CROSSING THE MIDLINE

CROSSING THE MIDLINE: AN EXPLORATION OF REFERENCE FRAME CONFLICT

BY

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Abstract

Multiple reference frames are used to interact with our surroundings. When these reference frames are in conflict, processing errors can occur. For tactile stimuli, this conflict is highlighted when the hands are crossed over the midline of the body. In this posture, vibrotactile temporal order judgments (TOJs) presented to the hands are impaired compared to an uncrossed posture. This decrease in temporal processing is known as the crossed-hands deficit. The deficit was explored in depth throughout this thesis. In Chapters 2, 3 and 4 different elements of the crossed-hands deficit were evaluated including its connections to the rod and frame test, individual and sex differences within the TOJ task, as well as the influence of vision and body position. These elements were framed with underlying goal of investigating the root cause of the deficit. The data presented here provided evidence for a conflict model of crossed hands processing. A conflict between the internal and external reference frames produced the deficit in temporal processing when the hands were crossed. The role of the body's midline in understanding multisensory integration was further considered in Chapter 5 through the rubber hand illusion, which is a visuotactile phenomenon whereby an unseen real hand is mislocalized towards a seen rubber hand. When the real hand, rubber hand, or both were crossed over the midline the illusion did not occur. It was hypothesized that a failure to integrate the tactile information presented to the real hand with the visual rubber hand was responsible for the absence of the illusion. Taken together, the data presented in this thesis contribute to the greater understanding of how reference frame conflicts are resolved, particularly when the conflict occurs across the body's midline.

This dissertation is dedicated to my husband, Riziq.

Thank you for your love and support.

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List of Abbreviations

ANOVA	Analysis of variance
PCD	Proportion correct difference
RFT	Rod and frame test
RHI	Rubber hand illusion
RT	Reaction time
TOJ	Temporal order judgment

Declaration of Academic Achievement

Chapter 1 – Introduction

Author: Michelle L. Cadieux

Chapter 2 – Crossing the hands is more confusing for females than males

Authors: Michelle L. Cadieux, Michael Barnett-Cowan & David I. Shore

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Chapter 3 – Response demands and blindfolding in the crossed-hands deficit: An exploration of reference frame conflict

Authors: Michelle L Cadieux & David I Shore

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Chapter 4 – Supine body position and the crossed hands deficit

Authors: Michelle L Cadieux, Megan O'Connor, Crystal Rankin, & David I Shore

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Chapter 5 – Rubber hands do not cross the midline

Authors: Michelle L Cadieux, Katelyn Whitworth, & David I Shore

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Chapter 6 – Discussion

Author: Michelle L. Cadieux

1. Introduction

We view and interact with our environment in many ways. The different perspectives we take influence how we relate to our surroundings. Take for example preparing a meal with a friend. As chef, you must regularly ask your friend to hand you the necessary items and ingredients. You can base your directions on either your internal perspective or you can use their location with regards to the other items on the counter. You can ask your friend to hand you the knife on your right or the knife to the left of the salad bowl. Both refer to the same item but they rely on different reference frames. The first makes use of the internal reference frame, in which the observer is the center of the world; the second requires an external reference frame, in which objects are references to each other and the position of the observer plays no role. The goal of the present thesis is to assess how internal and external reference frames influence behaviour. Specifically, it will address situations in which the information provided by these frames of reference is in conflict.

Conflict between an internal and an external reference frame is seen when we cross our hands over the midline of our body. In this posture, our right hand is on the left side of our body and our left hand is on the right. If we view our right hand in this scenario from an internal perspective, it is still considered "right"—crossing our right hand over the midline does not stop it from being our right hand. However, if we view this situation from an external viewpoint, our right hand is now on the left side of visual space. Using external world coordinates, it would be considered "left". In this crossed-hands position, the internal and external reference frames are providing different information. This conflict of information can cause a deficit in temporal processing.

1.1 Temporal Order Judgments and the Midline

Performance on tactile temporal order judgments (TOJs) is significantly impaired when observers place their hands in a crossed posture (Azañón & Soto-Faraco 2007; Cadieux et al 2010; Craig & Belser 2006; Drew 1896; Heed et al., 2012; Holmes et al 2006; Kobor et al 2006; Roberts & Humphreys 2008; Roder et al 2004; Shore et al. 2002; Wada et al 2004; Wada et al., 2012; Yamamoto & Kitazawa 2001). Two main explanations have been proposed to address this crossed-hands deficit (Yamamoto and Kitazawa 2001; Shore et al. 2002). Both explanations involve transformation from an internal reference frame to an external one. Yamamoto and Kitazawa (2001) attribute the deficit to a delay in processing time when a crossed-hands posture is adopted. They propose that the hands must first be localized in external space before temporal order can be determined. The final determination of stimulus order is based on external coordinates only. In contrast, Shore et al. (2002) propose that both reference frames remain active after the translation, but these reference frames provide conflicting information when the hands are crossed. It is this conflict between the reference frames that causes the deficit. The data presented here will provide further evidence for a conflict model as opposed to a delay in the transfer of information from an internal to an external reference frame.

Temporal order judgments (TOJs) allow for the assessment of temporal processing. Several factors can influence our ability to judge temporal order. When stimuli are presented to the hands, the physical distance between them affects performance, with accuracy improving as distance between the hands is increased (Shore et al. 2005). Shifting the perceived difference between the hands using mirrors shows a similar effect (Gallace & Spence 2005). Performance on TOJs is reduced in older adults (Craig et al., 2010), sleep deprived individuals (Babkoff et al., 2005), and dyslexics (Ben-Artzi et al, 2005). With dyslexia, the TOJ deficit indicates that it is not a language-specific disorder but a general dysfunction in temporal processing (cf. Farmer & Klein, 1995). In Chapters 2, 3, and 4, I used TOJs as a tool for measuring temporal processing across the midline.

Vibrotactile TOJs are impaired when hands are crossed over the midline. This deficit is not an all or none effect. An intermediate deficit can be produced when the hands but not fingers or the fingers but not hands are crossed over the midline (Heed et al., 2012). While the hands are most commonly studied, the deficit is not unique to this area of the body; it has also been found in the feet (Schicke & Roder, 2006). The crossed-hands deficit provides us with a tool to study the role of the midline in temporal processing and reference frame conflict.

The crossed-hands deficit develops in childhood. Children younger than 5 years of age do not show the deficit (Pagel et al., 2009). Visual experience during the early years of life appears to play a key role in its development. Only the performance of late-blind but not congenitally blind individuals is hindered when the hands are crossed over the midline. While the deficit is typically set after childhood, it can be drastically reduced with training (Craig & Belser, 2006). The malleability of the deficit may help to account for some of the individual differences present in the crossed-hands deficit, which will be further explored in Chapter 2.

1.2 Crossing the Midline

Although accuracy is currently the most popular method to examine the crossed-hands deficit, reactions times (RTs) are also an interesting avenue of research (Nicoletti, Umilta, & Ladavas, 1984; Riggio, Gawryszewski, & Umilta, 1986). During a choice RT task, RTs are increased when a crossed-hands posture is adopted (Nicoletti, Umilta, & Ladavas, 1984). However, during a simple RT task where no decision must be made to respond accurately, RTs are not increased in the crossed position. This result provides some evidence for a conflict model of crossed-hands effects. When both hands have to be taken into account, a reference frame conflict occurs that does not happen during a simple one-hand RT task. When both hands are crossed over the midline, the internal reference frame is not only in conflict with external visual space, but also the hands with regards to themselves—the right hand now lies to the left of the left hand and vice-versa. Crossing the hands over the midline allows for the examination of reference frame conflicts on many levels. In the current thesis I will examine the importance of the midline using two tasks: temporal order judgments and the rubber hand illusion.

1.3 Measures of Reference Frames

Although TOJs are an important tool in exploring reference frames and was the main paradigm used in this thesis, other tasks can provide us with different measures of reference frame interaction. Mental rotation, navigation and the rod and frame test all require the use of multiple reference frames. Additionally, visual space and the effects of gravity on our body can influence our perception of reference frames, thus changing how they interact with one another. Examining these tasks and effects can create a more complete picture of how reference frames are measured.

1.3.1 Mental Rotation

Mental rotation typically requires an individual to rotate a three dimensional object along one of its axes. As with the crossed-hands deficit, mental rotation tasks provide insight into how we manipulate and manage reference frames. The basic task is to determine, as quickly as possible, whether or not two objects are the same—except for a rotation in space. Reaction time for correct responses increases linearly with the angle of rotation (Shepard and Metzler, 1971). In other words, the greater the disparity in rotation between the two objects, the longer it takes to resolve the rotation.

Two types of mental rotation are commonly used—block and body (hand). In a block mental rotation task, observers are typically presented with two line drawings of three-dimensional interconnected blocks. Block rotation utilizes the external reference frame, in the sense that one object is rotated with regards to another. Body rotation uses drawings of human bodies in different positions. It may also sometimes use a single body with a dark circle placed either the right or left hand. In this case, observers are required to indicate on which hand the target is present. Body rotation uses a more body centered reference point for its completion (Bonda et al., 1995), indicating that it taps into an internal reference frame. Although the two bodies are still rotated with regards to each other, participants tend to picture themselves as the body being rotated. Comparing these two types of mental rotation can provide insight into how reference frames function together to determine the orientation of objects in space.

1.3.2 Navigation

Navigation is possible using both the internal and external reference frame. For example, if we are giving directions, we can base them on a traditional map perspective (i.e., go east on Main Street) or we can base those directions on our own view point (i.e., turn right on Main Street). These two descriptions convey the same information, but rely on different reference frames: the first demands an external reference frame in which the actor plays no part in the world view, while the second requires an internal reference frame in which the actor is the center of the world. This same idea can be applied to walking towards a target. We can use both locomotor information (internal) or visual information (external) to achieve our goal. Both types of information provide us with the same level of precision and when conflict occurs, an average is taken (Ellard and Shaughnessy, 2003). When both sources provide accurate information, individuals show a preference for using an internal or external representation (Gramann et al., 2005). However, switching to the non-preferred frame has little consequence.

Environments are coded for navigation in different ways. Novel environments are coded using an internal representation whereas familiar locations are represented using an external reference frame (Iachini et al., 2009). This shift in coding can be seen with the different errors made during area learning. In novel environments, errors are made with respect to the position of the observer. However, in familiar locations errors occur between structures with reference to each other. The initial body centered representation is used to form an external map of one's surroundings over time.

1.3.3 Rod and frame test

The rod and frame test (RFT; Witkin and Ash, 1948) examines reference frame bias. The RFT can involve physically setting a rod to the subjective vertical or indicating if a visual straight line is vertical or tilted, or to which direction it is tilted (left or right relative to gravity; e.g. Figure 2.4, Chapter 2). The rod or line is fixed within a frame tilted about its centre. Observers are told to ignore the frame and base their judgments on the position of the rod alone. The degree to which the frame influences judgment of vertical is known to as the 'frame effect'. This effect provides an estimate of an individual's visual dependence. When the line is set closer to the direction of the frame, observers are considered to be more visually dependent (Witkin et al., 1954). Those who are more visually dependent are more likely to use visual cues to estimate both the perceived direction of vertical and their own body position.

In Chapter 2, I examined the connections between the RFT and the crossed-hands deficit. The goals of this chapter were twofold. First, I was interested in possible correlations between these two tasks. Both tasks required the use of an internal and external reference frame for accurate performance. During the crossed hands phase of this experiment, participants were required to use external coordinates for their responses. Information needed to be transferred from an internal somatosensory representation of the tactile stimuli to an external reference frame. Under these response demands, the internal and external reference frames would provide opposing information. This conflict mirrors the reference frame opposition seen in the RFT. Participants are required to ignore the visual tilted frame and base their judgment of vertical on the upright position of their body and gravity. It is this similarity that leads to the hypothesis that performance on the RFT could predict the size of the crossed-hands deficit. The second goal was to provide a more in-depth examination of the crossed-hands deficit itself. Particularly the wide range of individual differences present in a crossed-hands TOJ task, as well as possible sex effects within the task.

1.3.4 Visual space

Visual space plays an important role in the crossed-hands deficit. Crossed performance can be improved with the sight of uncrossed rubber hands (Azañón & Soto-Faraco, 2007). Performance can also be improved by crossing the hands out of sight behind the observer's back (Kobor et al., 2006). In these cases, vision is a defining factor. Both rubber hands and crossing behind the back shaped the participant's perception of their hands in external space.

The primary goal of Chapter 3 was to explore the effects of vision on the crossed-hands deficit. The amount of visual information available to participants was reduced through blindfolding. By restricting vision, the information provided by the external reference should be degraded given that it is a primarily visual frame of reference. Under these conditions, when the hands are crossed, the two theories detailed earlier predict opposing outcomes. With a degraded external frame, the time required to remap stimuli to that frame should increase. Based on the hypothesis put forward by Yamamoto and Kitazawa (2001), the increase in remapping time should result in the size of the deficit being increased as well. On the other hand, according to Shore et al. (2002), degrading the external reference frame should reduce the size of the deficit. Under this framework, the reduced reliability of the external frame should push observers to depend on the information provided by the more stable internal reference fame. In response to this shift, the conflict between the two frames of reference would be reduced.

