trials. Following each set of practice blocks, participants completed 6 experimental blocks of 64 trials, with 3 blocks in the uncrossed hand posture and three blocks in the crossed hand posture. Participants completed the first block of trials with their hands in their assigned counterbalance posture and alternated between this posture and the other posture on each subsequent block. Participants were given a short break between each block and between the different attentional conditions.

Results

Mean accuracy scores, calculated as the proportion of trials in which the participant correctly responded with the hand that vibrated first, (see Figure 1A; results plotted as proportion right first responses are available in Appendix A for the interested reader) were submitted to a 2x2x2x2 mixed-factor ANOVA that included hand posture (uncrossed/crossed) and attentional condition (focused/relaxed) as within-subjects variables, and the counter-balancing order variables of hand posture first (uncrossed first/crossed first) and attentional condition first (focused first/relaxed first) as between-subjects variables. Partial eta squared and Cohen's *d* are used as measures of effect size for *F*- and *t*-tests respectively throughout the present work.

As expected, responses were overall more accurate in the uncrossed (M=.86, SD=.09) than in the crossed (M=.65, SD=.12) hand posture, producing a significant main effect of hand posture, $F(1,44)=26.29$, $p<.001$, $\eta_p^2=.374$. Although the two-way interaction between hand posture and attentional condition was not significant, $p=.244$, there was an unexpected three-way interaction between hand posture, attentional condition, and hand posture first, $F(1,44)=4.87$, $p=.032$, $\eta_p^2=.100$ (see Figure 1B).

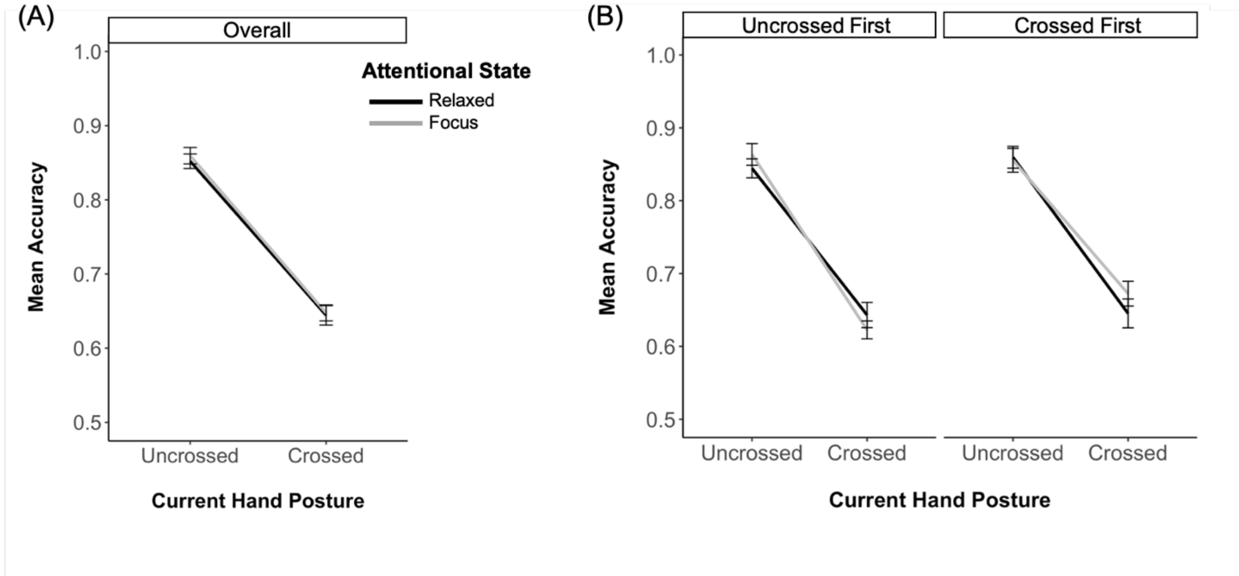

Figure 1. Mean accuracy data from Experiment 1 plotted as (A) overall data and (B) data separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

This three-way interaction was decomposed by examining hand posture (uncrossed/crossed) and attentional condition (focused/relaxed) separately for participants who experienced the uncrossed hand posture first and those who experienced the crossed hand posture first. The predicted interaction of posture and attention was observed when the uncrossed hand posture was completed first, $F(1,23)=7.42$, $p=.021$, $\eta_p^2=.238$, but not when the crossed hand posture was completed first, $p=.183$.

The significant two-way interaction in the uncrossed first condition was driven by a larger difference between uncrossed and crossed performance (i.e., a larger CHD) in the focused attentional condition (difference between means=.24, $t(23)=11.31$, $p<.001$, $d=2.39$), than in the relaxed attentional condition (difference between means =.20, *t*(23)=8.2, *p*<.001, *d*=1.99). This smaller difference between uncrossed and crossed performance in the relaxed attentional condition was driven by a numerical trend toward worse performance in the relaxed uncrossed condition than in the focused uncrossed condition, but a numerical trend toward better performance in the relaxed crossed condition than in the focused crossed condition, as predicted. There were no effects of body posture first (all *p*s>.131).

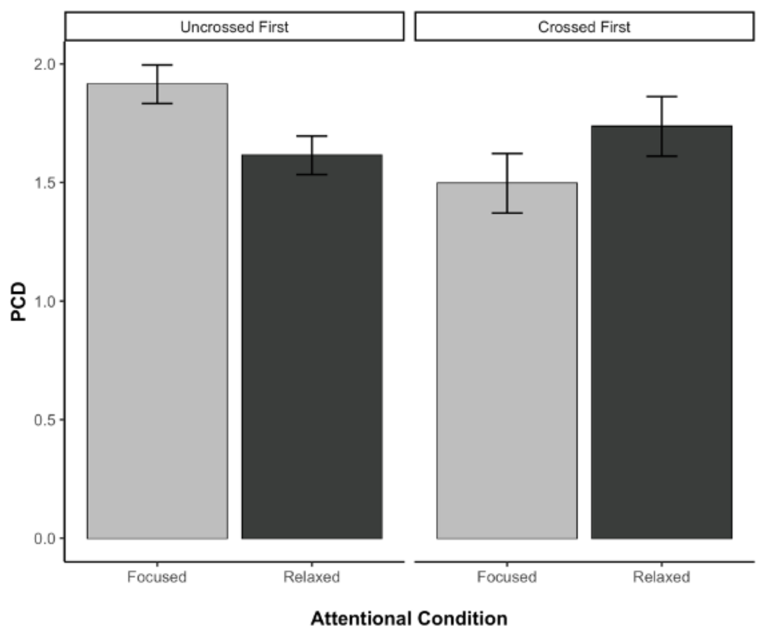

Figure 2. Data from Experiment 1 plotted as PCD score separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Another way to understand the three-way interaction between hand posture, attentional condition, and hand posture first derives from the use of proportion correct difference scores (PCD scores; Cadieux et al., 2010; see Figure 2). PCD scores were computed by taking the difference in performance between the uncrossed and crossed posture at each SOA and then summing the values to get a single number that represents the magnitude of the CHD. PCD scores were significantly smaller in the relaxed condition than the focused condition for uncrossed hands first, $t(23)=2.61$, $p=.016$, $d=.032$ and there was no statistical difference between the relaxed and focused condition PCDs in the crossed hands first condition, $p=.190$.

Discussion

Experiment 1 sought to evaluate the impact of a focused versus relaxed attentional set on the crossed-hand deficit. We observed the expected pattern of a smaller deficit in the relaxed condition when the uncrossed posture was tested first, but not when the crossed-hands posture was tested first. As such, the results of Experiment 1 provide initial evidence that attentional sets can alter the weights applied to the two reference frames during tactile localization. These results support the findings of Cadieux and Shore (2013) and Badde, Heed, and Röder (2014), who found that task-demands can influence attention to consequently influence the relative weighting of the two reference frames. However, our results uniquely suggest that internally generated attentional sets can influence performance.

This result comes with a caveat, however, as participants' performance only matched predictions made by the attentional account when they began the experiment in the uncrossed hand posture. If the participant began the experiment in the crossed hand posture, there was no significant effect of attentional condition on the performance observed in each hand posture. Although this result may seem surprising at first, it can be understood from an attention account.

At its core, our manipulation of attention was instructional. The change in posture simply supported those instructions. Ideally, participants followed the instructions, but we have no independent assessment of instruction compliance. One way to understand our findings proposes that the uncrossed-first group successfully engaged in the desired attentional set in each block of the experiment, whereas the crossed-first group did not. Consider that the uncrossed hand posture presents an easier task, which, when done first, may allow participants to learn and engage in the instructed attentional set. In contrast, those participants who began the experiment in the crossed-hands posture had a more difficult task to face while trying to implement the attentional instructions. Because this group found the task to be difficult from the outset, they likely dedicated all available attentional resources to simply trying to engage with the tactile TOJ task, with no resources left to engage in the attentional manipulation. Put another way, the participants who started the experiment in the harder condition never learned to apply the correct attentional set, but rather engaged in a focused attentional set throughout the experiment.

The expected value of control (EVC; Shenhav et al., 2013) parameter of cognitive control suggests that control will only be executed if the benefits of doing so outweigh the costs, and specifically if the task demands are not too high. When cognitive control is not evoked, the default response is instead executed. In the present experiment, not evoking control is akin to ignoring the attention instructions and instead using their default response to complete the experiment (i.e., to complete the entire experiment with a focused attentional set). Similarly, attentional inertia describes the phenomenon whereby the attentional set used at the outset of the experiment is carried throughout the rest of the experiment, despite instructions to the contrary (Longman et al., 2014). Taken together, these findings provide empirical precedent for our proposal that the attentional set evoked at the beginning of the experiment based on initial hand posture can influence the attentional set engaged in subsequent blocks of the experiment.

Experiments 2a and 2b

Our proposed attentional explanation for the effect of hand posture experienced first in Experiment 1 produces an important corollary argument: attentional manipulations should be modulated by the hand posture experienced first. The attentional manipulation should influence performance in the expected direction when the uncrossed hand posture is experienced first, as participants in this condition have sufficient capacity to engage in the desired attentional set. But the attentional manipulation should not influence performance when the crossed hand posture is experienced first, as these participants adopt an attentional set that does not engage in the desired manipulation throughout the experiment. To be clear, we expect to see order effects when the manipulation in question requires a specific attentional set. In contrast, manipulations that directly influence information quality should not be affected by hand posture first: perceptual changes should result regardless of the attentional set of the participant.

To test this hypothesis, we re-analysed previously prepared data in which tactile TOJ performance was compared when participants sat upright versus when they were on their back (Unwalla et al., 2020, Exp 2.6) or on their side (Unwalla et al., submitted). The original rationale for these studies was that lying on the back or the side should degrade perceptual information about the external reference frame and consequently decrease the magnitude of the CHD. Here we propose that lying on the back does not change the nature of the perceptual information provided by the vestibular system as it relates to left–right decisions. Instead, lying on the back changes how much attention is paid to information in the external reference frame. In contrast, lying on the side changes the nature of the perceptual information, such that information about spatial left and right is degraded. This difference between an attentional manipulation and a perceptual manipulation accounts for the smaller magnitude of the effect observed when lying on the back compared to when lying on the side—as mentioned above, attentional manipulations can be influenced by outside attentional factors, but perceptual manipulations should not. Thus, we expected that the order of hand posture should affect performance when participants lie on their back, but not when participants lie on their side. Specifically, when participants perform the uncrossed posture first, they should be able to take advantage of the lying-on-the-back posture.