1.3.5 Gravity

Two measures are used to evaluate which way is up: the subjective visual vertical (SVV) and the perceptual upright (PU) (Dyde et al. 2006). The SVV represents the influence by gravity on the perception of up. Like vision, gravity is most closely tied to the external reference frame (Barnett-Cowan & Harris, 2008). To assess this measure, observers are asked to judge when the orientation of a line appears vertical and aligned with the perceived direction of gravity. On the other hand, the PU is directly linked to the internal reference frame. It represents the influence of the body's orientation on the perceived direction of 'up'. For its evaluation, observers are asked to judge the orientation of a visual stimulus. For example, 'p' and 'd' are the same stimulus except for their orientation. Which of the two letters is perceived hinges on the direction of 'up'. These two measures capture different elements to the perception of which way is 'up'.

Chapter 4 examined how body position – upright versus supine – would influence the crossed hands deficit. In the upright position, both the PU and SVV are aligned and provide congruent information. In the supine position, the PU remains aligned with the direction of the body, separating itself from the SVV, which is constant with the direction of gravity. In the supine position, the PU and SVV provide conflicting information with regards to which way is up. This confusion in the direction of up should cause a degradation of the external reference frame. As in Chapter 3, this should drive participants to adopt the more reliable internal reference frame, resulting in the same predictions as the previous chapter. If the crossed-hands deficit were due to a delay in remapping time, the deficit should increase in the supine position. However, if the deficit were caused by a conflict between the two reference frames, performance should improve in the crossed posture when an internal reference frame is adopted.

1.4 Rubber Hands

The 5th chapter shifted from the use of TOJs to exploring the rubber hand illusion (RHI). In the RHI, a person mistakes a fake rubber hand for his or her own hand (Botvinick & Cohen, 1998). The real hand is hidden from view and replaced with a fake rubber hand. Both the real hand and the rubber hand are stimulated—typically using paintbrushes. After a relatively brief period of synchronous brushing (Ehrsson et al., 2004), the illusion can be induced. The participant not only reports that the rubber hand feels like their hand but they also tend to mislocalize the position of their real hand towards the rubber hand.

An integration of reference frames is required to produce the rubber hand illusion (see Makin et al., 2008 for review). As with the crossed-hands deficit, the internal and external reference frames provide conflicting information. It is the multisensory integration of these opposing reference frames that induces the illusion. The touch on the real hand (internal) and the visual information from the rubber hand (external) are erroneously combined, which produces the illusion that the touch is occurring on the rubber hand and therefore that the rubber hand is the real hand. If the hands are brushed asynchronously, the illusion does not occur. The integration of the tactile and visual information only occurs when they are temporally matched.

The RHI can be separated into two components: Visual capture of touch and proprioceptive drift. Visual capture refers to the feeling that the tactile stimulation of the brush is being felt on the rubber hand. In other words, the visual fake hand is capturing the touch felt on the real hand. Proprioceptive drift alludes to the mislocalization of the real hand towards the rubber hand. The visual information provided by the rubber hand dominates the proprioceptive information from the real hand. During the illusion, the perceived location of the real hand drifts towards the fake hand.

Several factors influence the degree of illusion that is experienced. An unusual or varied brushing pattern and a more realistic looking rubber hand increases the illusion (Armel & Ramachandran, 2003). The rubber hand must also be anatomically aligned with the body (Pavani, 2000). If the hand is too far away, flipped around, or in an impossible position, the RHI cannot be induced.

The final data chapter explored the importance of the midline in the RHI. For the illusion to occur, information from an internal (tactile) and external (visual) reference frame has to be integrated into a single representation. When the hand is crossed over the midline, the hand is not only harder to locate in space but multisensory integration is also impaired (Shore, Spry, & Spence, 2002; Spence, Kingstone, Shore, & Gazzaniga, 2001). Confusion with regards to the position of the real hand may increase the RHI—participants might be more likely to mislocalize the rubber hand. However, given the disruption of multisensory integration when the hands are crossed, the illusion may be reduced. This result would occur if the tactile and visual information could not be integrated.

1.5 Goals

The main goal of this thesis was to explore reference frame conflict. This was done primarily through addressing the underlying cause of the crossed-hands deficit—an effect in which at its core is conflicting information from reference frames. Although the crossed-hands deficit is well documented, the root cause of the deficit has not been directly addressed. Secondary goals included comparing the crossed-hands deficit to the putatively related rod and frame test (Chapter 2), examining both individual and sex differences within the task (Chapter 2), analyzing the effects of both vision (Chapter 3) and body position (Chapter 4) on the deficit, and finally considering how multisensory integration is affected across the midline (Chapter 5).

Chapter 2: Crossing the hands is more confusing for females than males

2.1 Abstract

A conflict between an egocentric and an external reference frame can be highlighted by examining the marked deficit observed with tactile temporal order judgments (TOJ) when the hands are crossed. The anecdotally reported large individual differences in the magnitude of this crossed-hands deficit were explored here by testing a large group of participants (48; 24 female). Given that females have been shown to be more visually dependent than males in the potentially related rod-and-frame test (RFT), we hypothesized that females would show a larger influence of the external reference frame (i.e., a larger crossed-hands deficit). As predicted, female participants produced larger tactile TOJ deficits compared to our male participants. We also administered the RFT in these participants with hands crossed and uncrossed. Crossing the hands increased the effect of the frame in the RFT, more so for females than males, further highlighting the potential difference in the way that each sex accommodates reference frame conflicts. Finally, examining the relation between the two tasks revealed a significant correlation, with larger frame effects associated with larger crossed-hands TOJ deficits, but this only held for males. We speculate that sex specific differences in multisensory processing and

spatial ability may explain why females are less able to disambiguate a crossed-hands posture than are males.

2.2 Introduction

Performance on a tactile temporal order judgment (TOJ) task is drastically impaired when observers place their hands in a crossed posture (Drew 1896; Yamamoto and Kitazawa 2001; Shore et al. 2002; Röder et al. 2004; Wada et al. 2004; Sanabria et al. 2005; Holmes et al. 2006; Craig and Belser 2006; Röder et al. 2007; Azañón and SotoFaraco 2007). This crossed-hands TOJ deficit can be as large as 300% when compared to an uncrossed posture (Shore et al. 2002; Röder et al. 2004). One striking finding concerns the vast individual differences in the magnitude of this deficit—some observers show only a small deficit, while others show almost a complete reversal in response pattern (Yamamoto and Kitazawa 2001). One goal of the present study was to assess this variability. A second goal was an attempt to find a measure that covaries with these individual differences in the hopes of better understanding the deficit through a comparison with a putatively related measure. Specifically, we evaluated the correlation between the tactile TOJ crossed-hands deficit and the influence of a visual frame on the perception of subjective vertical (rod-and-frame test: Witkin and Asch 1948).

We predicted a relation between performance on the rod-and-frame task and the tactile TOJ crossed-hands deficit for several reasons. First, both measures are associated with large individual differences (Witkin et al. 1954; Cadieux and Shore, unpublished data). Second, there appears to be a large visual component to the crossed-hands deficit, and this is the source of the effect in the rod-and-frame illusion. Finally, both tasks require a transformation between an egocentric frame of reference and an external one. For the purposes of the present paper, an external reference frame refers to either a visual or gravitational reference frame which is defined as body-centered aligned with the orientation of the body[1], whereas egocentric refers to a reference frame tied to the body surface (i.e. somatotopic). While somatotopic and egocentric reference frames represent different information and cannot be considered the same thing, it is our assumption that the transformation processes required to relate one frame of reference with the other are closely related. Both somatotopic and gravitational reference frames influence our interpretation of body position and our relation to an external reference frame. It is the need to transform an internal representation into an external one in both tasks that motivates our hypothesis that the two tasks will be related.

2.1.1 Reference frames in the crossed-hands deficit

Two main explanations have been proposed for the crossed-hands deficit in TOJ performance (Yamamoto and Kitazawa 2001; Shore et al. 2002) both of which involve transformation of information from an egocentric frame of reference to an

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[1] The term 'allocentric' is sometimes used to describe this type of visual reference frame. However, this term usually applies to a frame of reference based on an external object rather than on the subject. In our case, external objects are classified with reference to the participant's midline, therefore we have chosen to use the term 'external' as opposed to 'allocentric'.

external one. Yamamoto and Kitazawa attribute the deficit to a delay in this process when the hands are crossed. They contend that the hands must first be localized in space (i.e., tactile stimulation must be translated into an external reference frame) before the temporal order can be determined. In contrast, Shore et al. proposed that both frames of reference remain active after the transformation, but these reference frames provide conflicting information when the hands are crossed (Shore et al. 2002). Within this latter framework, the deficit is attributed to the time required to resolve the conflict between the two reference frames. While these are different theoretical accounts of the observed deficit, they are by no means mutually exclusive—the transformation process may be slower with the hands crossed, and both frames may compete at the time judgments are made.

Many pieces of evidence support the existence of both reference frames at the time a TOJ is computed. For example, when participants are encouraged to code the tactile stimulation in an egocentric frame of reference, the deficit is reduced, but not eliminated (Shore et al. 2006, IMRF presentation). Here, two groups of participants were each given different response demands in a tactile TOJ task. The external reference frame group was required to respond by lifting the foot on the side of space that was stimulated first, whereas the egocentric group lifted the foot that corresponded to the hand that was stimulated first. With an uncrossed posture, these response demands were identical, whereas in the crossed posture they were not. Better performance was found with the crossed posture for the egocentric group (i.e., those encouraged to maintain a reference frame tied to the hand). Thus, changing the response demands maintained the stimulus coding in an egocentric frame of reference and reduced the size of the deficit. Additionally, the external reference group evidenced poorer accuracy with the uncrossed posture, even though the physical response demands were identical. These results implicate the involvement of both reference frames—egocentric and external—in determining performance in the crossed-hands TOJ task. In considering the nature of the external reference frame, the impact of vision on our awareness of limb position needs to be evaluated (cf. Lloyd et al. 2003).

2.2.2 Role of vision in the crossed-hands deficit

Visual information has been shown to dominate over other sensory stimuli in sensory-motor coordination (Batista et al. 1999; Pouget et al. 2002; Röder et al. 2004). Within the context of judging the location of tactile information, manipulating the sight of the limbs by varying the distance between the hands (Shore et al. 2005; Soto-Faraco et al. 2004; Gallace and Spence 2005), crossing the hands behind the back (Kobor et al. 2006), using mirrors (Holmes and Spence 2005), and substituting the hands with rubber hands (Botvinick and Cohen 1998; Pavani et al. 2000; Azañón and Soto-Faraco 2007) all influence the crossed-hands deficit. This implicates a strong role for vision in determining the size of the deficit.

Take as an example, the effect of seeing crossed rubber hands when the hands remain uncrossed and out of sight (Azañón and Soto-Faraco 2007). Here, a significant TOJ deficit was found, as if the hands were actually crossed. Likewise, when the hands were physically crossed and the viewed rubber hands were uncrossed, there was a drastic reduction in the deficit. Additional support for the role of a visual frame of reference in the tactile TOJ crossed-hands deficit comes from studies of congenitally blind individuals. Early blind individuals do not show this deficit and indeed appear to respond to tactile stimuli as if they are represented in an egocentric frame of reference (Röder et al. 2004). Further evidence comes from event-related potentials (ERPs), with congenitally blind individuals producing identical attention-related negativity regardless of hand posture (Röder et al. 2008). Sighted individuals, on the other hand, show early attention positivity in the uncrossed posture. Heed and Röder (2010) also showed increased positivity when limbs (hands and feet) were placed closer together during a tactile attention task, implicating the use of both anatomical and external coordinates in tactile localization. Together, these results provide strong evidence for how a visual external reference frame affects the magnitude of the tactile TOJ crossed-hands deficit.

The prediction of a relation between the deficit observed when completing a tactile TOJ with the hands crossed and visual dependence measured using the rod-and-frame test stems from a consideration of both the conflict between egocentric and external reference frames and the impact of vision in determining the size of both effects.

2.2.3 Rod-and-frame test

The rod-and-frame test (RFT; Witkin and Asch 1948) has been extensively administered to quantify individual and group differences in reference frame bias. The RFT consists of setting a visual rod or straight line to the subjective vertical (subjective visual vertical). The rod is embedded within a visual frame tilted about its centre. Observers who set the line closer to the direction of the tilted frame are said to be more ‘field (visually) dependent’ (Witkin et al. 1954) as they are more influenced by the visual frame of reference than the gravitational and egocentric frames of reference (which are aligned when the head and body are both oriented upright). It has been hypothesized that individuals who are visually dependent use mainly visual cues for estimating not only their subjective vertical but also their body position (Luyat 1997).