To examine this attention versus perception hypothesis, we re-analyzed results from a crossed-hands TOJ task when sitting upright versus lying on the back (Unwalla et al., 2020, Experiment 2.6) or side (Unwalla et al., submitted) and included hand posture first and body posture first as between-subject variables.

Method

The method used by Unwalla and colleagues was similar to that of Experiment 1 of the present work with the following exceptions.

Participants. 20 participants (10 female) were recruited from the McMaster University undergraduate student pool to complete the lying on the back experiment (Experiment 2a), and a separate group of 20 participants (10 female) completed the lying on the side experiment (Experiment 2b). It is important to note that the sample sizes of Experiments 2a (*N*=20) and 2b (*N*=20) are less than half that of Experiment 1 (*N*=48).

Apparatus & Stimuli. Participants were presented vibrotactile stimuli via an Oticon-A (100 Ohm) bone-conduction vibrator driven by a 250 Hz amplified sinusoidal signal. All stimulation was controlled by a set of reed-relays connected to the parallel port of a DELL Dimension 8250, running Windows XP software. Stimuli were created using MATLAB R2012b software (The MathWorks, Inc).

Design & Procedure. Lying on the back and lying on the side were manipulated separately across two experiments with two separate groups of participants. Participants in each experiment completed half of the experiment sitting upright in a chair, and the other half lying on their back on the table (Experiment 2a), or lying on their side on the table (Experiment 2b). Participants in each experiment were randomly assigned to complete the first block of trials sitting upright at a table or lying on the table (either on their back or side), such that approximately half of the participants began in the upright body posture. No instructional manipulations about attention were provided. Within each body posture, the participant completed the first 3 blocks of 64 trials in the uncrossed or crossed hand posture, and the last 3 blocks in the other hand posture. Initial hand posture was randomly assigned across participants, such that approximately half of the participants started in the uncrossed hand posture.

Experiment 2a: Upright versus Lie on Back

Mean accuracy scores were calculated the same as Experiment 1 and were submitted to a 2x2x2x2 ANOVA that included body posture (upright/back), hand posture (uncrossed/crossed) as within-subject factors, and body posture first (upright first/back first) and hand posture first (uncrossed first/crossed first) as between-subject factors (see Figure 3A for a summary of the data).

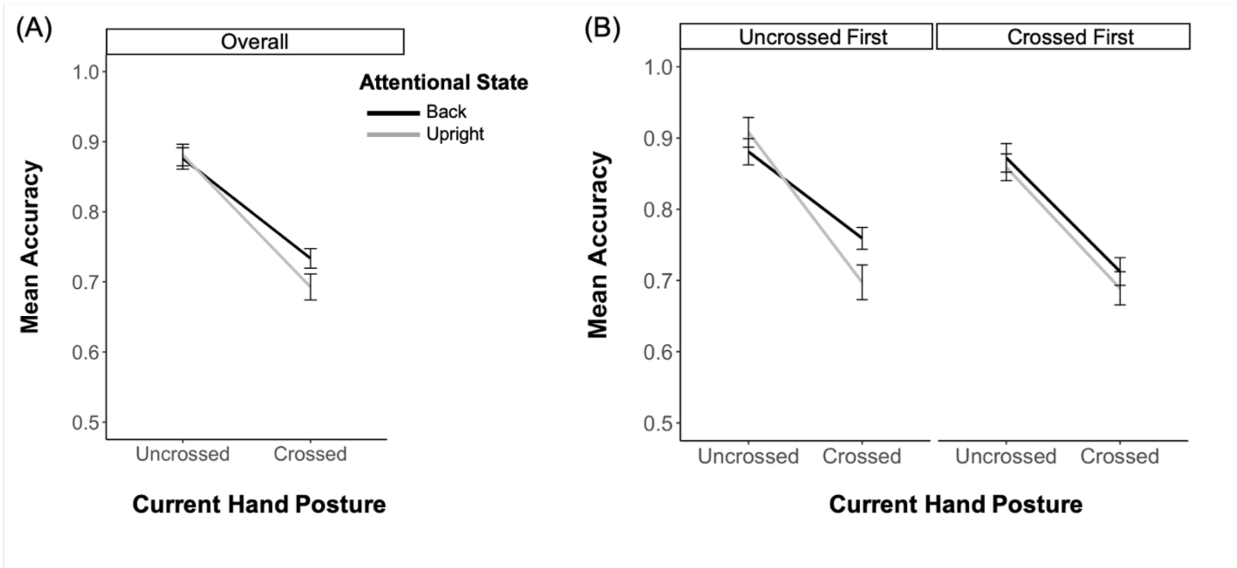

Figure 3. Reanalyzed data from upright versus lying on back study from Unwalla et al. (2020, Exp 2.6) plotted as (A) overall data and (B) the data separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

The three-way interaction between hand posture first, hand posture, and body posture was not significant, p=.744. However, given our *a prioi* interest in this relation, and the fact that the sample size was less than half of that in Experiment 1 (suggesting that this experiment was underpowered to find this effect), we further explored this interaction (see Figure 3B). Separate ANOVAs were run for uncrossed hand first data and crossed hand first data that included hand posture and body posture as within-subject factors. When participants completed the uncrossed posture first, the interaction between hand posture and body posture was significant, $F(1,10)=6.99$, $p=.030$, $\eta_p^2=.467$, but when the hands were crossed in the first blocks of trials, this interaction was not significant, p=.697.

The significant two-way interaction for the uncrossed-posture first data was driven by a smaller difference between uncrossed and crossed performance (i.e., a smaller CHD) in the back condition, $M_{Difference}$=.12, $t(8)$=4.72, p=.001, d=.964, than in the upright condition, $M_{Difference}$=.21, $t(8)$=5.23, p<.001, d=1.26. As in the uncrossed-hands first group in Experiment 1, for the uncrossed posture performance was numerically better (but non-significant), in the upright condition compared to the lying on the back condition, $t(8)$=.97, p=.36, d=.256, but in the crossed-hands condition the reverse was true with a numerical trend toward better performance when lying on the back than when sitting upright, $t(8)$=2.09, p=.07, d=.411.

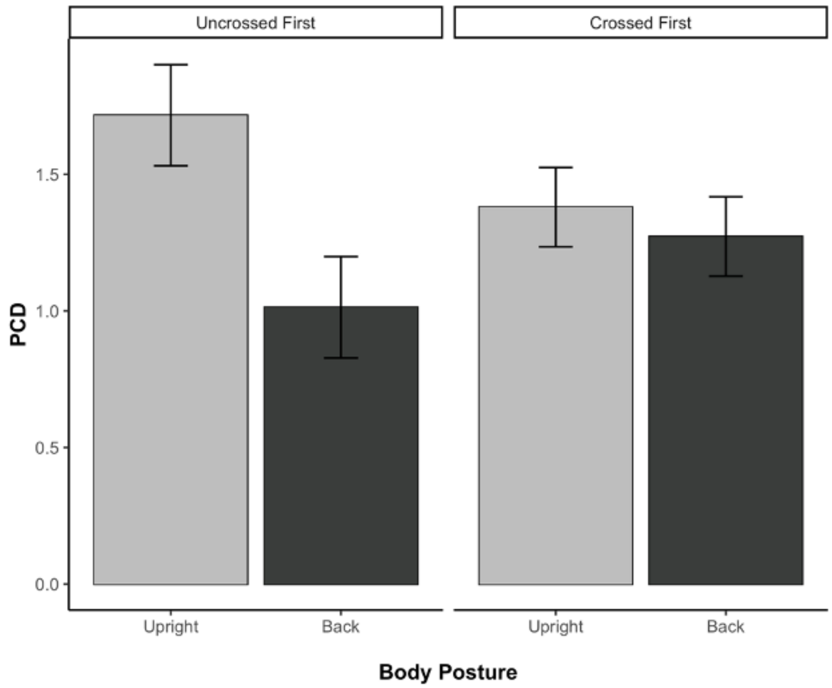

Figure 4. Data from Experiment 2a plotted as PCD score separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

As an additional way to measure this interaction, we calculated PCD scores as in Experiment 1. PCD scores were significantly smaller in the back condition than the upright condition for uncrossed hands first, $t(8)=2.68$, $p=.028$, $d=.856$ (see Figure 4). There was no statistical difference between the upright and back condition PCDs in the crossed hands first condition, $p=.612$.

As in Experiment 1, the analysis of accuracy scores found no effects of body posture first (all ps>.187).

Experiment 2b: Upright versus Lie on Side

Mean accuracy scores were submitted to a 2x2x2x2 ANOVA that included body posture (upright/side) and hand posture (uncrossed/crossed) as within-subject factors, and body posture first (upright first/back first) and hand posture first (uncrossed first/crossed first) as between-subject factors (see Figure 5A for a summary of the data).

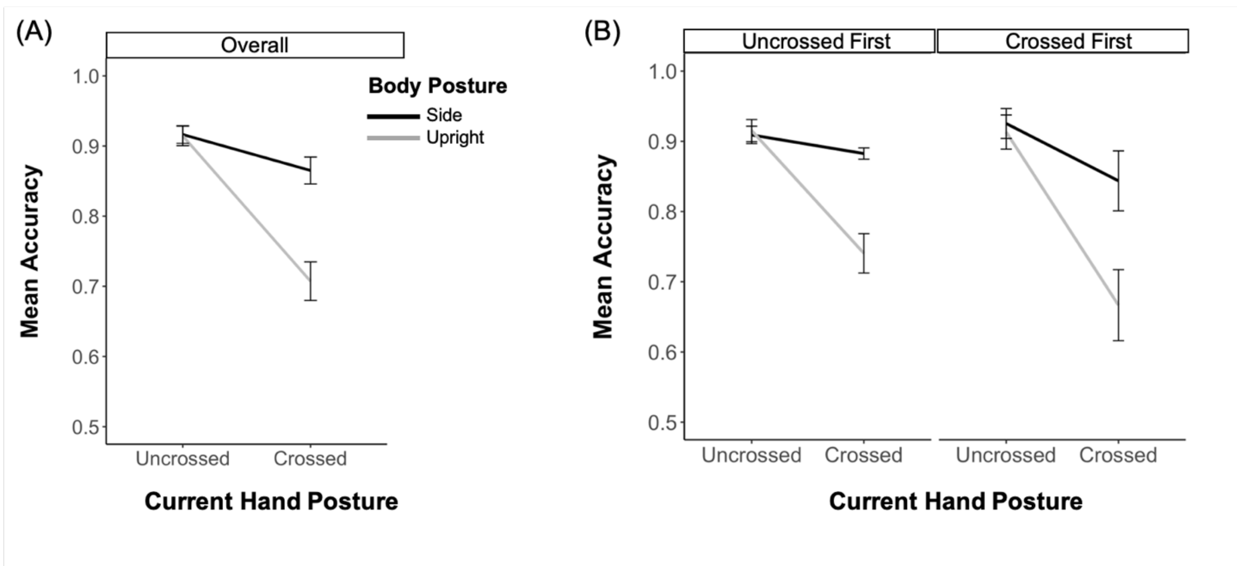

Figure 5. Reanalyzed data from upright versus lying on side study from Unwalla et al. (submitted) plotted as (A) overall data and (B) the data separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Again, the three-way interaction between hand posture first, hand posture, and body posture was not significant, p=.362, but given our *a prioi* interest in this relation, we further explored this interaction with separate ANOVAs for uncrossed hand first participant data and crossed hand first data that included hand posture and body posture as within-subject factors (see Figure 5B). The two-way interaction between hand posture and body posture was significant for both the uncrossed-hand first participants, $F(1,9)=19.61$, $p=.001$, $\eta_p^2=.661$ and the crossed-hand first participants, $F(1,8)=5.32$, $p=.050$, $\eta_p^2=.399$. Both interactions were driven by a difference between crossed and uncrossed performance in the upright condition (crossed hand first: $M_{Difference}=.25$, $t(8)=4.2$, $p=.003$, $d=1.41$; uncrossed hand first: $M_{Difference}=.17$, $t(10)=4.72$, $p<.001$, $d=1.83$), but not in the side condition (crossed hand first: $p=.114$; uncrossed hand first: $p=.053$). Regardless of hand posture first, uncrossed performance did not differ between the two body postures, all *p*s>.11, but crossed performance was consistently significantly better when lying on the back, uncrossed first $t(10)=5.03$, $p<.001$, $d=1.35$; crossed first, $t(8)=4.20$, $p=.003$, $d=1.41$.

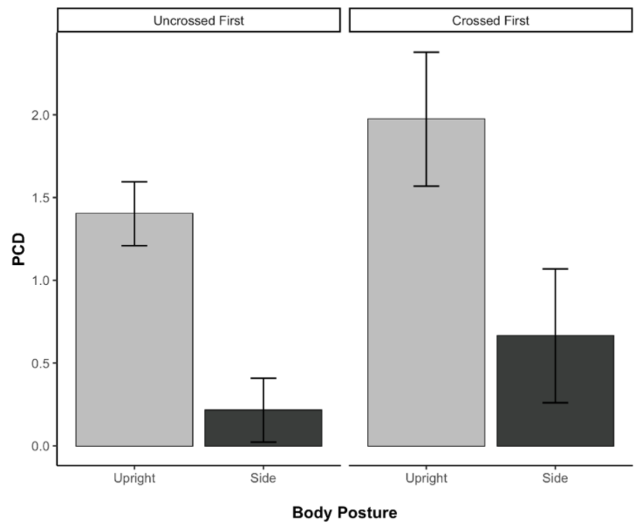

Figure 6. Data from experiment 2b plotted as PCD score separated by hand posture experienced first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

As an additional way to analyze this interaction, we calculated PCD scores as in Experiment 1. PCD scores were significantly smaller in the side condition than the upright condition for both the uncrossed hands first condition, $t(10)=4.35$, $p=.001$, $d=1.40$, and for the crossed hands first condition, $t(8)=2.29$, $p=.051$, $d=1.03$ (see Figure 6).

Unlike in Experiments 1 and 2a, in the analysis of accuracy scores for Experiment 2b, there was a significant interaction between body posture first and body posture, $F(1,16)=6.38$, $p=.022$, $\eta_p^2=.285$. The effect of body posture was significant regardless of body posture first, but was larger for side first, $M_{Difference}=.11$, $t(9)=4.05$, $p=.003$, $d=.955$, than upright first, $M_{Difference}=.05$, $t(9)=2.73$, $p=0.02$, $d=.693$.

Discussion

Lying on the back (Experiment 2a) reduced the crossed-hands deficit, but only for those participants who experienced the uncrossed hand posture first. For these participants, uncrossed performance was better when sitting upright and worse when lying on the back. Lying on the side (Experiment 2b) produced a different pattern of data. Regardless of hand posture order, lying on the side increased performance in the crossed-hand posture (a smaller crossed-hands deficit); uncrossed performance was not affected by lying down or by posture order.

This pattern of findings—influence of posture order for the manipulation that required attention and not for the one that changes perceptual signals—aligns with the predictions based on Experiment 1. Without considering order of presentation, we would conclude that lying on the back does not change the relative weights applied to the internal and external reference frames. However, including this factor in our analysis revealed the impact of lying down. Most papers on the crossed-hands deficit do not include this factor in their analyses, which may be masking some interesting findings as null results.

In considering the manipulation of lying on the back in Experiment 2a we posited this as an attentional manipulation. However, these data were collected before we considered the role of attention in the crossed hands deficit. We thought of lying on the back as a weaker version of lying on the side. To be clear, although lying on the back did not have any attentional instructions, the posture does provide a relaxed approach to the task. Future research will have to explore *how* this posture impacts attention. For our present purposes, we can simply say that the manipulation does not alter the perceptual quality of the information, but can affect how the participant interacts with the sensory information.

In Experiment 2b there was an interesting effect of which body posture (upright or lying on the side) was experienced first. Specifically, the effect of body posture was smaller for upright-first participants. We argue that laying on the side disconnects the external world (Unwalla et al., submitted); thus, it may be that experiencing the upright posture first locks participants into attending to this reference frame. As such, it may provide additional support for the role of attention in tactile localization. Clearly, we would want to replicate this pattern before making strong conclusions.

General Discussion

Adopting a relaxed set (Experiment 1), lying on your back (Experiment 2a), and lying on your side (Experiment 2b) all reduce the crossed-hands deficit in tactile temporal order judgments. The effect of a relaxed set and lying on the back are much smaller in magnitude compared to the benefit of lying on the side, and, critically, only occur for participants who experience the uncrossed posture first. We posit an attentional account for the two weaker findings and a change in the sensory quality for the larger effect. In the attentional account, a focused set pushes the observer to adopt an external focus whereas a relaxed set allows them to discount information from the external reference frame. In contrast, lying on the side fundamentally changes the perceptual experience of left–right because of its relation to gravity. Both reclining (Experiment 1) and lying down completely (Experiment 2A) maintain the orthogonal relation of left–right and up–down, and having a clear sense of upright allows a more reliable estimate of left–right in a reference frame that uses gravity (e.g., the vestibular system). When lying on the side, the sense of upright is noisier because vision, vestibular, and body-based cues do not line up with gravity. As such, the reliability of a gravity-based reference frame is compromised, and, thus, this reference frame would have a smaller contribution to location estimation (see Unwalla et al., submitted for a full discussion of this condition). Critically, we do not think of lying on the side as an attentional manipulation so will focus our discussion on the other two manipulations.

The idea that attention can affect multisensory perception is not new (see MacAluso et al., 2016 for a review). However, these discussions typically focus on whether multisensory integration occurs automatically, or whether attention is required for multisensory integration to occur (but see Kovshoff et al., 2015 for evidence of the importance of voluntary attention for perception). Indeed, the dual-task CHD experiments of Badde, Heed, & Röder (2014) were run for this purpose: the research question offered by the researchers was whether the integration of internal and external reference frame information occurs automatically, or whether attention is required for integration. Their observation of a smaller CHD in the dual-task condition compared to the single-task condition led to the conclusion that integration is not automatic. The results of the present work suggest that a further nuance to this argument is required by providing evidence that attentional modulations can alter the extent to which external reference frame information is weighted in the tactile localization estimate, not just simply whether integration of external reference frame information occurs at all.

Attention and Existing Theories of the CHD

The relation between attention and reference frame weights is important to consider when examining theories of the CHD. Both the conflict model (Shore, Spry, & Spence, 2002) and integration model (Badde, Heed, & Röder, 2016) suggest that the CHD occurs because conflicting information from the external reference frame is integrated into the tactile localization estimate when the hands are in the crossed posture. Support for this has come from evidence that CHD magnitude decreases when conflicting external reference frame information is removed in the crossed hands posture. The resulting explanation is that removing or degrading information from the external reference frame leads to a smaller CHD.

This explanation has important implications for thinking about mathematical models to describe tactile localization and multisensory perception more generally. Multisensory perception is modelled as a cue combination problem that uses maximum likelihood estimation to weigh different cues (see Ernst & Bulthoff, 2004 for a review). The extent to which each sensory signal (i.e., cue) is factored into the calculation is based on the 'weight' assigned to it. In optimal integration, the weight is the inverse of cue reliable, where the less reliable the sensory signal, the less it will be weighted. Within this context, the above conclusion makes sense: degrading the external reference frame reduces its reliability, and, thus, the weight applied to it in forming the final estimate of location. The present results suggest that attention can also alter the weights applied to specific reference frames.

Considering attention in the model opens the door to new explanations for existing and future CHD results. For example, the results of Experiment 2a suggest that lying on the back does not degrade external reference frame information. Instead, lying on the back makes it less likely for external reference frame information to be attended to, and it consequently receives a lower weight. In contrast, the results of experiment 2b suggest that lying on the side does, in fact, degrade external reference frame information, leading to a lower weight due to decreased reliability of the signal.

Considering the role of attention also allows for a better understanding of the response demand results discussed in the introduction (Cadieux & Shore, 2013; Crollen et al., 2019; Unwalla et al., submitted). The nature of the external reference frame information was identical in both the side of space response and hand response conditions. The information was not ‘degraded’ in one condition, yet, there were differential influences of the external reference frame information. This suggests that the different response conditions altered the weight of the external reference information via attention, rather than through changes to reliability of the external reference frame sensory signals.

Future Directions

As mentioned above, there are many examples of how attention alters multisensory perception (see Macaluso et al., 2016; Tsalma et al., 2010 for reviews) and even tactile processing generally (see Spence, 2002 for a review), so it is no surprise that attention would alter the extent to which internal and external reference frame information contribute to tactile localization. However, the evidence presented here suggests that attention may play a previously unknown role in tactile localization. Importantly, incorporating attention into existing theories of tactile localization and the CHD offers many exciting avenues for future research.

Although considering attention in tactile localization in the capacity proposed in the present work adds another parameter to the tactile localization equation, it may actually introduce parsimony across the field. Consider the response demand results of Cadieux & Shore (2013) and the dual-task demand results of Badde & Heed, & Röder (2014). We propose that both observations are a result of attentional modulation of reference frame weights due to the demands of the task. Thinking this way allows for a single mechanistic explanation for the changes in reference frame weights of two seemingly disparate results. It also allows for this mechanistic explanation to be applied to mathematical modelling of changes in reference frame weights (Badde & Heed, & Röder, 2016; Unwalla, Goldreich, & Shore, submitted) that have been discussed in more abstract terms, such as top-down control (Badde & Heed, 2016). And we believe that there are sure to be more examples of this in the future.