A common observation from the RFT concerns the difference between females and males. Females have been shown to be less precise (i.e., higher within subject variance) in estimating the perceived vertical and to be more visually dependent than males in the RFT (Witkin et al. 1954; Gross 1959; Bogo et al. 1970; Hyde et al. 1975; Linn and Petersen 1985; Barnett-Cowan et al. 2010). There have been a number of explanations as to why females may be more visually dependent than males. Sex differences are also present in mental rotation (Linn and Petersen 1985; Voyer et al. 1995; Parsons et al. 2004), maze navigation (Gron et al. 2000; Shore et al. 2001), and path integration (Chaudhury et al. 2004), suggesting that females generally perform poorer than males in measures of spatial ability. Another explanation that has been put forward states that sex differences in the RFT are attributable to sex differences in the size of the vestibular organs. Tremblay et al. (2004) and Tremblay and Elliot (2007) hypothesized that females depend more on vision as a result of relying less on gravitational cues because the otoliths, which detect tilt of the head relative to gravity, are smaller in females (Sato et al. 1992). This latter hypothesis has recently been rejected by Barnett-Cowan et al. (2010) in favor of a hypothesis that females and males integrate sensory cues differently, with vision being more highly weighted in females than in males (Kennedy et al. 1996; Darlington and Smith 1998; ViaudDelmon et al. 1998; Berthoz and Viaud-Delmon 1999) at equal cost to gravitational and the internal representation of the body information (Barnett-Cowan 2009).

The visual nature of the RFT and the role that differential weighting of conflicting reference frames plays in causing the deficit reinforced our prediction that RFT performance would predict the size of the crossed-hands deficit. Conflicting sensory information of an external frame of reference has been shown to affect judgments in egocentric tasks (Dassonville et al. 2004; Dassonville and Bala 2004; Barnett-Cowan and Harris 2008). Thus, we also hypothesized that degradation of the egocentric representation of the body, by crossing the hands, might alter performance on the RFT. Given the sex differences in this task, this effect may be more evident for females compared to males.

2.2.4 Scope of the present study

The primary goal of the present research was an exploration of the individual differences that have anecdotally been reported for the tactile TOJ crossed-hands deficit. At the same time, we sought to better understand the cause of the deficit, by evaluating the relation between the individual differences in the TOJ task and those observed in the putatively related RFT. To this end, 44 participants (22 females) were tested on both the TOJ task and the RFT while adopting a crossed and an uncrossed posture. We predicted a correlation would exist between the magnitude of an individual's crossed-hands deficit in the tactile TOJ task and the amount with which they are influenced by the frame in the RFT. We anticipated this correlation would differ between sexes due to the fact that females show a greater reliance on an external frame of reference compared to males (Witkin et al. 1954; Gross 1959; Bogo et al. 1970; Hyde et al. 1975; Linn and Petersen 1985; Barnett-Cowan et al. 2010). This design also afforded us the opportunity to address two related questions: first, is there a sex difference in the tactile TOJ crossed-hands effect? And, second, does crossing the hands in the RFT increase visual dependence? We anticipated that there would be a sex difference present in the TOJ task and that women would show a larger crossed-hands deficit because of their greater dependence on a visual reference frame. We also predicted that crossing the hands would increase the effect of the visually tilted frame by reducing the reliance on body-centered cues.

2.2.5 Measuring the tactile TOJ crossed-hands deficit

To examine individual differences in the tactile TOJ crossed-hands deficit, a metric is required to assess the size of the deficit for a given individual. Some authors have used the just noticeable difference (JND), computed from a fitted function for the crossed and uncrossed posture, specifically the slope of the fitted functions for these two postures were compared (e.g., Kobor et al. 2006; Shore et al. 2002). However, negative slope values (negative JNDs) and the volatility in the slope value around zero make the tactile TOJ crossed-hands deficit difficult to interpret. Small differences in the fit around a flat line can lead to very large differences in the computed values of the fit. Others have estimated the crossed-hands deficit using a 'flip' function based on a Gaussian fit of the difference between the crossed and uncrossed data (Yamamoto and Kitazawa 2001,2005; Wada et al. 2004; Azañón and Soto-Faraco 2007). The major assumption here is that performance with the hands uncrossed is related to performance with the hands crossed—this assumption has not been directly tested to our knowledge. Additionally, there are theoretical assumptions in this method of quantifying the deficit that may not permit a comparison of different underlying models. Finally, one needs a very large range of stimulus onset asynchrony (SOA) values to provide reliable and reasonable fits. In the present paper, we have adopted a much simpler approach that appears to yield very reasonable estimates of individual variation. For each participant, the difference in proportion of correct responses for crossed and uncrossed posture was computed for each SOA, and these values were summed. This proportion correct difference (PCD) score essentially provides an estimate of how much crossed performance would have to change to be the same as uncrossed performance. This score has the virtue of being a model-free estimate of the performance difference. That is, both the slope difference and the flip function require an assumption of normality in performance, which is clearly violated in the crossed posture. We will provide an evaluation of this metric in the results to Experiment 1 where we compare it to a more traditional approach.

2.3 Experiment 1: Tactile temporal order judgment

There were several goals of the present experiment. The first goal was to assess individual variation in the tactile TOJ crossed-hands deficit by examining a relatively large group of participants in a standard implementation of the task (i.e., Shore et al. 2002). A second goal was to evaluate any sex effects in this deficit. The final goal was to assess a new metric of the deficit—the proportion correct difference score—by comparing the deficit as described using traditional measures and this new measure.

2.3.1 Method

Participants

Forty-eight participants were recruited from the McMaster University undergraduate psychology subject pool. There were 24 females and 24 males with an average age of 19.5 (19 for males; 20 for females). Participants received one extra course credit as compensation for their participation in the experiment. All participants were right handed except for five (3 females) who were left handed as reported on a handedness questionnaire, and all provided written informed consent prior to participation. All participants were naïve to the purpose of the experiment and reported normal or corrected-to-normal vision and tactile sensitivity.

Apparatus and stimuli

Participants were seated at a table (73.7 cm in height) in a well-lit testing chamber. They held two foam cubes separated by 18 cm with their thumbs and index fingers in contact with Oticon-A (100 Ohm) bone-conduction vibrators. The surfaces of the vibrators were 1.6 cm in width and 2.4 cm in length. The vibrators were driven by a 250-Hz sine wave signal that was amplified to a comfortable, clearly suprathreshold level. On each trial, two 20-ms vibrations, one to each index finger, were delivered separated by a variable stimulus onset asynchrony (SOA): ± 400, ± 200, ± 100, ± 50 ms, where negative SOAs indicated that the vibration was presented to the left side of space first. Four red LEDs (10 mm in diameter) were located next to the four vibrators. Two foot pedals were used (one under the toes of each foot) for participant responses. All stimulation was controlled by a set of read-relays connected to the parallel port of a DOS-based PC computer. The program to administer stimulation and collect responses was written in Turbo C. Throughout the experiment, participants wore earplugs, and white noise was continuously played over two loudspeakers to mask sound produced by the tactile vibrators and foot pedals.

Procedure

Participants held one foam cube in each hand during the experiment. The cubes were held so that the index fingers were in contact with the top vibrator. On each trial, participants received two short vibrations, one to each index finger. Participants lifted the toe of the foot corresponding to the side of space, which was stimulated first, regardless of hand posture.

Each trial began after the participant pushed their toes down on both foot pedals. The first vibration occurred 800 ms after the start of the trial. The second vibration was delivered after a variable SOA determined randomly from the fixed set of SOAs for each trial. After the second vibration, participants indicated which stimulus had been presented first by lifting the corresponding toe (e.g., the left toe if vibration was delivered to the left side of space—left finger in the uncrossed posture, and right finger in the crossed posture). The next trial began when participants pushed with both toes on the pedals. If participants did not respond within three and a half seconds, the four vibrators and the four LEDs would turn on and off until the participant lifted both of their feet. Trials in which the participant did not answer within the allotted time or where reaction times were less than 10 ms were not included in the analysis. This equaled less than one percent of the overall data.

At the start of the experiment, participants were given instructions as to how to complete the task and then completed two blocks of 20 practice trials each. One block was completed with the hands uncrossed and the other was completed in the crossed-hands posture. Hands were crossed right over left with the arms touching. The experimenter remained in the room during the practice trials to provide feedback and answer any questions. After the practice trials, the experimenter left the room, and participants completed ten blocks of 64 experimental trials, alternating crossed and uncrossed postures for each block. This resulted in 40 trials per SOA for each hand posture. The order of which hand posture to adopt first was counterbalanced across participants.

Analysis

The following three analyses were conducted: (1) A repeated measures analysis of variance (ANOVA) on the proportion of 'right first' responses across SOA, with sex as a between-participant factor; (2) An analysis of the slope for crossed and uncrossed postures for males and females. The slope was computed by converting each proportion of 'right first' responses to its associated z-score from a normal distribution and then using a least-squares fit to a linear function (i.e., a probit analysis; cf. Finney 1971). To further explore any sex-related effect on performance, the difference between slope produced in the crossed and uncrossed postures was compared between males and females. Additionally, the normality of the slope difference was evaluated since this is one estimate of the size of the deficit; and (3)

An analysis of the new measure proposed by this paper: the proportion correct difference (PCD) score. The PCD score is computed by taking the difference, at each SOA, between performance in the crossed and the uncrossed postures and summing these differences. Since there is no score independent of the crossed and uncrossed postures, a one-way between-participants ANOVA was conducted comparing performance for males and females.

2.3.2 Results

ANOVA results

For each participant, the proportion of 'right first' responses was calculated for the crossed and uncrossed postures at each SOA (see Figure 1 for the average performance across participants and Figure 2 for individual participant graphs). These values were submitted to a repeated-measures ANOVA. The Greenhouse–Geisser epsilon value (ε) and adjusted probabilities are reported for any violations of the assumption of sphericity. The proportion of right first responses, as evident in Figure 1, increased monotonically with increasing SOA ($F_{(7, 322)} = 359.8$, $p < 0.0001$, $\varepsilon = 0.24$). The increase was steeper and more complete when observers adopted an uncrossed posture compared to a crossed posture, resulting in a significant interaction of posture by SOA ($F_{(7, 322)} = 140.8$, $p < 0.0001$, $\varepsilon = 0.25$). The sex of the participant influenced the shape of this interaction such that females showed a smaller effect of SOA for the crossed posture than males ($F_{(7, 322)} = 10.3$, $p = 0.0003$, ε

= 0.23) while for the uncrossed posture there was a smaller difference between the sexes ($F_{(7, 322)}$ = 3.1, p = 0.05, ε = 0.28). These differences led to a significant three-way interaction between posture, SOA, and sex ($F_{(7, 322)}$ = 6.2, p = 0.0043, ε = 0.25). To summarize, the typical posture-related effect was observed with steeper slopes for the uncrossed posture than the crossed posture. This difference was smaller for males than for females.

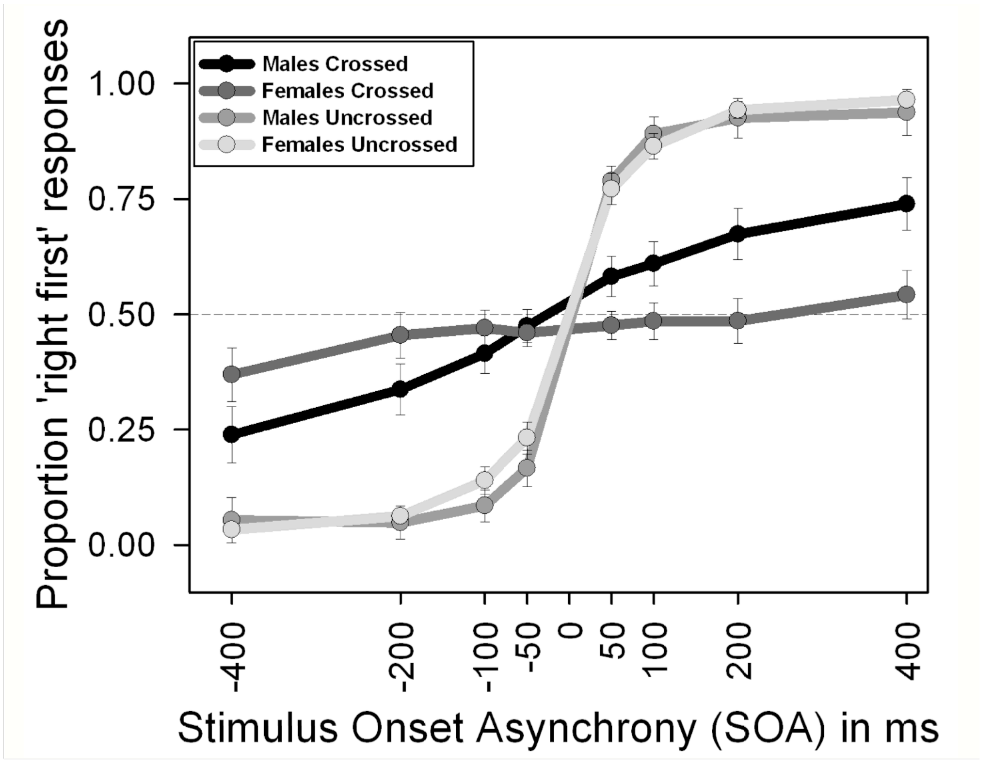

Figure 2.1 Proportion of 'right first' responses across stimulus onset asynchrony (SOA) for all 48 participants (24 males and 24 females).

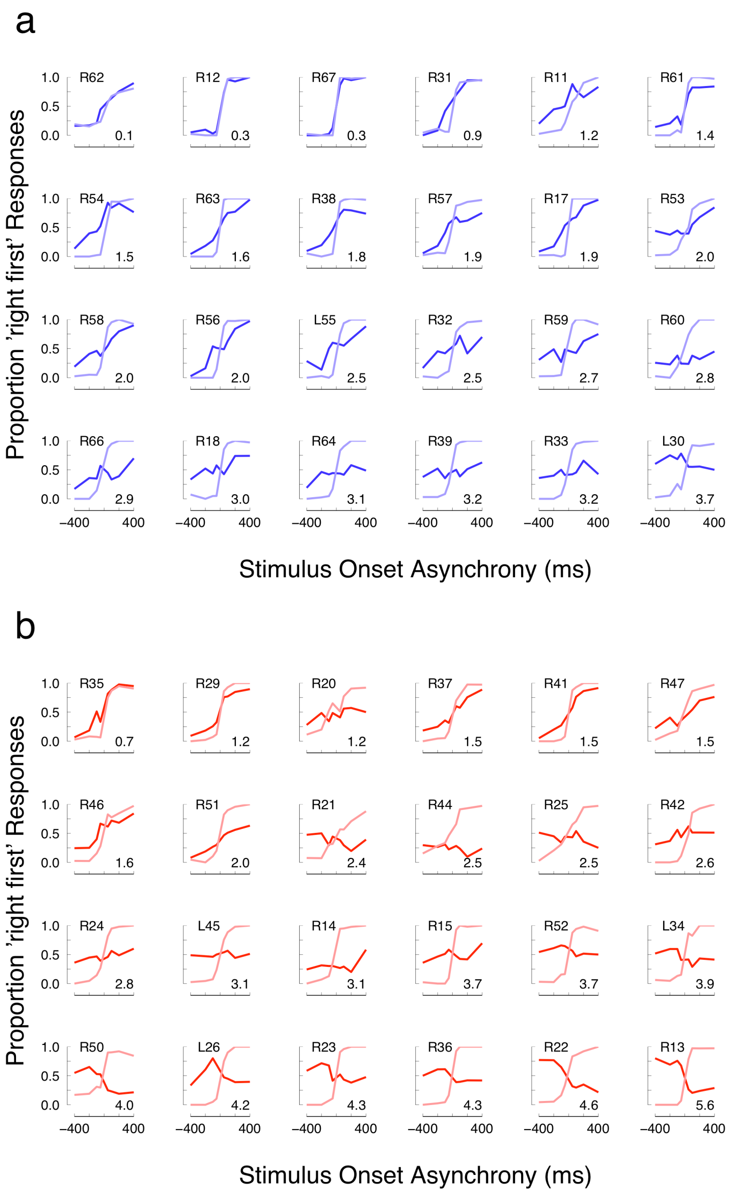

Figure 2.2 Proportion of 'right first' responses across stimulus onset asynchrony for individual participants. Number in bottom right corner of each graph indicates the participant's proportion correct difference (PCD) score. The text in the top left of each graph indicates the handedness of the participant (R for right handed and L for left handed) and participants' identification number. See Figure 1 for legend. Males (a) Females (b).

Analysis of slope

Slope values were calculated for males and females in both the crossed and uncrossed conditions. These values were submitted to a 2x2 ANOVA with factors of posture and sex.

The slope for the uncrossed posture (mean = 6.3 proportion 'right first' responses/second (prfr/s), s.d. = 1.2 prfr/s) was much higher than for the crossed posture (mean = 1.6 prfr/s, s.d. = 2.2 prfr/s; $t_{(47)} = 14.8$, $p < 0.0001$) replicating the basic crossed-hands deficit.

In examining the effect of sex on performance in this task the slopes in the uncrossed posture were slightly steeper for male participants (mean = 6.56 prfr/s, s.d. = 1.06 prfr/s) than for female participants (mean = 6.02 prfr/s, s.d. = 1.26 prfr/s) but the effect was not significant ($F_{(1, 46)} = 2.59$, $p = 0.115$). A significant difference was observed in the crossed posture (mean = 2.66 prfr/s, s.d. = 1.94 prfr/s for males; mean = 0.61 prft/s, s.d. = 1.93 for females; $F_{(1, 46)} = 13.47$, $p = 0.006$). A significant interaction between sex and posture was observed ($F_{(1, 46)} = 6.46$, $p = 0.015$).

In examining the relation between the crossed and uncrossed slope there appeared to be a significant correlation ($r = 0.28$, $p = 0.05$). However, once the effect of sex was partialled out, this correlation was no longer significant ($r = 0.19$, $p = 0.19$). In essence the significant correlation resulted from the significant effect of sex on both slope values. To our knowledge this is the first evaluation of this assumption in the literature. To be clear, we see no evidence that performance in the crossed posture is related to performance in the uncrossed posture, except as related to the effect of sex on both. The slope difference was normally distributed, (χ^2 criterion = 0.87, df = 2, χ^2 statistic = 0.648; see Figure 3a) as determined by the D'Agostino-Person's test of normality (Zar, 1999). As mentioned in the Introduction, there are difficulties in using the slope difference as a measure of the crossed-hands deficit. The main issue concerns the fitting procedure used as the slope approaches zero, as is common with a crossed-hands posture. Small changes in performance can lead to large changes in the fit. That is, there are non-linearities in the slope as it approaches zero because of the poor fit at these levels. For this reason, we propose a new measure, the PCD score, which is less theory laden and thus more closely tied to the data.

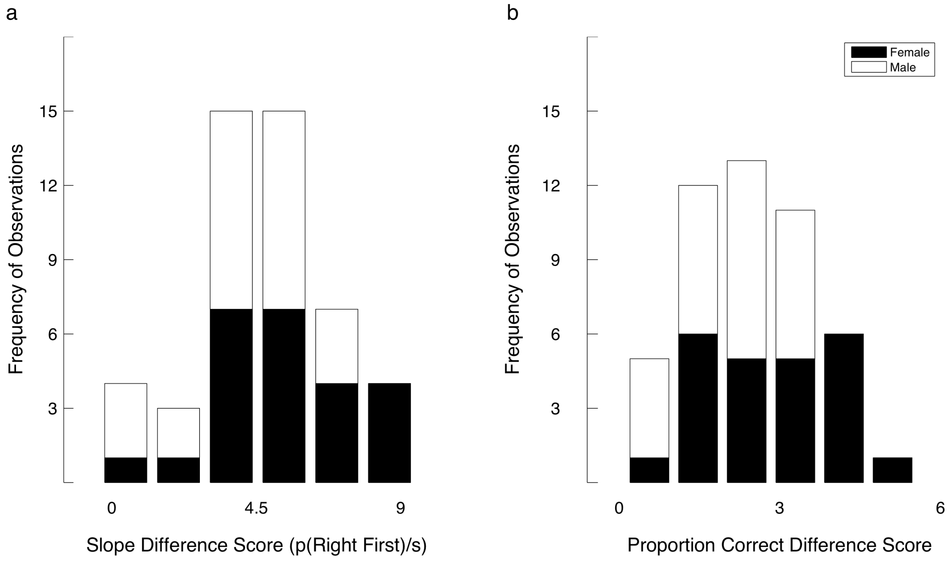

Figure 2.3 Distribution of the slope difference (a) and the proportion correct difference (PCD) score (b) for males and females.

Analysis of proportion correct difference score (PCD)

The PCD score was calculated by summing the differences between the proportion of correct responses in the crossed and uncrossed postures at each SOA. This allows a participant's performance to be reduced to a single value. A between-participants ANOVA with the factor of posture was conducted. The PCD score was significantly smaller for males (mean = 2.01, s.d. = 0.96), than for females (mean = 2.85, s.d. = 1.30; $F_{(1, 46)} = 6.35$, $p = 0.0153$) supporting a larger crossed-hands deficit for females than for males. Specifically, men were 10.4% more accurate then women across all SOAs. These values were normally distributed (χ^2 criterion = 0.031, df = 2, χ^2 statistic = 0.628; see Figure 3b) [2].

2.3.3 Discussion

Individual difference in the crossed-hands TOJ deficit

Experiment 1 replicated previous results of a dramatic decrement in the precision of tactile temporal order judgments when stimuli were delivered to each hand in the crossed-hands posture (Shore et al. 2002; Röder et al. 2004). The anecdotally reported variation in the size of this deficit across individuals was quantified and shown to be normally distributed (see Figures 2, 3). This variation

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[2] In previous research (e.g., Spence et al. 2001) the most extreme SOAs (±400ms) were removed from the calculation of the slope. If this was done to the present data, the main effect of sex was not observed for slope ($F_{(1,46)} = 1.3$, $p = 0.26$). If the extreme values were removed from the calculation of the PCD scores, the main effect of sex was marginally significant ($F_{(1,46)} = 1.91$, $p = 0.06$).

was quantified by the new metric proposed here—the proportion correct difference score (PCD). The variation in the observed PCD scores spread from a small deficit of 0.11 to a large deficit of 5.56. The largest deficit possible is 8.0. This would occur if the participant were 100% accurate in the uncrossed posture and 100% inaccurate in the crossed posture. The advantage of this score over the traditional slope measure concerns its linear nature. As the deficit increases, there is a monotonic increase in the value, whereas with slope, for the crossed postures there are nonlinearities around the flat slope of zero.

The large degree of variation between participants in the tactile TOJ crossed-hands deficit helps to demonstrate the contrast in reliance on different reference frames between individuals. As mentioned in the Introduction, we are working under the assumption that the deficit is caused by a conflict of information between egocentric and external frames of reference. The individual differences seen here likely represent differences in the weights ascribed to one frame of reference over another. The more a person places himself or herself in a single frame of reference, the less they will be influenced by conflicting information provided by the other frame of reference.

The large degree of individual variation in performance seen here brings into question the validity of group-based analysis. As can be seen in the average data (Figure 1), females in the crossed-hands condition perform close to chance for the given SOAs. However, at the level of each individual participant (see Figure 2b), a large portion of females perform well, while an equally large portion of females perform poorly, some even showing a complete reversal. It is the combination of the two that create a group performance at chance levels, which does not reflect actual participant performance. In the future, these individual differences need to be carefully considered when examining group differences.

Sex effects in the tactile TOJ crossed-hands deficit

Experiment 1 revealed a significant effect of sex in the vibrotactile TOJ task—a smaller crossed-hands deficit for males compared to females. The TOJ task requires a participant to make judgments based on tactile stimuli presented to the hands. This deficit appears to stem from a conflict of egocentric and external frames of reference. Females have been shown to have a greater reliance on a visual (external) frame of reference (Witkin et al. 1954;Gross 1959; Bogo et al. 1970; Hyde et al. 1975; Linn and Petersen 1985; Barnett-Cowan et al. 2010). We believe this increased dependence on vision causes females to have a larger conflict in the crossed-hands condition when compared to males who more easily ignore or resolve conflicting information from an external reference frame.

A second possibility is that the deficit is caused by a higher degree of left-from-right confusion in females. Past studies have shown females to be more prone to these kinds of errors (Wolf 1973; Harris and Gitterman 1978;Hannay et al. 1990; Ofte and Hugdahl 2002; Gormleyet al. 2008). The left and right hands serve as an egocentric frame of reference for distinguishing left-from-right. Normally, the left and right hands are aligned with the left and right sides of space respectively. In this hand posture, distinguishing left-from-right is not affected by reference frame dependence. Crossing the hands, however, would most likely add to the error associated with left-from-right confusion. Thus, it is possible that the reference frame conflict mentioned above increases these types of errors as participants are required to integrate left and right information from two different sources (external and egocentric). The exact relation between left–right confusions and the crossed-hands deficit should be addressed in future research.

To provide additional information about the potential source of the crossed-hands TOJ deficit, and specifically the newly-noted sex effect we evaluated the relation between this deficit and the frame effect in the rod-and-frame test.

2.4 Experiment 2: rod-and-frame

The primary goal for Experiment 2 was to assess the hypothesis that the size of the frame effect on estimating the perceived vertical, as measured in the RFT, would increase when the hands used to respond to the RFT were crossed. We hypothesized this to be the case based on the assumption that decreased reliability on the egocentric reference frame, as induced with the crossed-hands posture, would increase reliance on the other available information (i.e., visual reference frame). We also expected an effect of sex, such that females would show a larger frame effect than males. Finally, based on the results from the first experiment, we hypothesized that the effect of hand crossing (i.e., larger frame effects with the hands crossed) would be larger for females than for males. The second goal concerned the comparison of visual dependence, as measured in the RFT, with the tactile TOJ crossed hands deficit measured in Experiment 1 (see ''The relation between the tactile TOJ crossed-hands deficit and the rod and-frame-effect'').

2.4.1 Method

Participants

Fifty-four participants were recruited from the McMaster University undergraduate psychology subject pool. Forty-four of these participants also took part in Experiment 1. Participants received one extra course credit as compensation for their participation in the experiment. All participants were right handed except for five (3 females) who were left handed as reported on a handedness questionnaire, and all provided informed written consent prior to participation. There were 28 females and 26 males with an average age of 19.5 (20 for males, 19 for females). All participants were naïve to the purpose of the experiment, reported normal or corrected-to-normal vision, and reported no history of vestibular dysfunction.

Apparatus and stimuli

Participants were seated upright and observed images presented in the fronto-parallel plane on an Apple MacBook laptop computer with a resolution of 48 pixels/cm (21 pixels/° at the viewing distance of 25 cm). Peripheral vision was masked to a circular screen of diameter 35° using a circular aperture shroud (Figure 4a).