Lastly, and possibly most interestingly, allowing for the role of attention in tactile localization also leads to the prediction that an internally generated attentional set can also alter tactile localization, and the results of Experiment 1 provide initial behavioural evidence for this. This means that differences in attentional set can lead to differences in performance. A corollary of this proposal is that baseline tactile localization may differ across typically-developed individuals due to their baseline attentional set. This provides a new lens with which to examine the individual differences that have been observed in the CHD literature (Cadieux et al., 2010; Figure 2). It may also challenge implicit assumptions of the CHD literature, including that uncrossed performance serves as the natural or baseline performance for tactile localization, or the idea that tactile localization is carried out by the same manner across all typically-developed individuals and, thus, follows the same psychophysical properties.

Conclusion

The results of the present work provide evidence that attention plays a role in the relative weighting of internal and external reference frame information during tactile localization. Allowing for this role of attention will invite new interpretations of existing results and require more critical and careful procedures in future CHD studies to control for the potential confounding effects of attention.

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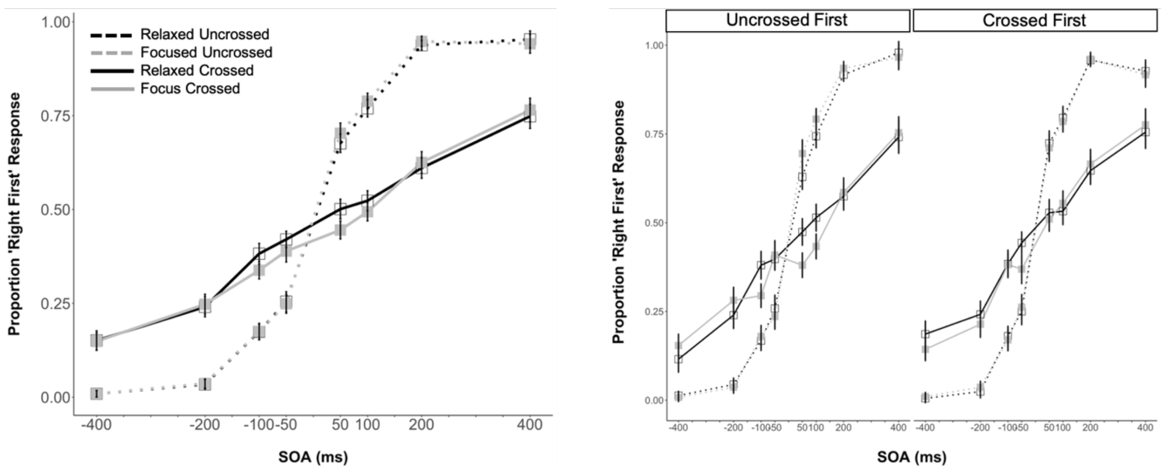
Appendix A: Experiment 1 Proportion Right First Responses



Appendix A. Data from Experiment 1 plotted as proportion right first responses with left-first trials denoted by negative stimulus onset asynchronies (SOAs). The left panel depicts overall data and the right panel depicts data separated by hand posture tested first. Error bars represent ±*SEM* with between-subjects variability removed (Morey, 2008).

Chapter 4

A Paradigm Shift for the Crossed-Hands Deficit: Re-Evaluating Theory and Approach

Lisa Lorentz and Sandra Monteiro

Abstract

Our understanding of the perception of tactile location has grown substantially over the past two decades. Research in this area has largely been informed through the study of crossing effects. The crossed-hands deficit (CHD), arguably the most common crossing effect, is examined using a perceptual task known as the tactile temporal order judgment (TOJ) task. Although much has been uncovered using this task, the present work argues that our understanding of tactile localization has actually been limited by the underlying assumptions and statistical methods associated with the task. We explore how the use of the probit slope and proportion correct difference score as measures of the CHD have influenced the methods used to study the effect and the theories used to explain the observed data. We also explore how examining the CHD through a new lens of individual differences may help to explain questions that have evaded understanding for years. We propose that the literature must critically examine the conscious and

unconscious biases that have influenced our experiments and theorizing, and that engaging in this paradigm shift will allow for broader investigations of the CHD and its potential clinical implications.

Introduction

The study of perception and cognition is the study of intangible concepts. We create theories to explain things we cannot see and use proxy measures in attempt to triangulate processes we cannot directly measure. This often requires us to “break” a system, in order to understand how it functions when it is “working properly” or “doing its job”. If we can successfully implement experimental manipulations to put the system back into working order, we can say we understand how the system works under typical conditions. Although this experimental framework allows us to investigate and understand cognitive and perceptual processes, it does not come without cost. It requires us to first have a theory about how a process works. This theory then informs the manipulations we employ in our experiments, which in turn determine the dependent measures we use. The statistical tests used to investigate the implications of differences in dependent variable across different manipulations depends on the research question, meaning that theory determines the statistics we subject our observations to.

Although this seems like a textbook definition of the scientific process, it is important to note that theory both begins and ends this cycle. Theory determines what questions we ask and how we interpret the results we observe. We, as cognitive and perceptual psychologists, may see ourselves as uncovering objective truths about cognitive or perceptual processes, but in reality, we are unintentionally influenced by our biases about theory. In the present work, we examine how theory and statistical measures have biased our study of a tactile perception through investigations of the crossed-hands deficit.

The Crossed-Hands Deficit

Investigations of the crossing effect, or the crossed-hands deficit (CHD), have been used to study the processes underlying tactile localization for decades (see Badde & Heed, 2016; Heed & Azañon, 2014 for reviews; see Shore, Spry, & Spence 2002; Yamamoto & Kitazawa, 2001 for seminal work). Studies of the CHD are prime examples of breaking the system to understand how it works under ideal conditions. In CHD studies, participants complete a tactile temporal order judgment (TOJ) task, in which they receive two successive vibrations, one to each hand, and are asked to respond with the hand that vibrated first (see Figure 1A). When the hands are in their typical uncrossed posture—when the system is working under ideal conditions—participants' performance is near ceiling. However, when participants simply cross their hands over the body midline performance suffers significantly, with more errors and slower responses (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). In the crossed hand posture, the system has been "broken".

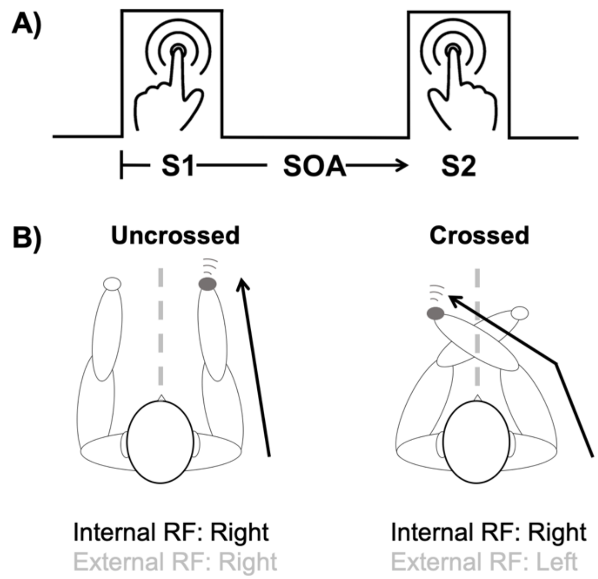


Figure 1. (A) A visual depiction of the tactile temporal order judgment (TOJ) task. Participants receive two vibrations, one to each hand, separated by a variable stimulus onset asynchrony (SOA). Participants are typically asked to respond with the hand that vibrated first. (B) A visual depiction of the integration theory of the crossed-hands deficit. In the uncrossed posture, the internal reference frame (RF) and external RF provide consistent information about the location of the tactile stimulus. In the crossed posture, the internal and external RF provide conflicting information. Integrating the conflicting external RF information with the internal RF information in the location of tactile location results in less reliable percept (i.e., the crossed-hands deficit).

Multiple experimental manipulations have been used to "put the system back together again" and have led to theories that rely on the existence of two reference frames (see Figure 1B; Badde & Heed, 2016; Badde, Heed, & Röder, 2016; Shore, Spry, &

Spence, 2002; Yamamoto & Kitazawa, 2001). The internal reference frame localizes tactile stimuli in bodily-map coordinates. In contrast, the external reference frame localizes tactile stimuli in external spatial coordinates, based largely on visual information (Azañon & Soto-Faraco, 2007; Cadieux & Shore, 2013; Kóbor et al., 2006; Lorentz et al., submitted; Röder et al., 2004), but also vestibular information (Unwalla et al., submitted). If the hands are in an uncrossed posture and a vibrotactile stimulus is applied to the right hand, the internal reference frame will localize the stimulus to the right hand and the external reference frame will localize the stimulus to the right side of space. In contrast, if a vibrotactile stimulus is applied to the right hand when the hands are in a crossed posture, the internal reference frame will localize to the right hand, but the external reference frame will localize to the left side of space.

The integration (Badde, Heed, & Röder, 2016) theory of the CHD proposes that localizing tactile stimuli requires information from the two reference frames to be integrated. This means that all available information, including somatotopic and visual information are integrated to localize tactile stimuli. In the uncrossed posture the two reference frames provide congruent information, and thus, integrating the information results in accurate tactile localization (see Figure 1B). However, when the hands are crossed, the reference frames provide incongruent information. Thus, integrating this information will lead to error-prone responding, as is observed in the CHD.