We measured the RFT using a variant of the 'luminous line' technique. A simple line probe (3° x 0.5° of visual arc) was presented for 500 ms and oriented about a central fixation point (0.45° of visual arc). The probe line was presented in 41 orientations (from -20° to +20° relative to gravity, in 1° increments). The orientation of stimuli is defined with respect the body midline of the observer which was aligned upright relative to gravity; 0° in our convention. Clockwise errors relative to gravity are positive. The line probe was superimposed on a 35° circular background picture which consisted of a white frame (29.7° x 29.7° of visual arc) against a neutral gray background. The frame was randomly displayed either as upright at 0° or at +18° or -18° relative to gravity (Figure 4b). After 500 ms, stimuli were replaced with a neutral gray screen containing a central fixation point.

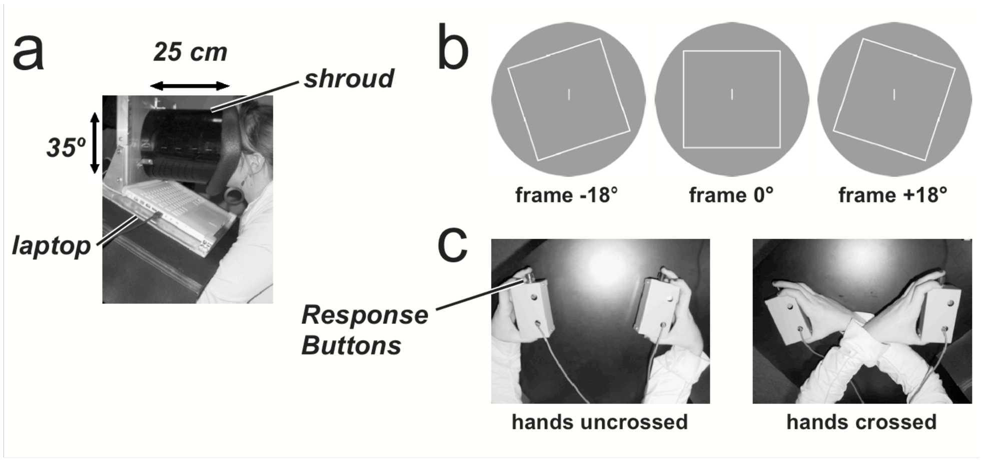

Figure 2.4 Rod-and-frame test apparatus. The viewing distance for the laptop screen viewed through an aperture shroud (a). Rod oriented from -20° to +20° at 1° intervals relative to upright (0° shown here) embedded within frames oriented at -18°, 0°, and +18° relative to upright (b). Hands uncrossed and crossed postures while holding response push buttons (c)

Procedure

Participants were asked whether the line probe was oriented counter-clockwise or clockwise relative to the direction of gravity. The direction of gravity was defined as the "direction in which a ball would fall if dropped". Participants completed the RFT in hands uncrossed and crossed postures and unspeeded responses were collected using push buttons for each of the hands held 18 cm apart (Figure 4c). As in the TOJ task, participants responded according to the side of space and not according to the hand. Participants completed a total of 1968 trials over the course of approximately 30 min: 41 (lines) x 3 (frames) x 8 (repeats) x 2 (hand postures). No feedback was given.

Analysis

A sigmoidal function (Eq. 1) was fit to the proportion of times the line was judged as clockwise relative to gravity as a function of line orientation. The orientation of the line probe where it was equally likely to be judged tilted clockwise or counter-clockwise from gravitational vertical was taken as the perceived vertical.

$$y = (1-\lambda_{upper}) + (1 - \lambda_{lower})\ (1 / (1 + e^{-((x-PSE)/JND)})) \tag{1}$$

Where: y = probability of line being clockwise, λ_{upper} and λ_{lower} = lapse rates for the upper and lower asymptotes of the psychometric function (see Wichmann and Hill 2001; Yamamoto and Kitazawa 2001), x = line orientation, PSE = point of subjective equality; JND = just noticeable difference (i.e., standard deviation).

To assess the maximum effect of the RFT, we took the difference between the PSE for the frame oriented -18° minus the PSE for the frame oriented -18°. We call this the frame effect (FE). FE quantifies the influence of visual information on estimates of the perceived vertical, where positive FE values indicate bias toward the direction of the frame's orientation. The FE, the average JND, and the average combined upper and lower lapse rates ($\lambda_{\text{upper}} + \lambda_{\text{lower}}$) across both tilted frames were entered into separate 2 (hand posture) x 2 (sex) mixed-design repeated measures ANOVAs. The effects of hand posture and sex in the absence of a tilted frame were similarly assessed with the upright frame. Greenhouse–Geisser corrections for multiple comparisons and violations of sphericity were employed when appropriate. Bonferroni pairwise repeated measures comparisons as well as independent and paired sample t-tests were used when following up interactions or testing our a priori predictions concerning the difference between males and females (two-tailed; a = 0.05).

2.4.2 Results

A larger FE was observed with hands crossed (mean = 4.0°, s.d. = 3.4°) compared to uncrossed (mean = 3.2°, s.d. = 3.9°; $F_{(1,52)} = 5.43$, $p = .024$; Figures 5 & 6). A main effect of sex was also found ($F_{(1,52)} = 4.57$, $p = .037$), but not a sex by hand interaction ($F_{(1,52)} = 0.27$, $p = .609$). The main effect of sex was driven by a significant difference between females and males with hands crossed ($t_{(1,52)} = 2.40$, $p = .020$; Figure 6a). The difference between females and males with uncrossed hands did not reach significance ($t_{(1,52)} = 1.67$, $p = .101$). Females were more influenced by the tilted frames with hands crossed (mean = 5.1°, s.d. = 3.6°) compared to the uncrossed hand posture (mean = 4.1°, s.d. = 4.0°; $t_{(1,27)} = 2.71$, $p = .012$; Figure 5b-c). This was not the case for males whose FE values with hands crossed (mean = 2.9°, s.d. = 2.8°) and uncrossed (mean = 2.3°, s.d. = 3.7°) were not significantly different ($t_{(1,25)} = 1.04$, $p = .307$).

There was a trend suggesting a higher lapse rate with hands crossed (mean = 14.7%, s.d. = 19.2%) compared to uncrossed (mean = 9.6%, s.d. = 12.6%; $F_{(1,52)} =$

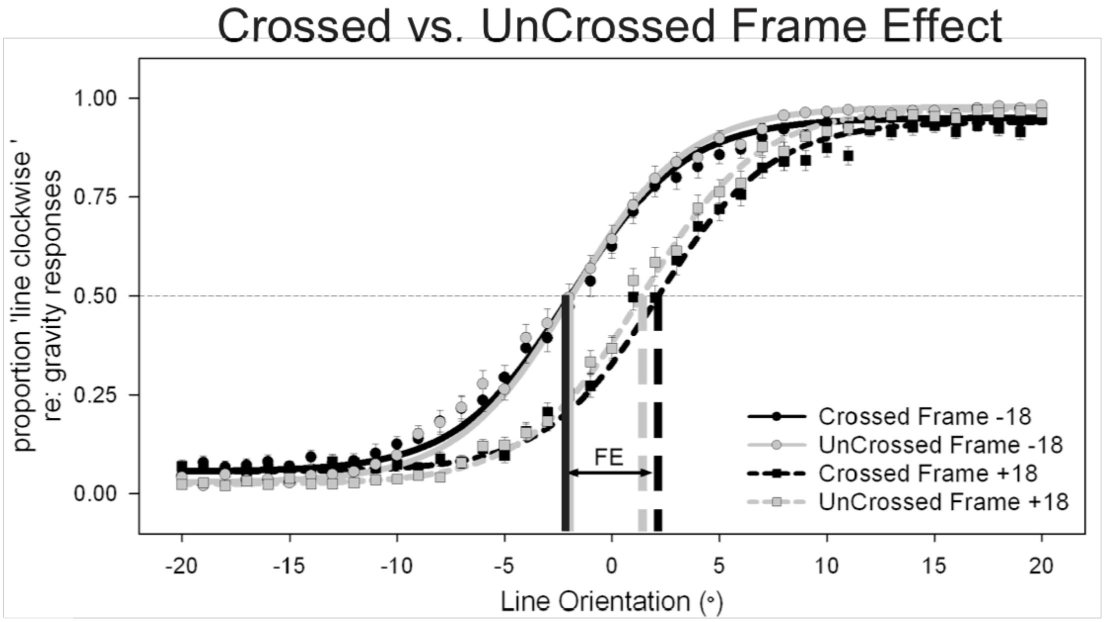

Figure 2.5 Average rod-and-frame effects with tilted frames observed with hands crossed and uncrossed with sigmoids fit to the proportion that the line was judged to be clockwise relative to gravity as a function of line orientation with the frame oriented at -18° (circle symbols, solid curves) and +18° (square symbols, dashed curves) with hands crossed (black) and uncrossed (gray). Curves were fit to line orientations from -20° to +20° in 1° increments. The maximum effect of the RFT (frame effect: FE) is the difference between the points of subjective equality (PSE; vertical lines) for when the frame is oriented at ± 18° (see Fig. 6a)

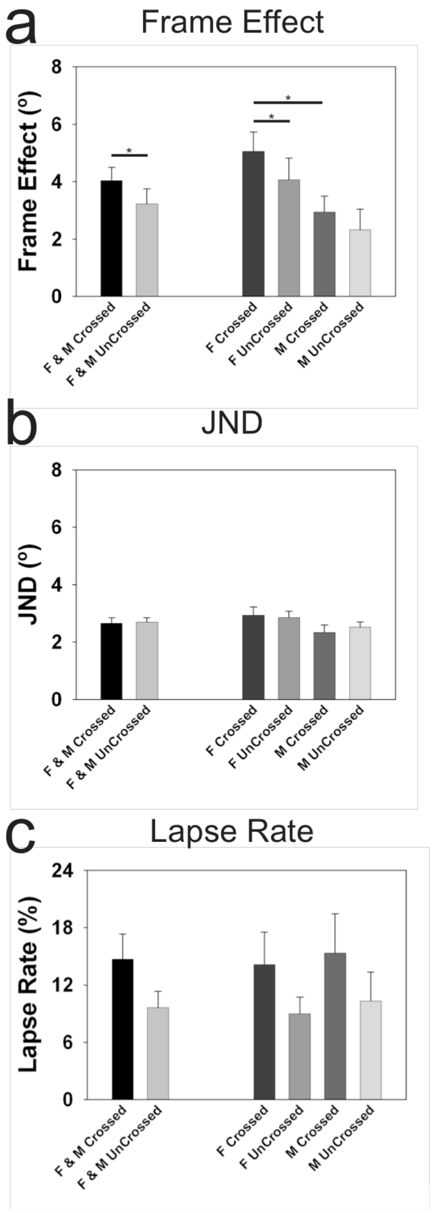

Figure 2.6 The average FE (a), JND (b), and lapse rate errors (c). Data are shown for females (F) and males (M) combined (data from Fig. 5; left series), as well as separately for females (middle series) and males (right series) for both crossed and uncrossed postures. Error bars are standard error; * $p < 0.05$

3.40, $p = .071$; Figure 6c). A main effect of sex and a sex by hand interaction were not found for lapse rates ($F_{(1,52)} = 0.13$, $p = .719$; $F_{(1,52)} = 0.0003$, $p = .987$). No significant effects of hand posture ($F_{(1,52)} = 0.12$, $p = .734$), sex ($F_{(1,52)} = 2.34$, $p = .132$), or a sex by hand posture interaction ($F_{(1,52)} = 0.79$, $p = .377$) were found for the JND values (see Figure 6b). No significant differences were found for the PSE, JND or lapse rate values with the upright frame (all $p > .05$).

2.4.3 Discussion

Crossing the hands significantly increased the rod-and frame effect. Why does the frame effect increase when the hands are crossed? We suggest that by crossing the hands, the representation of the body becomes less reliable and must be disambiguated to perform the task accurately. The results from Experiment 1 and Experiment 2 both suggest that females are less able to disambiguate a crossed-hands posture than males. One could ask whether the effect observed here has its roots in the perception of upright, as we assume, or instead in some response-based increase in errors when the hands are crossed. There is good evidence that changes in response demands can change the perception of stimuli. For example, Gallace et al. 2008 demonstrated a change in tactile spatial congruency by altering the relevant response demands of the task (indicate finger/ thumb vs. up/down). In our laboratory, we have shown that changing the response demands from an external reference frame (i.e., indicate the side of body) to a somatotopic reference frame (i.e., indicate which hand was stimulated) can drastically reduce the crossed-hands

TOJ deficit (Shore et al. 2006). Finally, the RFT was no more error-prone with the hands crossed than uncrossed. This can be seen in both the JND measure and the lapse measure, which were not significantly different between the two postures. For all of these reasons, we assume that the effect of hand crossing on the FE was caused by a change in perception. This assumption needs to be evaluated in future research.

Why is the internal representation of the body implicated in the RFT, particularly for females? It has previously been shown that the extent to which females are influenced by vision in the RFT is reduced when instructed to attend to the internal representation of the body (Reinking et al. 1974). Similarly, the misperception of the morphological horizon, which is biased toward the feet in females when pitched backward by 45°, is reduced when given similar instructions (Tremblay et al. 2004). This difference has been attributed to sex differences in neural strategies in performing spatial orientation tasks. Our data support this hypothesis and further suggest that females are less able to disambiguate disturbances of the internal representation of the body.