How Measurement Informed Theory

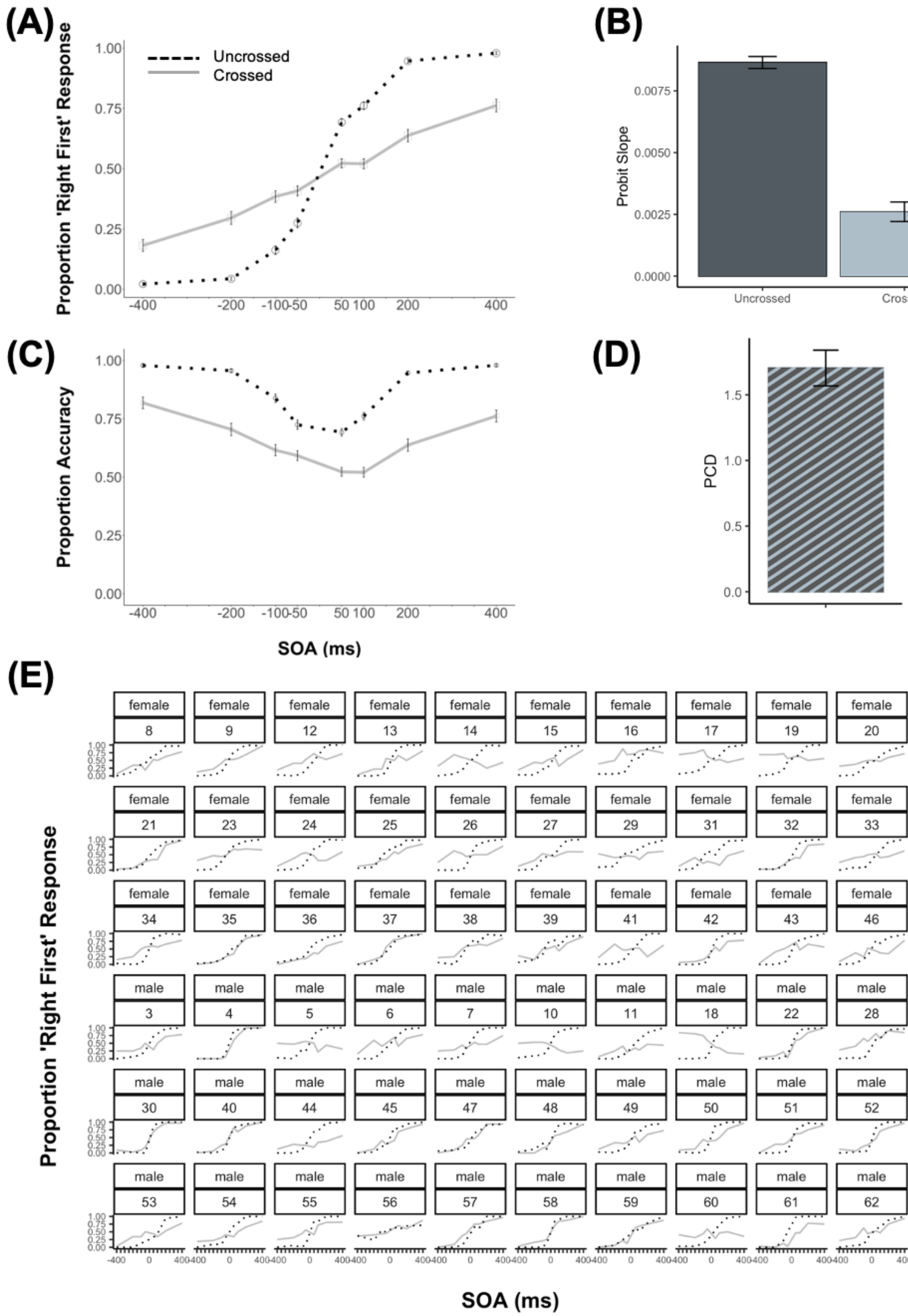
As was mentioned in the introduction, the goal of the present work is to identify how the task used to measure the CHD and the theoretical assumptions associated with it have influenced the ways in we have studied this deficit. In this section, we discuss how the measurements used to evaluate the CHD have influenced our understanding of the deficit. More specifically, we will examine how the use of each measurement has, likely unintentionally, lead to unconscious assumptions about the mechanisms underlying the CHD, and consequently narrowed the scope with which we investigate and understand the deficit. This is true of both traditional measurements of perception used to evaluate the CHD, such as the probit slope and the just noticeable difference (JND), as well as the newer proportion correct difference (PCD) score measure, which was designed specifically for evaluating the CHD (Cadieux, Barnett-Cowan, & Shore, 2010). Although previous work has evaluated how each measurement is associated with mathematical pros and cons (Heed & Azañon, 2014), the goal here is to evaluate the unintended consequences that these measurements have had on theories of, and consequently on investigations of, the CHD.

The Tactile TOJ Task

The CHD is studied using the tactile temporal order judgment (TOJ) task. This task has been used to study a variety of perceptual effects. Importantly, it is believed that the perceptual nature of this task allows for an understanding of the perceptual mechanisms underlying behavioural outcomes, such as the CHD, but also more applied applications, such as the understanding of clinical disorders like body integrity identity disorder (BIID; Bloom et al., 2012; Ayoyama et al., 2012). Thus, the use of a TOJ task comes with an important assumption: what is being measured by a TOJ task is perceptual in nature. This means that performance on the task ought to be fundamentally similar across individuals, so long as the perceptual system under examination is typically developed.

The assumption that performance on a tactile TOJ task follows typical psychophysical parameters consequently leads to the assumption that performance on the tactile TOJ task should be similar across typically-developed individuals. Any variations in performance should be viewed as noise, rather than be viewed as systematic differences in tactile localization ability. These assumptions are clearly realized in the traditional measures used to explain behaviour on the task, such as the probit slope and just noticeable difference measures. Importantly, these measures themselves come with a set of assumptions, further constraining how we examine CHD results.

In the following section we examine how use of the probit slope and the (sometimes unconscious) assumptions that go hand-in-hand with its use have influenced study of the CHD (JND measures that are calculated as a parameter of an underlying Gaussian distribution fall prey to the same issues that are discussed about probit slope). Following our discussion of probit slope, we examine how a new measure of the CHD, the proportion correct difference (PCD) score, was created to avoid falling prey to the assumptions associated with using probit slope as a measure of the CHD. However, we detail how the PCD score is fraught with its own issues that have potentially limited our understand of the CHD and tactile localization as well.


(A)
Proportion 'Right First' Response
Uncrossed
Crossed
-400 -200 -100-50 50 100 200 400
(B)
Probit Slope
Uncrossed
Crossed
(C)
Proportion Accuracy
SOA (ms)
(D)
PCD
(E)
female 8
female 9
female 12
female 13
female 14
female 15
female 16
female 17
female 19
female 20
female 21
female 23
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female 25
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male 56
male 57
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male 60
male 61
male 62
Proportion 'Right First' Response
SOA (ms)

Figure 2. Data from an unpublished crossed tactile TOJ study completed by the Multisensory Perception Lab at McMaster University. Participants first completed 6 blocks of 64 trials with the hands uncrossed, followed by 6 blocks of 64 trials with the hands crossed. Each block contained 8 of each of the following SOAs, with negative values indicating that the left hand was stimulated first: ±50, 100, 200, 400. (A) Proportion right first responses at each SOA, collapsed across all participants, (B) probit slope calculated by excluding ±400 SOAs, collapsed across all participants, (C) proportion accuracy at each SOA, collapsed across all participants, (D) PCD scores, collapsed across all participants, (E) proportion right first response graphs for each individual participant in the study, with participant number and sex listed above each graph. All error bars represent ±*SEM.*

Probit Slope

The probit slope measure of the CHD is a typical method of measuring psychophysical effects. To calculate the probit slope, performance on the tactile TOJ task is first computed as the proportion of right-first responses as a function of SOA (with left-first SOAs being denoted by a negative value; see Figure 2A). When the data from a tactile TOJ task are plotted this way, they *usually* form a standard S-shaped psychophysical curve (however, see Yamamoto & Kitazawa, 2001 for evidence of another systematic distribution shape). The proportion right-first values at short SOAs are then probit-transformed separately for the uncrossed and crossed hand postures and linearly regressed. The slope of this probit line (see Figure 2B) is then used to evaluate performance in each hand posture, with a steeper slope indicating better performance.

The Gaussian assumption. The first issue with using probit slope as a measure of the CHD is that it assumes a specific underlying pattern of data. More specifically, it assumes a Gaussian fit that is typical of psychophysical measurements. However, previous work has highlighted that there is ample variability across individuals (Cadieux, Barnett-Cowan, & Shore, 2010, Fig. 2), with some individuals showing no evidence of an underlying Gaussian distribution to their data (Yamamoto & Kitazawa, 2001). A visual inspection of Figure 2E in the present work demonstrates the variability in performance across individuals completing a typical crossed tactile TOJ task. Some may argue that this is a non-issue, given that the data typically reaches a Gaussian fit when collapsed across a pool of participants (see Figure 2A); however, this is not necessarily true.

The issue we would like to highlight with the assumption of an underlying Gaussian distribution isn't about its statistical properties, because, as previous work has suggested, an inverse slope will simply be fitted with a negative value (such as in the N-shaped curve observed by Yamamoto & Kitazawa, 2001), and a flat slope can be assigned a value of zero (Heed & Azañon, 2014; see Figure 3). Instead, we would like to highlight the theoretical consequence of assuming an underlying Gaussian pattern of data. Assuming a Gaussian distribution means that participants who do not fit this model are considered noise and thrown away. Indeed, even though Yamamoto and Kitazawa (2001) demonstrated the reliability with which some participants exhibit a N-shaped response curve, this non-Gaussian pattern of data is often ignored as noise, under the guise that it is unclear whether these participants are performing the task differently than those who display the S-shaped curve. This means that systematic variability across participants is being ignored if their data do not fit the Gaussian distribution.

However, there are many valid reasons why a participant's data will deviate from the Gaussian function. In fact, the assumption that the data will be Gaussian comes from the more hidden assumption described above that the CHD represents an observation of a psychophysical behaviour: The CHD will be exactly the same across individuals because the CHD results from properties of basic physics and neuroscience (so long as the individual being measured is typically-developed). However, there is ample evidence to suggest that this is not true, with both task demands (Cadieux & Shore, 2013; Badde, Heed, & Röder, 2014) and attentional focus (Lorentz et al., Chapter 3) affecting the CHD. These results demonstrate that the CHD manifests differently depending on a number of factors both within and outside of a participant's control. Thus, ignoring participants who do not meet a Gaussian fit is to ignore valuable data that could actually aid in our understanding of the mechanisms underlying the CHD. Essentially, the use of the probit slope has, likely unintentionally, kept researchers from exploring the very variability that is captured by exploring individual differences.

Ignoring long SOAs. The second issue with using probit slope to measure the CHD is that the probit slope requires that only data collected at short SOAs be analyzed. This is because the tactile TOJ data typically plateau at longer SOAs, and thus, must be fit using a different statistic (see Heed & Azañon, 2014 for a review). The issues associated with relying on shorter SOAs due to the use of probit slope as the measure of the CHD has led to a number of theoretical and experimental issues.

Ignoring data from longer SOAs has supported the unconscious assumption that the crux of what causes the CHD occurs at shorter SOAs. We agree that most of the variability is captured at the shorter SOAs, but what about when effects do occur at the longer SOAs? Are we to assume that these effects are due to different mechanisms than those that occur at shorter SOAs? And importantly, how would this implied assumption influence our understanding of tactile localization more generally? We argue that this assumption that the CHD is only captured at short SOAs has led researchers away from the original goal of studying the CHD, which was to use the CHD to tap into how tactile localization occurs at large. Focusing on this niche range of SOAs has stopped researchers from investigating effects that may necessarily occur at longer SOAs, such as the effects of volitional attention or decision-making, which has limited our understanding of tactile localization more generally.

In addition, it is unclear whether influences on the CHD in the literature may have different effects as the extremes, simply because experiments aren't including these longer SOAs in their experimental design. Although previous work has found that the CHD effectively disappears around 300 ms (Shore, Spry & Spence, 2002; Yamamoto & Kitazawa, 2001), this was determined under the most basic conditions under which the CHD is measured. There is ample evidence that changes in task parameters can greatly influence performance on the CHD task (Badde, Heed & Röder, 2014; Cadieux & Shore, 2013). Thus, we should go back and examine whether manipulations that have been examined alongside uncrossed and crossed hand posture behave at the extremes, rather than not measuring these extremes and assuming that nothing of interest happens.

A final critique of the issues with respect to SOAs introduced by using probit slope as a measure of the CHD is that there is no standardized cut-off to delineate ‘short’ SOAs from ‘long’ SOAs. Instead, researchers choose a handful of shorter SOAs, typically shorter than or close to 300 ms. They then eyeball where the data seem to plateau and include non-plateau SOAs in their calculation of probit slope. These differences in SOA make is difficult to compare across experiments completed by different researchers, and sometimes even across different experiments completed by the same research group. In addition, given the influences of task parameters (Badde et al., 2014; Cadieux & Shore, 2013) and an individual’s attentional focus (Lorentz et al., Chapter 3) mentioned above, one can argue that there is a wealth of information hidden in differences between cut-off points. Knowing when performance plateaus under different task and individual parameters would provide us with a more refined understanding of the processes underlying tactile localization.