As mentioned earlier, females are known to be more likely to confuse their left-from-right than are males (Wolf 1973; Harris and Gitterman 1978; Hannay et al. 1990; Ofte and Hugdahl 2002; Gormley et al. 2008). The RFT, as used in the present study, requires observers to judge whether a visible line is oriented clockwise or counter-clockwise relative to the direction of gravity and therefore requires observers to distinguish clockwise from counter-clockwise. As clockwise and counter-clockwise are easily substituted for right and left respectively, it is possible that sex differences in making left-from-right discriminations might explain sex differences in the RFT but more for when the hands are close together than apart. We suggest that a within-participants experiment addressing the effects of hand distance, left-from-right confusion and sex in the RFT should be conducted to address these factors.

The relation between the tactile TOJ crossed-hands deficit and the rod-and-frame-effect

In order to assess the relation between the tactile TOJ crossed-hands deficit in the first experiment and the extent to which participants were more influenced by visual information as measured using the RFT in the second experiment, we performed correlations between the tactile TOJ crossed-hands deficit with the frame effect in both crossed and uncrossed postures for females and males. Forty-six participants completed both Experiments 1 and 2. Two participants (1 male and 1 female) were removed due to a frame effect that was larger than 2.5 standard deviations from the mean. All participants were right handed except for five (3 females) as reported on a handedness questionnaire. There were 22 females and 22 males with an average age of 19.5 (20.0 for males, 19.0 for females).

Before reporting the correlations between these tasks, one must be certain that the measures to be correlated have the reliability to produce a significant correlation. For the RFT task, we have two estimates of the frame effect—one from the crossed-hands posture and one from the uncrossed-hands posture. These two values were highly correlated (r = 0.82, P \ 0.001, partialling out the influence of sex) indicating a reliable index of performance. For the crossed-hands TOJ deficit, we have only one measure, so we cannot as easily test the reliability. As such, we performed a bootstrap resampling simulation on all of the data. For each participant, their trials from each cell in the design were split in half. A best-fitting slope difference measure (''Analysis of slope'') and a PCD score (''Analysis of proportion correct difference score (PCD)'') were determined, one for each half of the sampled data. Across the 44 participants, the two scores were correlated one with the other. This sampling was completed 999 times, and the 95% confidence intervals for the correlation of the two samples were used as the metric of reliability (see MacLeod et al. 2010, for an example of this method). For both measures—PCD and slope difference—the mean correlation was quite high (r = 0.92; 95% CI = 0.88–0.95 for the PCD score; r = 0.86; 95% CI = 0.77–0.90 for the slope difference score) indicating quite reliable measures.

The relation between the crossed-hands TOJ deficit and the effect of the visual frame from the RFT was examined by correlating the PCD score with the frame effect (FE) from both the crossed-posture and uncrossed-posture conditions. Confidence intervals were computed using a bootstrap sample technique with 999 samples. Overall, neither of these evaluations was significant (r = 0.12, *p* = 0.44; 95% CI = -0.20–0.40 for the uncrossed posture and r = 0.07, P = 0.63; 95% CI = -

0.25–0.38 for the crossed posture). However, given the different performance on both tasks by males and females and our a priori prediction that this correlation may be different for each sex, we tested the relation separately for each sex. For the uncrossed RFT task, a significant positive correlation was found between the tactile TOJ crossed-hands deficit and the frame effect for males (r = 0.42, *p* = 0.05; 95% CI = 0.10–0.67), while the correlation for females was non-significant and negative (r = -0.17, *p* = 0.42; 95% CI = -0.66–0.27; Figure 7a). With a crossed posture, neither correlation was significant, (r = 0.33, *p* = 0.13; 95% CI = -0.02–0.60 for males and r = -0.33, *p* = 0.13; 95% CI = -0.73–0.14 for females). Using the slope difference measure, none of the correlations tested was significant.

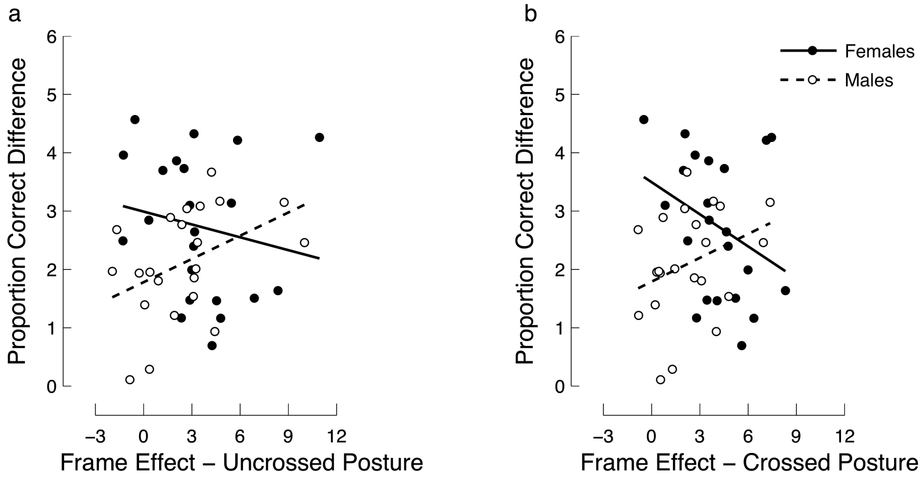

Figure 2.7 Scatter plot for males and females of the proportion correct difference (PCD) score from the tactile TOJ task by the uncrossed frame effect (a) and the crossed frame effect (b)

2.5 General discussion

2.5.1 Summary

There were four main findings from the present study. First, females show a slightly larger average tactile TOJ crossed-hands deficit than do males. This sex difference was seen in the context of large individual differences in the size of the deficit. Second, the crossed-hands TOJ performance was not correlated with performance in the uncrossed posture once sex was partialled out as a factor. This was somewhat surprising given the assumption that similar processes are engaged in the two postures. Future work needs to consider the impact of this finding on the use of difference scores to assess performance. That is, does performance in the uncrossed posture provide a good baseline against which to compare performance in the crossed posture? Third, crossing the hands significantly increases the effect of frame orientation on the subjective vertical, with females being significantly more influenced by frame orientation in the crossed-hands posture than males. Finally, there was a significant correlation between the tactile TOJ crossed-hands deficit and the frame effect for males but not females. Below, we discuss these findings in greater detail and speculate on their origin and implications.

2.5.2 Possible role of spatial ability

Why are females less able to disambiguate a crossed-hands posture as compared to males? In addition to sex differences in left-from-right confusion, differences in spatial ability are well established between females and males (Sherman 1967; Hyde et al. 1975; Shute et al. 1983; Linn and Petersen 1985; Voyer et al. 1995; Parsons et al. 2004). The RFT is a measure of spatial ability and is classified along with other tests such as the water level task (Inhelder and Piaget 1999) as a measure of spatial perception (Linn and Petersen 1985). Linn and Petersen (1985) defined spatial perception tests as those in which the observer determines spatial relations with respect to their body despite distracting information. We suggest therefore that spatial ability is used to mentally uncross the hands in order to perform the tasks required of Experiments 1 and 2 and could very well explain sex differences in the tactile TOJ crossed-hands deficit. Note that the effect of crossing the hands need not affect perception per se—measures of spatial ability including spatial perception are quantified by response time or error rate—rather, response conflict arising from the crossed-hands posture may increase the time or error rate when performing spatial tasks. From this, we predict that the tactile TOJ crossed-hands deficit may also be affected by hormones (Resnick et al. 1986; Gouchie and Kimura 1991; Collaer and Hines 1995; Hampson 1995; Moffat and Hampson 1996), sex–linked genes (Stafford 1961; Garron 1970; Hartlage 1970; Bock and Kolakowski 1973; Yen 1975), and academic performance (Peters et al.

2006), which have all been shown to affect spatial ability. Other measures of spatial ability (e.g., mental rotation) may allow further testing of this hypothesis.

2.5.3 Correlation

This experiment was originally designed to assess the hypothesis that the tactile TOJ crossed-hands deficit and the frame effect both tap into a common underlying process related to visual dependence. In this vein, it was hypothesized that the ability to ignore the visual frame of reference in the RFT would correlate with the ability to ignore this same reference frame in the TOJ task. We have shown this to be true for males but not for females. It was, however, expected for both men and women given the large similarities between the two tasks. Both tasks are influenced by visual information (Witkin and Asch 1948; Holmes and Spence 2005; Gallace and Spence 2005; Maravita et al. 2002; Soto-Faraco et al. 2004; Azañón and Soto-Faraco 2007) and involve the transformation of information between external and egocentric frames of reference (Shore et al. 2006; Witkin and Goodenough 1981). With respect to individual differences, both tasks show a significant crossed-hands deficit that is larger for females than it is for males. The sex differences seen in these two tasks may be the underlying cause for the fact that a correlation was found for males but not for females. Specifically, men may be using the same spatial abilities and reference frame transformation processes in both the tactile TOJ task and the RFT, while women might approach the two tasks in different ways. To be specific, under this proposal, males have a single process for translating between reference frames, and this process works very well. Females, on the other hand, use different processes for vestibular-visual transformations and for visuohaptic transformations with mixed success. Obviously, this proposal requires further testing to validate the claim and tease apart these sex differences.

The RFT specifically asks participants to judge the orientation of a line relative to gravity. The direction of gravity's force is externally referenced, the internal representation of the body is an egocentric frame of reference, and the visual frame an external reference. All of these contribute to estimating the subjective visual vertical (Howard 1982; Mittelstaedt 1988; Dyde et al. 2006). When the body is upright, gravity and the body are aligned, leaving only vision to manipulate the subjective vertical. Thus, the two external cues are directly put into conflict in the RFT. This is not the case in the crossed-hands tactile TOJ task where only one external reference frame is relevant. Given women's greater dependence on visual external cues, it is possible that they are responding differently than men when visual cues provide conflicting information. This would help to explain why a performance on the crossed-hands frame effect was related to PCD scores for male participants but not for female participants.

Given the significant correlation between the PCD score and the FE for males, future research should explore the underlying causes of this relation. Conducting the crossed-hands TOJ task while tilted to one side might provide insight into this relation. When tilted to one side, the external gravity-based reference frame is misaligned from the egocentric body-centered reference frame, and this should disrupt the conflict between the two reference frames and reduce the size of the crossed-hands deficit. Given the sex-related difference in the correlation, we expect this manipulation to have a larger effect for males than for females.

2.5.4 Neural correlates of reference frame conflict

Possible neural correlates of the conflict may reside in the parietal or precuneus areas. Consider the Roelofs effect. Here, the perceived location of an object shifts in the opposite direction of an enclosing offset rectangle, indicating that the perceived egocentric straight ahead can be affected by visual stimulation (Roelofs 1935; Bridgeman et al. 1997; Dassonville and Bala 2004; Dassonville et al. 2004; Walter and Dassonville 2008). Similarly, the perceived long-axis of the head is perceived to shift in the same direction of the visual surround (Barnett-Cowan and Harris 2008). These studies indicate that conflicting sensory information of an external frame of reference can affect egocentric judgments. Likewise, the results of the present study indicate that conflicting information in an egocentric frame of reference can affect external judgments. Recently, Walter and Dassonville (2008) reported that the superior parietal cortex and precuneus areas (areas which are believed to contain maps of the body schema; Cavanna and Trimble 2006) are implicated in the Roelofs effect, where the illusory distortion of egocentric space is thought to arise from converging visual and egocentric sensory information. In addition, sex differences in cortical activation associated with mental rotation have also been implicated in parietal (Thomson et al. 2000; Jordan et al. 2002; Weiss et al. 2003) and precuneus (Butler et al. 2006) areas despite controlling for equal performance between females and males. The effects found in the present study may likewise have their origins in this network.

Alternatively, one might postulate the inter-parietal sulcus (IPS) as the locus of the effects observed in both of the tasks used here (Lloyd et al. 2003). In that study, placing the hands across the body midline resulted in a robust activation in the contralateral fronto-parietal network responsible for limb coordination and representation (cf. Rizzolatti et al. 2002), but only when the eyes were open. The most striking finding was a shift of activation to the ipsilateral IPS when the eyes were closed. Further, with the eyes closed there was no concurrent activation in the frontal areas, as one would expect. Although there have been a number of studies supporting the role of vision in the tactile TOJ crossed-hands deficit, no one has directly compared performance with the eyes open or closed. The present results, in combination with the IPS findings with crossed hands, lead us to predict that there may be significant sex differences in the morphology of or functioning in the IPS.

There is also evidence to suggest that cortical activation from tactile stimulation (Sadato et al. 2000; Gron et al. 2000) and hand movement (Gron et al. 2000; Gorbet and Sergio 2007) is different in the somatosensory cortices of males versus females. Sadato et al. (2000) found that somatosensory activity associated with tactile discrimination is lateralized in males while female activity is symmetric.

Gron et al. (2000) showed differential somatosensory activity among females and males using buttons in a virtual maze navigation task. Finally, Gorbet and Sergio (2007) found that sex differences in somatosensory activation were most evident when the visual information used to guide arm movements was spatially incongruent arm movements. Such differences in somatosensory cortical functioning in males and females likely contribute to the sex differences found here in the tactile TOJ and RFT crossed-hands deficits. We suggest that the neural correlates of these deficits should be measured using functional imaging techniques while controlling for sex differences.

2.6 Conclusion

Both the TOJ task and the RFT show many similarities, including large individual differences, sex effects, and effects of crossing the hands. In examining the relation between the two tasks, we observed a significant correlation between the frame effect in the RFT and the size of the crossed-hands deficit in the tactile TOJ task, but only for men. The lack of a correlation for females again highlights the robust sex differences in these tasks and thus in the way information is coded in egocentric and external reference frames. In particular, we postulate a key sex difference in the processes that transform the representations between reference frames. Clearly, this claim requires further examination given the relatively weak correlational nature of the supporting evidence. We conclude that the individual differences found for perceptual judgment deficits of these tasks are partially attributable to the sex of the observer. Critically, future research needs to consider carefully the mix of sexes in their sample.

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Chapter 3: Response demands and blindfolding in the crossed-hands deficit: An exploration of reference frame conflict

3.1 Abstract

Performance on tactile TOJs are impaired when the hands are crossed over the midline. The cause of this effect appears tied to the use of an external reference frame, most likely based on visual information. Across three experiments we measured the effect of degrading the external reference frame on the crossed-hand deficit through restriction of visual information. Experiments 1 and 2 examined three visual conditions (eyes open – lights on, eyes open – lights off, and eyes closed – lights off) while manipulating response demands; No effect of visual condition was seen. In Experiment 3, response demands were altered to be maximally connected to the internal reference frame and only 2 visual conditions were tested: eyes open – lights on, eyes closed – lights off. Blindfolded participants had a reduced crossed-hands deficit. Results are discussed in terms of the time needed to recode stimuli from an internal to an external reference frame and the role of conflict between these two reference frames in causing this effect.

3.2 Introduction

Effective interaction with the environment requires accurate detection and localization of tactile events. Adopting an unusual posture can complicate this task; for example, crossing the hands over the midline drastically impairs our ability to judge the order of two tactile stimuli delivered to the hands in close temporal proximity (Azañón & Soto-Faraco 2007; Cadieux et al 2010; Craig & Belser 2006; Drew 1896; Heed et al., 2012; Holmes et al 2006; Kobor et al 2006; Roberts & Humphreys 2008; Röder et al 2004; Shore et al. 2002; Wada et al 2004; Wada et al., 2012; Yamamoto & Kitazawa 2001). This effect is known as the crossed-hands deficit. While it is easily replicable, the source of the effect is still debated. Two theories have been proposed to explain the cause of this deficit (Yamamoto and Kitzawa, 2001; Shore et al., 2002). The present study manipulates visual stimulation to test which of the two proposals more accurately represents the underlying cause of the crossed-hands deficit.

Both theories posit an interaction between an internal and an external reference frame. An internal reference frame, for the purpose of this article, is closely tied to the body surface (i.e. somatotopic); an external reference frame is world based, primarily visual, and centered on the body midline of the observer. The two reference frames can provide congruent information (i.e., when the right hand lies to the right of the midline), or incongruent information (i.e., when the right hand crosses and lies to the left of the midline). The two theories differ on how the interaction between the reference frames causes the deficit. Yamamoto and Kitazawa (2001) propose that each stimulus in a vibortactile temporal order judgment (TOJ) task must be localized in space before their temporal order can be determined. Errors arise when the onset of the second stimulus occurs before the first stimulus has been localized in space. Based on their data, they propose that it takes approximately 300 ms to remap from the internal (ie., somatotopic) representation to the external reference frame when the hands are crossed. Within this framework, response selection is based exclusively on the information provided by the external reference frame. On the other hand, Shore et al. (2002) hypothesized that stimuli are quickly localized into external space, which may or may not take more time when the arms are crossed, and that both the internal and external reference frames are active when a response is made: the conflict between the two reference frames, and the need to integrate information from the two, causes the deficit.

Integration of information is essential for coherent perception. Across sensory modalities several factors including space, time, and the relative reliability of the individual signals determine the speed and accuracy of integration. For adults, visual-tactile (Ernst & Banks, 2002; Gori et al., 2008) and visual-auditory (Alais & Burr, 2004; Parise, Spence, & Ernst, 2012) information appear to be integrated in a statistically optimal fashion. The information is weighted based on its reliability and combined to form a single representation of the stimulus. This representation is biased towards the more reliable source. We maintain that the same type of process allows for integration between the internal and external reference frames. In the present study, we degraded the external reference frame by manipulating the available visual information while performing a TOJ task.

Visual information impacts tactile perception. Simply viewing the stimulated skin surface, either directly (Driver & Grossenbacher, 1996) or through a video camera (Tipper, Lloyd et al. 1998), enhances tactile acuity. These behavioural results are supported by imaging studies that point toward neural connections between vision and touch: PET scans show activation of visual cortex during tactile orientation discrimination (Sathian & Zangaladze, 2001); TMS applied to visual cortex impairs tactile performance (Zangaladze et al., 1999); fMRI data support the important role of vision in encoding tactile stimuli with crossed hands (Lloyd et al., 2002). Additional evidence comes from the effect of visual deprivation: short-term (45 minute) visual deprivation can improve accuracy on a grating orientation task (Facchini & Aglioti, 2003; Weisser et al., 2005; although see Wong et al., 2011); at the longer term, Braille reading is improved in sighted individuals after several days of blindfolding (Kauffman, Theoret, & Pascual-Leone, 2002). Together, these separate lines of evidence point to close connections between visual and tactile modalities.

Within the context of tactile TOJs, there is also evidence that visual factors can influence performance. Manipulating the distance between the hands by physically separating them in space (Shore et al., 2005) or by using mirrors to misrepresent the perceived distance (Gallace & Spence, 2005) can influence performance on TOJs. Specifically, performance is improved when perceived distance between the uncrossed hands is increased. Substituting the participant's hands for rubber hands (cf. Botvinick & Cohen, 1998; Pavani et al., 2000) also influences performance on the crossed-hands deficit (Azañón & Soto-Faraco, 2007; see also Cadieux, Whitworth & Shore, 2011). Accuracy with hidden crossed-hands was improved with the sight of uncrossed rubber hands (Azañón & Soto-Faraco, 2007). Performance can also be improved by crossing the hands behind the observer's back (Kobor et al., 2006). Vision is not typically used behind the back due to our anatomy; therefore, it is possible that the external reference frame, being primarily visual, is not well established in that area. In all of these examples, vision is a defining factor. Mirrors, crossing behind the back, or the use of rubber hands, all manipulate the participant's perception of their hands in the external visual world.

The present experiment directly manipulates vision and measures the crossed-hands deficit. We reduce the information available in the external reference frame by eliminating visual perception. Participants performed the experiment in a dark room, with their eyes open or closed under different response demands. Participants were asked to respond using external coordinates (Experiments 1a and b) or internal coordinates (Experiments 2 and 3)

The two theories predict opposite results for the manipulation of vision. Removing visual inputs should degrade the fidelity of the external reference frame and increase the time taken to remap the stimuli into this reference frame. According to Yamamoto & Kitazawa (2001), the increased time for remapping, which is a critical factor in their theory, should produce a larger crossed-hands deficit. In contrast, according to Shore et al., (2002), degrading the external reference frame should reduce the conflict between reference frames, which is critical for their theory, and thus produce a smaller crossed-hands deficit.

3.2 Experiment 1a

Three visual conditions were used for this experiment: (1) Participants' eyes open with lights on (2) Eyes open with lights off and (3) Eyes closed with lights off. In both the second and third condition, participants could not see their hands or the room around them while performing the TOJ task; both conditions were included based on fMRI data demonstrating differences in brain activation when individuals have their eyes open or closed in the dark (Marx et al., 2003, 2004). When eyes are open during visual or auditory stimulation, there is activation of the ocular-motor and attention systems; however, when the eyes are closed, there is activation of the somatosensory and visual systems. These types of observations have lead to the belief that two different mental states exist: An "exteroceptive" state when the eyes are open and an "interoceptive" state when the eyes are closed. During an exteroceptive state, the body is alert and attending to the visual environment (Marx et al., 2003). These can easily be compared to the external and internal reference frames discussed above. Given the main goal of the present study was to determine the interactions of these two reference frames, we felt it was important to examine both possible eye conditions.

3.2.1 Methods

Participants

33 participants were recruited from the McMaster University undergraduate psychology subject pool. Each participant received one extra course credit as compensation for their participation in the experiment. All participants were right handed except for 3 who were left handed (1 male) as reported by a handedness questionnaire and all provided informed consent prior to participation. There were 21 females and 12 males with an average age of 20.2 (18.5 for males; 20.2 for females). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment.

Apparatus and Stimuli

Participants were seated at a table (73.7 cm in height). They held two foam cubes separated by 18 cm with their index fingers and thumbs in contact with Oticon-A (100 Ohm) bone-conduction vibrators (1.6 cm in width and 2.4 cm in length). The vibrators were driven by a 250 Hz sine wave signal that was amplified. A single amplitude was used for all participants, which was set by the experimenter to be comfortable and clearly suprathreshold—no detection measurement was taken, but all participants could clearly detect the stimuli. Both vibrators received the same amplitude of vibration, and were of the same vintage providing some assurances that the stimulus was the same to both vibrators. On each trial, two 20 ms vibrations, one to each index finger, were delivered separated by a variable stimulus onset asynchrony (SOA): ±400, ±200, ±100, ±50 ms, where negative SOAs indicate that the vibration was presented to the left side of space first. Four red LEDs (10 mm in diameter) were located next to the four vibrators. Two foot pedals were used (one under the toes of each foot) for participant responses. All stimulation was controlled by a set of read-relays connected to the parallel port of a DOS-based PC computer. The program to administer stimulation and collect responses was written in Turbo C. Throughout the experiment participants wore earplugs and white noise was continuously played over two loudspeakers to mask sound produced by the tactile vibrators and foot pedals.

Procedure

Participants held one foam cube in each hand during the experiment. The cubes were held so that the index fingers were in contact with the top vibrators. On each trial, participants received two short vibrations, one to each index finger. Participants lifted the toe of the foot corresponding to the side of space that was stimulated first, regardless of hand posture.

Each trial began after the participant pushed their toes down on both foot pedals. The first vibration occurred 800 ms after the start of the trial. The second vibration was delivered after a variable SOA determined randomly from the fixed set of SOAs for each trial. After the second vibration, participants indicated which stimulus had been presented first by lifting the corresponding toe (e.g. the left toe if vibration was delivered to the left side of space—left finger in the uncrossed posture and right finger in the crossed posture). The next trial began when participants pushed both toes down on the pedals. If participants did not respond within three and a half seconds after the second vibration, the four vibrators and the four LEDs would turn on and off until the participant lifted both of their feet. Trials in which the participant did not answer within the allotted time or where reaction times were less than 100 ms were not included in the analysis (less than one percent of the overall data in all experiments).

At the start of the experiment, participants were given instructions as to how to complete the task and then completed two blocks of 16 practice trials each. One block was done with the hands uncrossed and the other was completed in the crossed-hands posture. Hands were crossed right over left with the arms touching. The experimenter remained in the room during the practice trials to provide feedback and answer any questions. After the practice trials, the experimenter left the room and participants completed 12 blocks of 64 experimental trials, alternating crossed and uncrossed postures each block. This results in 48 trials per SOA for each hand posture. Participants were encouraged to take breaks between blocks. They remained in the previous block's eye condition during these breaks. For example, if participants were in the eyes-open condition, they remained in that condition during their break. Participants were transitioned to the next eye condition at the end of the break. Breaks were on average around 30 seconds. The order of which hand posture to adopt first was counterbalanced across participants. Each participant completed the entire task in one of the three conditions: their eyes open and the lights on, their eyes open and the lights off, or with their eyes closed (blindfolded) and the lights off. Participants were randomly assigned to a condition.

Analysis

Participants performance was evaluated using the proportion correct difference (PCD) score (see Cadieux et al., 2010). This score was computed by taking the difference in proportion of correct responses for crossed and uncrossed postures at each SOA and summing these values. An analysis of variance (ANOVA) was conducted on theses scores with eye condition as a between-participant factor. This score was used over more traditional measures for several reasons: it is model free; it provides a single number representing participants' performance; it takes into account both the crossed and uncrossed postures and thus provides a direct measure of the crossed-hands deficit. In contrast, the more traditionally used slope measure (cf. Shore, et al., 2002), assumes normality in performance, which is clearly violated in the crossed hands posture. The flip measure proposed by Yamamoto &

Kitazawa (2001) assumes an underlying model, which may not be reflective of the data (see Heed, Backhaus & Roeder, 2012 for measure comparison). Additionally, one-sample t-tests were run on each visual condition's PCD score to evaluate whether they differed from zero, indicating a crossed-hands deficit. All p-values were adjusted using a Greenhouse-Geisser correction where appropriate. Unadjusted degrees of freedom were reported.

3.2.2 Results

A between-participants' ANOVA with the factor of visual condition was conducted on the PCD scores (Fig. 1). PCD scores were unaffected by the three visual conditions ($F(2,30) = 0.10$, $p = 0.91$). Three one sample t-tests determined that PCD scores (means: eyes open/lights on = 2.54; eyes open/lights off = 2.60;eyes closed/lights off = 2.37) differed significantly from zero ($t(10) = 7.95$, $p < 0.001$; $t(10) = 7.37$, $p < 0.001$; $t(10) = 5.34$, $p < 0.001$), indicating a crossed hands deficit was observed in all visual conditions.