Summary. The use of probit slope as a measure of the CHD has, unintentionally, limited the ways in which we view the CHD and consequently, the ways in which we have explored the deficit. This has consequently limited our understanding of tactile localization more generally. The requirement that underlying data fit a Gaussian distribution has led researchers to ignore non-Gaussian data by labelling it as ‘noisy’.

This has led to the removal of interesting variability that would be the basis of a novel way to enhance our understanding of the CHD, such as the exploration of individual differences. In addition, the requirement that data included in a probit slope calculation do not come from a 'plateaued' portion of the curve has limited our focus of what may influence the CHD, and consequently, influence tactile localization, such as the influences of volitional attention and decision-making.

The Proportion Correct Difference Score (PCD)

Another example of the complex relation between measurement and theory is the emergence of a measure specific to the CHD known as the proportion correct difference score (PCD; Cadieux, Barnett-Cowan, & Shore, 2010). As was mentioned above, the PCD score was created as a response to the criticisms about the Gaussian distribution assumption associated with the probit slope measure. The PCD measure's creators specifically point out the extreme variability in performance across individual tactile TOJ performance as an impetus for creating the measure (see Cadieux, Barnett-Cowan, & Shore, 2010, Fig. 2). However, the PCD score itself is associated with assumptions that have also limited our ability to use it to understand the CHD and tactile localization more generally.

The PCD score is based on a different metric of performance than the probit slope. More specifically, whereas the probit slope is based on proportion-right-first responses, the PCD calculation is based on accuracy (see Figure 2C). Participant proportion accuracy is calculated at each SOA separately for the uncrossed and crossed hand postures. Crossed accuracy at each SOA is then subtracted from uncrossed accuracy at the same SOA. These difference scores are then summed into an individual value: the PCD score. Thus, the PCD represents a simple difference score between uncrossed and crossed performance, with a larger difference leading to a larger PCD score, signifying a larger CHD (see Figure 2D).

Although this measure does not rely on a specific underlying distribution of the data, it does rely heavily on another assumption. More specifically, the assumption that uncrossed performance represents baseline performance, or performance when the tactile localization system is “working as it should”. Understanding this assumption requires consideration of the integration theory of the CHD (Badde, Heed, & Röder, 2016). This theory suggests that the CHD is a result of conflicting information from the internal and external reference frames when the hands are crossed. An important corollary of these proposals is that information between the two reference frames is congruent when the hands are uncrossed. This leads to the assumption that the system is “working” when the hands are uncrossed, and thus, we can use uncrossed performance as a baseline for tactile localization performance. Investigations of practice effects in the CHD literature provide some evidence to support this, with uncrossed performance being relatively unaffected by increased experience with the tactile TOJ task (Azañon, Stenner, Cardini, & Haggard, 2015; Craig & Belser, 2006), suggesting that an individual’s uncrossed TOJ performance is fairly stable.

However, this assumption that uncrossed performance represents baseline tactile localization feeds into the assumption that uncrossed performance shouldn’t differ within an individual, or across individuals. Thus, collapsing across uncrossed and crossed data in the PCD score is not detrimental, because interesting changes in crossed performance will be captured and the stable uncrossed performance will be absorbed. However, this way of thinking presents significant challenges if one wishes to explore group or individual differences in the CHD. More specifically, using the PCD as a measure of the CHD does not allow for an examination of whether "baseline" uncrossed performance differs between the groups, and such differences are critical to consider when proposing a theory to explain group differences.

Sex differences as an example of PCD weakness. One example of the weakness in using the PCD score as a measure of the CHD comes from the investigation of sex differences in the deficit. Previous work has found that females have a larger CHD when measured by PCD than males (Cadieux, Barnett-Cowan, & Shore, 2010). The authors proposed that females rely more on external reference frame information in the crossed posture than males, leading to their larger CHD. However, this proposed mechanism for the larger CHD in females does not fully align with their observed results.

Both PCD scores and probit slopes were provided as measures of the CHD. The PCD results were simple and in line with their proposed mechanism: the difference between uncrossed and crossed performance was larger for females than for males. However, the probit slope results are at odds with the results they observed in the uncrossed posture—results that are obscured by the calculation of a difference between uncrossed and crossed postures (i.e., the PCD score). The authors reported that females had a significantly shallower slope than males in the crossed posture. This is in line with their proposed mechanism that females rely heavily on conflicting external reference frame information, leading to a larger CHD. However, they also reported that there was a trend toward females having a shallower slope than males in uncrossed posture. This latter finding is at odds with the authors' proposed mechanism. More specifically, work by Badde et al. (2016) found that participants use the same relative weighting of the internal and external reference in the crossed and uncrossed postures. This means that if participants weight external reference frame information heavily in the crossed posture, the same would be true for the uncrossed posture. Relying heavily on external reference frame information that is congruent with internal reference frame information in the uncrossed posture would lead to a more reliable percept, and consequently, enhanced tactile localization. But a trend in the opposite direction was observed for the difference between male and female uncrossed performance.

It may be suggested that this trend was not emphasized because it was not statistically significant. However, it is likely that an overarching reliance on PCD scores, and the theoretical assumption that underlies them, led to this small trend being largely overlooked. Interestingly, recent work by Unwalla, Kearney, & Shore (2020) found that the sex difference, as measured by PCD, is not observed across all experiments.

Implications for theory. The PCD measure relies, likely unintentionally, on the assumption that uncrossed performance represents a "baseline" level of performance for when tactile localization processes are working "as they should". This leads to the assumption that this baseline is the same across groups, which does not appear to be true for sex-based group differences. And these differences in baseline performance have two important implications. The first is that uncrossed performance is not a true “baseline” that would be expected if tactile localization were a physiological principle that was constant across individuals. It is interesting to note that Cadieux, Barnett-Cowan, & Shore (2010) explored sex differences, but focused on differences in crossed performance, although it is clear that there are also differences in uncrossed performance in their data. If uncrossed performance differs across individuals, then relying on the differences between uncrossed and crossed performance to explain tactile localization may not be as theoretically sound as it is currently considered to be, meaning that a fundamental principle of the PCD score calculation is flawed.

In addition, uncrossed performance between males and females must be considered when proposing a theory about sex differences in the CHD. Specifically, it cannot be that females are simply less able to ignore external reference frame information, because this would lead to better uncrossed performance than males, which is the opposite of the observed trend. There must be a more nuanced argument. Although the effect toward worse uncrossed performance by females in Cadieux, Barnett-Cowan, & Shore, (2010) was not significant, this study was likely underpowered to find an effect if it truly exists. And although there appear to be differences across individuals in uncrossed performance, the variability across individuals is smaller in the uncrossed condition than in the crossed condition. This fact is interesting in itself, but also points to the likelihood that Cadieux, Barnett-Cowan, & Shore (2010) were underpowered to find a sex difference in uncrossed performance.

Recent work has also found that this sex difference is not as reliable as originally thought, with the effect being small or absent in a variety of CHD experiments (Unwalla et al., 2020). This raises the question as to whether this group differences approach is obscuring a more nuanced individual differences in tactile TOJ performance across individuals—a difference that is partially confounded with sex. Given the ample variability observed within each sex in Figure 2E of the present work, it is not surprising that this group-level factor of sex does not always account for a significant portion of the variability observed in an experiment. The next section examines this possibility in greater detail.

Group Differences versus Individual Differences

The interest in differences in CHD magnitude across the sexes stems from a broader research question about group differences that can alter the magnitude of the CHD. The basic premise for investigating group differences is to investigate factors across groups that should alter the CHD based on existing theory. If the group differences follow the direction predicted by the integration theory, it is taken as further support in favour of this theory. As outlined in the previous section, the integration theory of the CHD (Badde, Heed, & Röder, 2016) posits that the deficit results from the integration of conflicting external reference frame information when the hands are crossed. Thus, the natural direction to look for group differences is to examine individuals who should have enhanced or limited control over their ability to ignore external reference frame information compared to a control group.

Take, for example, the sex difference outlined above. The initial interest in examining whether sex influenced the magnitude of the CHD was based on substantial evidence that females have poorer spatial abilities than males (Cadieux, Barnett-Cowan, & Shore, 2010). If true, this should extend to the CHD task, because the deficit is proposed to be due to integrating *spatial* information from the external reference frame. The finding of a larger CHD in females than males supported this argument, and the researchers proposed that females show this larger CHD because they simply cannot ignore external reference frame information in the crossed posture. However, recent work has found that this sex difference is not always observed, suggesting that the difference may not truly be driven by the factor of sex, but may rather be due to a currently unexplored confounding variable (Unwalla, Kearney, & Shore, 2020).

Other lines of interest have examined the magnitude of the CHD in individuals who have extensive experience acting with their hands in the crossed posture, rather than an innate or biological difference. The premise behind these studies was that extensive practice in the crossed hand posture should result in the ability to ignore conflicting external reference frame information. However, the results either did not support this prediction, or the evidence for this prediction was weak, with drummers showing an equal magnitude CHD to non-drummers (Craig & Belser, 2006) and pianists showing a reduced, but still present, CHD compared to non-pianists (Kóbor et al., 2006). Later work proposed that the CHD cannot be practiced away, with even the most experienced individuals still showing a CHD, and therefore, still integrating the conflicting external reference frame information. This is corroborated by evidence from practice effect studies of the CHD, which have found that although the magnitude of the CHD can be decreased with practice, the effect was never eliminated (Azañón, Stenner, Cardini, & Haggard, 2015; Craig & Belser, 2006).

In fact, there is only one case in which a group demonstrates no evidence of a CHD at all. Work with blind individuals found that congenitally blind individuals show no CHD, whereas late blind individuals do (Röder, Rosler, & Spence, 2004). Interestingly, however, a CHD can be induced in congenitally blind individuals under certain task parameters (Crollen et al., 2019). Given that the only group shown to have an absent CHD (i.e., congenitally blind individuals) can rather easily have a CHD induced in them begs the question of whether examining group differences is the correct way to examine the effects of different factors on the CHD.

Individual Differences and the CHD

As was discussed in the previous section, the CHD literature has focused largely on group differences: musicians versus non-musicians, males versus females, or congenitally blind versus typically-sighted. As was also discussed in the previous section, this exploration of group differences has been largely unsuccessful: males only sometimes show a smaller CHD than females (Unwalla et al., 2020) and a CHD can be induced in congenitally blind individuals.

Why has the exploration of group differences been unfruitful? It may be that the correct group difference hasn't be explored. But more likely, it is that the assumption underlying the exploration of group differences is misguided. More specifically, the CHD is treated as a perceptual phenomenon. All individuals perform more poorly on a TOJ task when the hands are crossed than when they are uncrossed, and this is a result of how tactile localization perception is carried out in a typically-developed individual. Any differences between individuals is simply noise in the measure that should be ignored.

In fact, although there is ample evidence that many individuals display an N-shaped response curve (Azañon & Soto-Faraco, 2007; Yamamoto & Kitazawa, 2001), most researchers exclude such participants from analyses because "it is unknown whether participants displaying N-shaped response curves process TOJ differently than S-type participants, or whether their response pattern is an extreme variant of systematic errors observed in the reduced steepness of S-curves in crossed conditions in other participants" (Heed & Azañon, 2014, pp. 2). Assuming that tactile localization is a perceptual phenomenon that shouldn't vary between individuals clearly leads to this conclusion. But what if performance on the task does truly vary across individuals? And what if understanding the variability in performance can actually help us understand the processes underlying tactile localization?

Asking and answering such a question requires investigation of individual differences. Studying group differences relies on the assumption that all individuals are the same, more or less, and that any given manipulation will affect everyone in the same systematic manner. This clearly follows the assumption that the CHD is a purely perceptual phenomenon and supports the assumption that all individuals should have a Gaussian response distribution. The study of individual differences relies on an inherently different assumption. All individuals are unique, and the presence of some trait in some amount will lead to a unique response pattern: an N-shaped response curve for some participants is just as valid as the S-shaped Gaussian response curve for other participants.

There is initial evidence that individual differences contribute to the magnitude of the CHD in clinical populations. And unlike studies of group differences, these studies of individual differences have been fruitful. However, the theoretical basis for these studies are rooted in group differences, with an interest in those who have experienced atypical development. More specifically, these studies have focused on individuals from clinical or sub-clinical populations who are likely to display altered reference frame weights based on the symptoms of their disorder. Ferri et al. (2016) found that individuals higher in schizotypal personality traits had larger CHDs, and Wada et al. (2016) found that individuals with higher Autism Spectrum Quotient scores showed a smaller CHD. However, there is also evidence to suggest that typically-developed individuals' CHD magnitude is influenced by individual differences, suggesting that reference frame weights can be altered on a much more nuanced basis (Lorentz et al., submitted; Lorentz et al., Chapter 2).

Lorentz et al. (submitted) demonstrated that a measure of an individual's visual imagery ability was correlated with the magnitude of their CHD. Lorentz (Chapter 3) also demonstrated that the attentional set of the participant at the outset of the experiment can influence responding to the CHD TOJ task. Cadieux et al. (2010; Figure 2) even went so far as to present individual participant graphs to demonstrate the significant variability in participant response patterns observed in a typically-developed population. Taken together, these findings suggest that the CHD may be much more variable than originally thought. Baseline performance likely differs across individuals in a systematic way due to their individual traits—be it visual imagery ability, or attentional set, or some other yet unexplored trait. Thus, we should attempt to examine and explain these individual differences, rather than simply treat the associated variability as noise. And doing so will help us to better understand the mechanisms underlying the CHD.

Important groundwork has already been laid for the investigation of individual differences in the CHD regarding important parameters that must be met for the study of individual differences. First, performance on the measure of interest—in our case, the crossed-hands tactile TOJ task—must be consistent across time, and recent work by Unwalla et al. (2020) found just that. Second, work by Lorentz et al. (submitted) and Lorentz (Chapter 3) has demonstrated initial evidence that cognitive processes under an individual's control can influence CHD performance (visual imagery and attentional processes, respectively). Knowing this information opens the exciting new door for researchers to examine individual difference measures to finally understand the incredible variability seen in CHD performance, rather than treating this variability as noise.

Considering Individual Differences, Attention, and Task Demands

A switch from viewing the CHD through a group differences lens to viewing it through an individual differences lens provides exciting avenues for applications of the

CHD task beyond the laboratory. Although it is often stated that the CHD task is a measure of tactile localization (but see Maij, 2020), research into the task has uncovered that it reliably indexes the relative reliance on difference sources of sensory information in the tactile TOJ task (Badde, Heed, & Röder, 2016; Unwalla et al., 2020). Focusing on the CHD as a measure of how an individual weights different sources of sensory information, such as vestibular information (Unwalla et al., submitted), visual information (Azañón & Soto-Faraco, 2007; Cadieux & Shore, 2013; Kóbor et al., 2006; Lorentz et al., submitted; Röder et al. 2004; but see Badde et al., 2019; Maij et al., 2020) and body side information (Badde et al., 2019), allows us to consider how we can apply the CHD in a clinical context. And importantly, viewing the task in this way alleviates many of the challenges proposed about what the CHD task actually measures (Maij et al., 2020) or the sources of information that it actually taps into (Badde et al., 2019).

Arguably the most important benefit that results from switching from a group differences to an individual differences approach is how exactly the CHD task can be used in a clinical setting. Using a group differences approach limits the CHD to a diagnostic tool: a group of individuals from one population will have a relatively larger CHD than a group of individuals from another population. However, an individual differences approach emphasizes that differences in the CHD between individuals tell us something important about the individual. Studies can examine whether CHD magnitude and the associated relative reference weights are correlated with indices of disorder, and if relations are found, treatments aimed at alleviating dysfunctional reference weights can be explored. Potential disorders of interest include those in which information from one sensory modality or frame of reference is prioritized to a dysfunctional degree such as complex regional pain syndrome (CRPS; Jänig & Baron, 2002; Moseley et al., 2009) and body integrity identity disorder (BIID; Bloom et al., 2012; Ayoyama et al., 2012). In fact, the CHD task has been used as an index of relative reference frame reliance in these disorders, but to our knowledge, no study of individual differences with the CHD task has been conducted.

The recent work demonstrating that CHD performance varies greatly based on task parameters (Cadieux & Shore, 2013; Unwalla et al., 2020; Unwalla et al., submitted) and also varies greatly based on things under an individual's control, such as attention and visual imagery (Badde et al., 2014; Lorentz et al., submitted), provides a foundation for clinical treatments: we can use the malleability of the CHD to alter dysfunctional reference weights. All of these considerations taken together position the CHD task to go beyond a diagnostic tool of CHD magnitude to a tool that can index and change the very reference frame weights that may contribute to disorder.

Conclusion

We have learned much about tactile perception from studies of the CHD over the past several decades. But the future of the CHD rests on a fundamental re-evaluation of the information collected to date and the theories used to explain these data. We must explore the assumptions made about the CHD in terms of the statistical tests used, as well as consider the consequences of using a "broken system" (i.e., crossed performance) to understand the processes underlying typical tactile perception (i.e., uncrossed performance). We must critically examine whether the CHD should be viewed as a basic tenet of tactile localization in the typically-developed individual, or instead move toward viewing the CHD as an index of behaviour under specific task parameters and individual attentional sets. In the present work we provided evidence that answering these questions will require a critical re-evaluation of probit slope and PCD scores as measures of the CHD. We also propose switching from a group differences approach to studying the CHD to an individual differences approach provides the necessary paradigm shift for the CHD, which will allow for a critical evaluation of statistics and theory, as well as provide a way to bring the CHD task out of the laboratory and into a clinical setting to help those who can benefit from decades of research on the CHD task.

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Chapter 5

General Discussion

Introduction

Our sense of touch is critical for our ability to interact with the world around us. Consider the classic example of feeling a bug crawl on your body. We need to be able to localize where that tactile stimulus is coming from to be able to then successfully shake that body part to fling off the unwanted visitor—or for the braver among us, to squash this tactile invader. But regardless of the final goal to shake or squash, our ability to localize tactile stimuli is the first critical step to keeping us safe from the potential disease vector.

Work in the tactile domain has found evidence that locating the tactile stimulus requires a more complex calculation than it seems in this simple example (Badde & Heed, 2016; Badde et al., 2016; Heed et al., 2015; Shore, Spry, & Spence, 2002). It may appear that just knowing where the bug is on your body is enough information to localize said bug. And in the case of shaking off the invader this may be true: Which limb is being touched? Shake that limb. But more often, we need additional information. This is because the tactile sense organ, which is essentially our entire body surface, is able to move throughout space, and our limbs can move relative to one another. This means that we must not only know where on the body this bug is, but also where the touched body part is in space so that another limb (usually the arm) can target that particular locus. For the squashing example, this spatial localization of the tactile stimulus relative to the limb of attack is critical so that you can accurately swat at the bug, lest you unintentionally scare it into running along your skin's surface with greater haste unharmed.

The study of tactile localization has focused extensively on the squashing example where information about location on the body and in space are required. However, the existing literature has not explicitly examined the difference between the shaking and squashing example and what this difference might mean for the processes underlying tactile localization. There is ample evidence to suggest that in general, integration of this additional information is the rule rather than the exception (see Stein & Meredith, 1993; Spence, 2002 for reviews), but new work suggests that the extent to which this information is considered during tactile localization varies depending on the task at hand (Badde et al., 2014; Cadieux & Shore, 2013; Lorentz, Chapter 3; Unwalla et al., submitted). In this thesis I presented novel empirical evidence and an updated theoretical framework that, when taken together, provide us with the more malleable approach required to consider how the tasks of shaking and squashing may differ—and crucially, what this difference means for our understanding of tactile localization more generally.

Studying Tactile Localization in the Lab

The tactile TOJ task. The most commonly cited theory of tactile localization, integration theory (Badde & Heed, 2016; Badde, Heed, & Röder, 2016; Heed et al., 2015; Shore, Spry, & Spence, 2002), is focused on the idea that we need multiple sources of information to successfully complete tactile localization. These sources of information are often described as two reference frames: the internal reference frame and the external reference frame. The internal reference frame provides information about where a tactile stimulus is located on our bodily map. Put more simply, where on our body's surface do we feel the bug? The external reference frame provides information about where the tactile stimulus is located in the space surrounding the body. Where is the bug in space?

Most of the evidence about the use of these two reference frames during tactile localization has been found using the tactile temporal order judgment (TOJ) task (see Azañon & Soto-Faraco, 2007; Azañon et al., 2015; Badde et al. 2014; Cadieux, Barnett-Cowan, & Shore, 2010; Cadieux & Shore, 2013; Craig & Belser, 2006; Crollen et al., 2016; Gallace & Spence, 2005; Kóbor et al., 2007; Röder et al., 2004; Röder et al., 2007; Unwalla et al., 2020; Unwalla et al., submitted; Wada et al., 2004; Yamamoto & Kitazawa, 2001 for examples; but see Badde et al., 2019; Maij et al., 2020 for variations on this typical task). In this task participants receive two vibrations, one to each hand, and are asked to respond with the hand that vibrated first. When the hands are in their typical uncrossed posture, participants' performance is near ceiling. However, simply asking participants to cross their hands over the body midline leads to a significant decrease in performance accuracy.

The integration theory suggests that this deficit observed in performance when the hands are crossed (often referred to as the crossed-hands deficit; CHD) results from integrating internal and external reference frame information during tactile localization. In the uncrossed posture the two reference frames provide congruent information: the stimulated right hand is in the right side of space. But in the crossed posture the two reference frames provide conflicting information: the stimulated right hand is in the left side of space. Integrating these conflicting sources of information leads to the error-prone responding that is referred to as the CHD.

Understanding an effect versus measuring perception. The exclusive use of the tactile TOJ task to measure tactile localization has inadvertently led us to ask a very specific set of questions. These questions have consequently taken us away from our original question about how tactile localization occurs in general to instead focus on questions specific to our task. The crossed tactile TOJ task requires that participants engage with tactile stimuli in a crossed and uncrossed posture. Because of this, our focus is largely on the difference between these two conditions, or more specifically, why crossed performance is worse when the hands are crossed when compared to our baseline uncrossed performance. However, it is important to remember that the crossed condition is an experimental artefact, rather than something that we routinely experience in the real world. Consequently, its merit in terms of illuminating our understanding of tactile perception is contingent on what the crossed-hands manipulation can tell us about the processes active during tactile localization more generally, including when the hands are in the uncrossed position. Only when performance in the uncrossed posture and in the crossed posture are considered together *and* independently can these two positions inform our understanding of tactile localization more broadly.

Our focus on crossed performance has led to an abundance of research about why crossed performance behaves the way it does. This evidence has been used to strengthen our theory that the CHD results from conflicting information provided by the two reference frames (but see Badde et al., 2019). Removing conflicting external reference frame information (Cadieux & Shore, 2013; Röder et al., 2004; Röder et al., 2007) or replacing it with information that is congruent with internal reference frame information (Azañon & Soto-Faraco, 2007; Lorentz, Unwalla & Shore, submitted) decreases the deficit. Similarly, asking the participant to respond in internal (i.e., which *hand* vibrated first) or external (i.e., which side of *space* vibrated first) coordinates influences how much external reference frame information is considered, and consequently, the how large the deficit will be (Badde et al., 2016; Cadieux & Shore, 2013; Unwalla et al., submitted).

In these studies, we are interested in whether the magnitude of the deficit changes. That is, we are interested in the difference between crossed and uncrossed performance. But our original reason for using the crossed tactile TOJ task was to understand tactile localization. The crossed tactile TOJ task is a tool to measure tactile localization, but understanding why crossed performance exists as it does is not the whole picture. We have failed to step back and consider what we have learned about tactile localization more generally. For example, most work to date has uncovered influences on crossed performance, but not uncrossed performance. This makes sense given that uncrossed performance is near ceiling. But this limitation of ceiling performance in the uncrossed posture should not deter us from trying to understand uncrossed performance. Understanding uncrossed performance is just as crucial to our understanding of tactile localization as understanding crossed performance. One could even argue that it is more important to understand uncrossed performance, given that this is the posture we typically reside in.

Interestingly, one study did find a difference in uncrossed performance across two different conditions. Badde, Heed, & Röder (2014) asked participants to engage in a secondary task concurrent with the tactile TOJ task, which decreased the magnitude of the deficit. However, a closer examination of their results demonstrates that the decreased difference in performance between uncrossed and crossed postures resulted largely from worse uncrossed performance in the divided attention condition, rather than the typical reporting of enhanced crossed performance. The implication of this unique finding about uncrossed performance was not discussed theoretically, and instead the task-oriented metric of deficit magnitude remained the focus. This lack of interest in systematic effects on uncrossed and crossed performance is leading us to ignore important signals in our data.

The CHD as a group-level effect. The effect name of “crossed-hands deficit” similarly leads us to focus on why crossed performance is worse when the hands are crossed than our baseline uncrossed performance. When averaged across participants, performance is worse in the crossed posture than in the uncrossed posture. But a quick visual inspection of individual participant data demonstrates that this is not a uniform effect (Cadieux et al., 2010, Fig 2; Chapter 3, Fig 2E). Not all individuals show decreased performance in the crossed posture, and even for those who do, there are significant differences across their behavioural data, including the magnitude of their CHD, and even the distribution that their crossed data follow (Yamamoto & Kitazawa, 2001; Wada et al., 2004), and some participants display worse uncrossed performance than others.

Because researchers are interested in finding the “deficit”, they label individuals who perform differently from their expected distribution as “noise” (see Heed & Azañon, 2016 for a review). In contrast, in this thesis I present evidence that the variability between individuals is, in fact, signal, not noise. Differences in sensory (Chapter 2) and cognitive (Chapter 3) signals that can differ across individuals systematically influence performance. Adopting this view allows us to easily incorporate individual differences measures into our understanding of tactile localization. More specifically, I propose that individuals can differ in the relative weights for their internal and external reference frame based on these sensory and cognitive signals under their control, and these weights systematically influence performance based on the modelling theories in the existing literature (Badde, Heed & Röder, 2016; Unwalla et al., submitted).

In Chapters 2 and 3 of the present work I provided novel empirical evidence to support this. In Chapter 2 I demonstrate that the internally-generated signal of visual imagery influences performance on the crossed tactile TOJ task, and more importantly, that an individual’s ability to successfully implement this visual imagery influenced how much this imagery impacted this tactile TOJ performance. This provides initial evidence of an individual difference that influences tactile TOJ performance, and by extension, tactile perception as well. In Chapter 3 I demonstrated that the attentional state of the participant (i.e., focused or relaxed) influences tactile TOJ performance, and interestingly, that this influence of attention was mediated by the differential impact of specific task parameters. The findings that visual imagery and attention can influence tactile TOJ performance in systematic ways provide us with a new path forward about how we can best study tactile localization to understand how it is carried out in each and every individual in each and every circumstance, not just how it occurs in the crossed tactile TOJ task at the group level.

But uncovering the systematic influences of individual traits on tactile TOJ performance is insufficient for a better understanding of the existing literature on the effects of perceptual changes (e.g., blindfolding in Cadieux & Shore, 2013) and task demands (e.g., response demands in Cadieux & Shore; Unwalla et al., submitted). In Chapter 4 of this thesis I provided an overview of the aspects of our theory, scientific approach, and statistics that we must re-evaluate to incorporate individual differences and ultimately better understand the available data. In the next section I propose a framework that will allow us to realize this incorporation using a simple change highlighted in Chapter 1 of the present work.

A New Horizon for the CHD and Tactile Localization

We have a literature full of evidence that changes to perceptual information other than somatotopic information influence tactile TOJ performance (see Azañon & Soto-Faraco, 2007; Azañon et al., 2015; Craig & Belser, 2006; Crollen et al., 2016; Kóbor et al., 2007; Röder et al., 2004; Röder et al., 2007). This suggests that multiple sources of information contribute to tactile localization. We have other evidence that changes to task parameters can alter how much attention is paid to these various sources of sensory information (Badde et al., 2014; Cadieux & Shore, 2013; Unwalla et al., submitted). This suggests that the integration of multiple sensory signals for tactile localization is malleable. In Chapters 2 and 3 I provide evidence that internally-generated signals can also influence tactile TOJ performance, and that the influence of these signals can vary across individuals. This suggests that tactile localization is not only malleable at the level of the task, but also at the level of the individual. Critically, we must consider *all* of these findings when we devise a theory for tactile localization. Ignoring any component will lead to an incomplete theory and consequently leave us with seemingly contradictory behavioural findings.

Modelling behaviour. These ideas can be combined in a relatively straightforward manner when understood in terms of a Bayesian model of tactile localization estimates (see Ernst & Bulthoff for an overview). Information from multiple sensory signals are included in the calculation. The weights for these signals are partially driven by the reliability of that signal. However, task parameters and individual traits can also adjust the weights associated with each signal. When considered together, we have a single model that can explain not only the effects of perceptual changes and task demands established in the literature, but also the individual traits explored in Chapters 2 and 3 of the present work.

I propose that attention is critical to how we understand reweighting based on task demands and individual differences. Altering the availability or quality of perceptual signals affects reference frame weights through changes to the reliability of that perceptual signal. In contrast, altering task parameters affects the weights by changing how much attention is paid to information from each reference frame. Similarly, in the case of an individual difference, some individuals may be predisposed to pay more or less attention to information from the external reference frame, such as individuals with an eating disorder (Riva, 2012) or schizotypal personality disorder (Ferri et al., 2016) and individuals with autism, respectively (Wada et al., 2014), or individuals may approach the task in a more focused or relaxed attentional state (Chapter 3). Similarly, task parameters can change how much attention is paid to information from either reference frame by explicitly asking participants to respond in either internal or external coordinates (Cadieux & Shore, 2013; Unwalla et al., submitted) or by distracting attention away from external reference frame information with a secondary task (Badde et al., 2014). Thus, calculations of reference weights are the result of only two influences: reliability of perceptual signals and attentional focus on those perceptual signals.

This leads us back to our example of shaking or squashing the bug. The same perceptual information is available in both cases, but our different goals (i.e., shake or squash) may change how we interact with these different sources of information, much like how different task demands do the same. Thinking this way provides a lens with which to view new evidence that seems to question whether the tactile TOJ task measures tactile localization at all.

An explanation for contradictory results. Maij et al. (2020) found evidence to suggest that external information about space did not influence responding in their version of the crossed tactile TOJ task. In their task participants received two vibrations. They were asked to respond with the location of the first tactile stimulus by pointing to that location with the hand that vibrated first. Participants began each trial with their hands on a table in either the uncrossed or crossed posture, and then moved their arms toward the body to end in either the same posture or the opposite posture from their starting posture. The two vibrations could occur at any time during this trajectory. The results demonstrated that rather than the spatial location of the tactile stimulus influencing responding, the response actually influenced perception of tactile location. More specifically, participants constructed tactile location post-hoc by determining which hand vibrated first, and then calculating where that hand was during the first vibration.

They consequently suggested that the tactile TOJ task does not index tactile localization and proposed that it instead indexes hand assignment. But these same authors provided evidence that hand assignment is used as a heuristic to post-hoc index tactile localization. In essence, tactile localization did occur, just not in the way that the authors conceive of tactile localization. However, conceptualizing tactile localization as the result of the integration of multiple sensory signals that is influenced by reliability of the signal, task parameters, and cognitive influences or individual characteristics can explain why information is used differently or even discounted in this atypical version of a tactile TOJ task. This can account for why location in external space did not appear to influence tactile localization performance. The same perceptual signals were available as those during a typical tactile TOJ task, but the addition of movement both during perception of the tactile events and during the response likely changed how the external reference frame information was used.

The same explanation can be used to understand why information about external space did not seem to influence responding in the task used by Badde et al. (2019). In their task, participants received two vibrations, one to the hand and one to the foot. Either the hands or feet could be a crossed posture, or both hands and feet could be in a crossed posture. An analysis of errors found that responses were not influenced by the side of space stimulated. However, it seems likely that this is due to specifics of the task used. Introducing both the hands and feet to the task likely changed how much attention participants paid to external information about space. Future work can examine whether this is the case. But viewing the results of Maij et al. (2020) and Badde et al. (2019) in light of the framework proposed in this thesis allows for a parsimonious account of all of the data collected to date.

Conclusion

In essence, viewing tactile localization as a dynamic ability that is influenced by a variety of factors, including reliability of perceptual signal, task demands (including task goal), and cognitive influences or individual traits allows us to account for the systematic group-level effects observed in the literature time and time again, but also the influence of internally-generated traits explored in Chapters 2 and 3 of the present work, as well as the seemingly contradictory new findings of Maij et al. (2020) and Badde et al. (2019). However, the variety of implicit assumptions we make when we approach studies of tactile localization discussed in Chapter 4 of the present work must be explicitly reevaluated for future research to be able to engage in experiments to test the assumptions of this new framework.

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