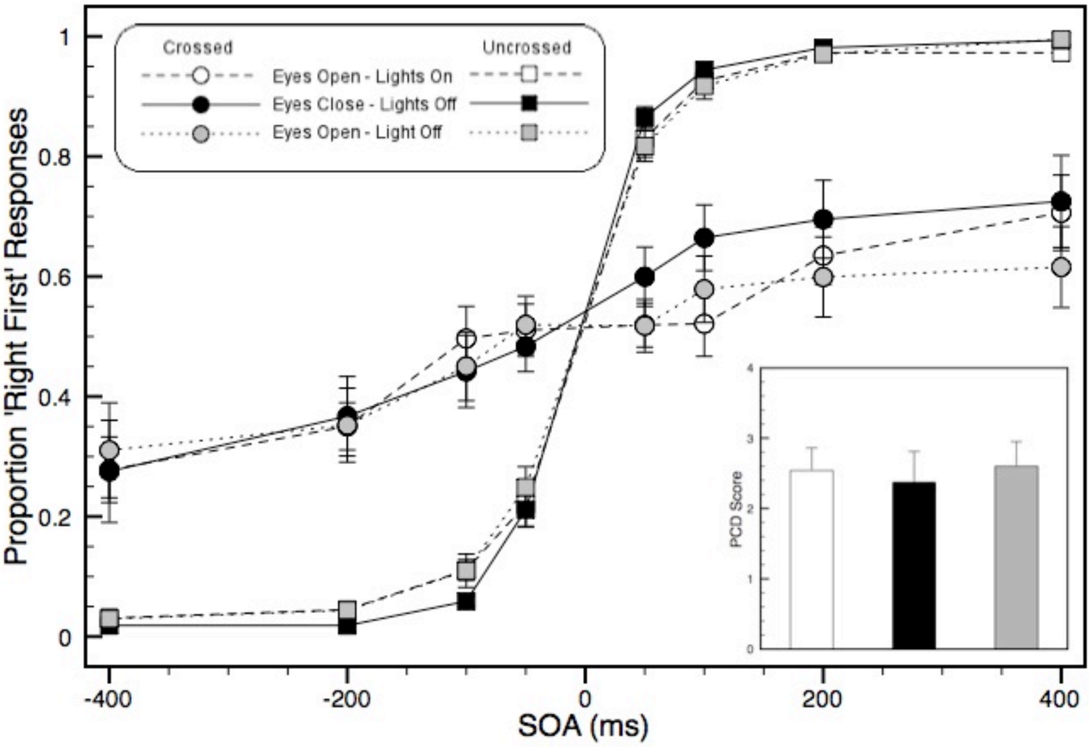

Figure 3.1 Data from Experiment 1a: a between-participant manipulation of visual conditions with “side of body” responses. The average proportion of ‘right first’ responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean. The average PCD score for each visual condition is represented in the inset bar graph. There was no difference across the visual conditions.

3.2.3 Discussion

Experiment 1a replicated a typical crossed-hands deficit: participants were less accurate with their hands crossed compared to uncrossed. However, there was no effect of visual information. Participants' performance was not improved nor diminished in either of the eyes closed conditions as would be predicted by the two theories presented earlier (Yamamoto & Kitazawa, 2001; Shore et al., 2002). Given the large amount of individual difference seen in this task (Cadieux et al., 2010) it was possible that any effect was being negated by differences between the groups. In an attempt to compensate for this possibility, Experiment 1b had participants undergo all three visual conditions in a within-participants design.

3.3 Experiment 1b

3.3.1 Methods

Participants.

34 participants were recruited from the McMaster University undergraduate psychology subject pool. Participants received one extra course credit as compensation for their participation in the experiment. All participants were right handed except for 5 who were left handed (2 males) as reported by a handedness questionnaire and all provided informed consent prior to participation. There were 25 females and 9 males with an average age of 19.8 (19.2 for males; 20 for females).

All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment.

Apparatus and Stimuli

This was identical to Experiment 1a

Procedure

The procedure was the same as Experiment 1a except the visual condition was a within-participant variable. Participants completed 12 experimental blocks: 4 for each of the three visual conditions (eyes open and the light on, eyes open and the lights off, and eyes closed (blindfolded) and the lights off)

Analysis

The analysis was identical to Experiment 1

3.3.2 Results

A repeated–measures ANOVA with the within-participant factor of visual condition was conducted on the PCD scores (Fig. 2). Again, visual condition did not impact the magnitude of the crossed-hands deficit ($F(2,64) = 2.36$, $p = 0.10$). Three one sample t-tests determined that PCD scores (means: eyes open/lights on = 2.75; eyes open/lights off = 2.58;eyes closed/lights off = 2.94) differed significantly from zero ($t(32) = 10.64$, $p < 0.001$; $t(32) = 9.09$, $p < 0.001$; $t(32) = 9.42$, $p < 0.001$), indicating a crossed hands deficit was observed in all visual conditions.

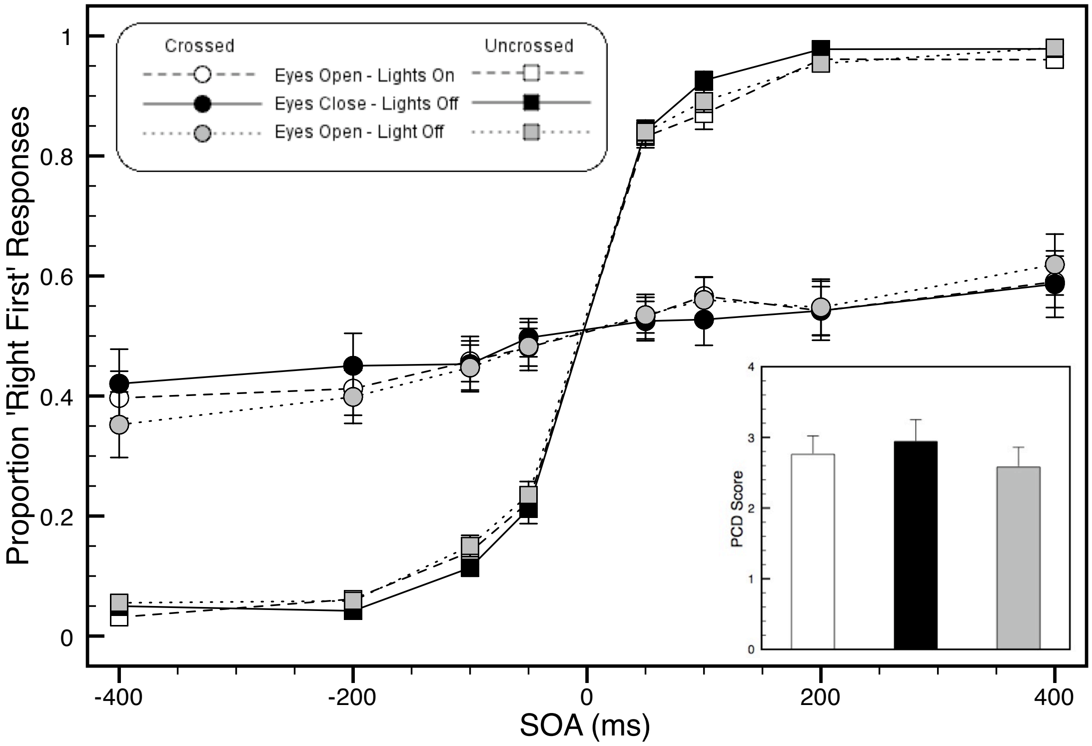

Figure 3.2 Data from Experiment 1b: a within-participant manipulation of visual conditions with "side of body" responses. The average proportion of 'right first' responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean corrected for a within-participant design. The average PCD score for each visual condition is represented in the inset bar graph. There was no difference across the visual conditions.

3.3.3 Discussion

Experiment 1b produced results similar to Experiment 1a: there was no effect of manipulating vision. With the combined results of these two experiments we are confident that there was no effect of vision on the crossed-hands deficit under these conditions. We predicted that visual information would influence the availability of the external reference frame while performing tactile TOJs. By removing visual information this should have increased (Shore et al., 2002) or decreased (Yamamoto & Kitazawa, 2001) performance on the task depending on the underlying cause of the deficit. Upon further reflection, the nature of the task used in Experiment 1a and 1b may be responsible for null results observed. In both experiments, participants were required to respond based on an external reference frame: the appropriate foot for response corresponded to the side of space where the stimulus was perceived (i.e., in the crossed-hands posture, they lifted their right foot for a left-finger stimulation—albeit on the right side of space). These response demands most likely made it impossible to eliminate the external reference frame through manipulations to the visual environment. To investigate this possibility, Experiment 2 was performed without the requirements of external coordinates: participants responded to which hand, as oppose to which side of space, was stimulated first (cf. Shore et al., 2006; in prep)

3.4 Experiment 2

3.4.1 Methods

Participants.

15 participants were recruited from the McMaster University undergraduate psychology subject pool. Participants received one extra course credit as compensation for their participation in the experiment. All participants were right handed as reported by a handedness questionnaire and all provided informed consent prior to participation. There were 9 females and 6 males with an average age of 19.7 (19.2 for males; 20 for females). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment. *4.1.2 Apparatus and Stimuli*

This was identical to Experiment 1

Procedure

The procedure was the same as Experiment 1 except participants now reported which hand was vibrated first regardless of hand position (e.g. if the left finger was vibrated first the participant always lifted their left toe, even when their left hand was on the right side of space).

Analysis

The analysis was identical to Experiment 1

3.4.2 Results

A repeated–measures ANOVA with the within-participant factor of visual condition and was conducted on the PCD scores (Fig. 3). The visual manipulation had no impact on the size of the crossed-hands deficit (F(2,26) = 1.39, p = 0.27). Three one sample t-tests determined that PCD scores (means: eyes open/lights on = 1.32; eyes open/lights off = 1.32;eyes closed/lights off = 1.57) differed significantly from zero (t(13) = 3.92, p = 0.002; t(13) = 3.79, p = 0.002; t(13) = 4.24, p = 0.001), indicating a crossed hands deficit was observed in all visual conditions.

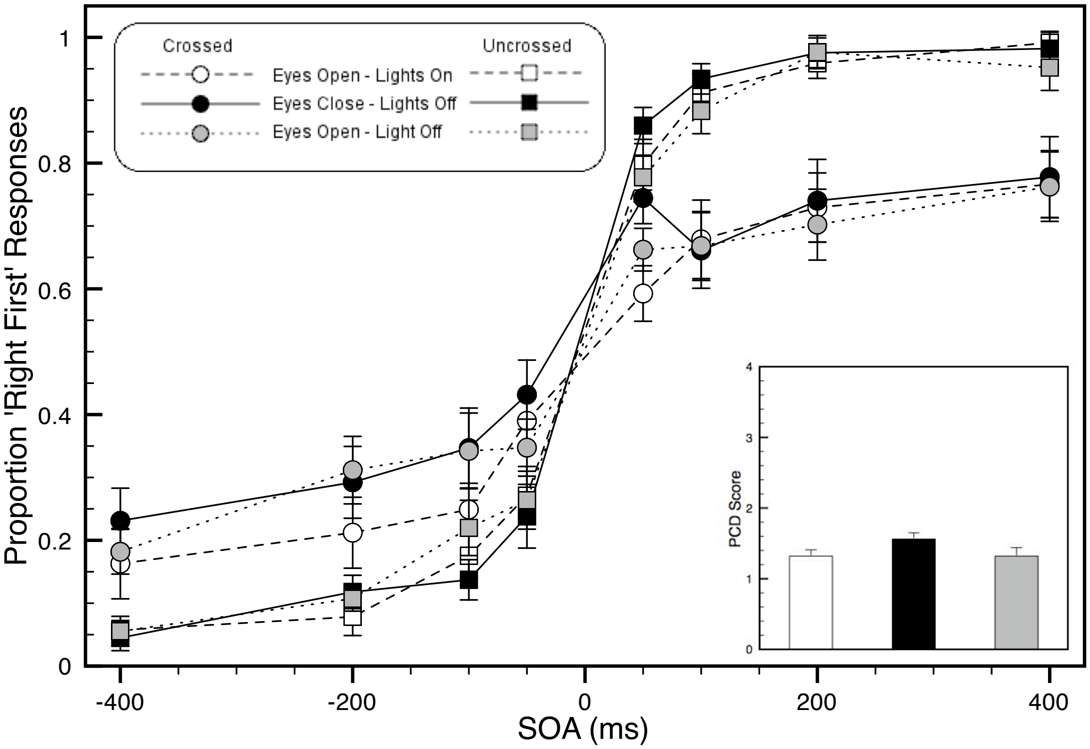

Figure 3.3 Data from Experiment 2: a within-participant manipulation of visual conditions with "which hand" responses. The average proportion of 'right first' responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean corrected for a within-participant design. The average PCD score for each visual condition is represented in the inset bar graph. There was no difference across the visual conditions.

3.4.3 Discussion

Experiment 2 produced results similar to Experiment 1. A crossed-hands deficit was seen and no effect of the visual conditions was present. While response demands were shifted in this experiment towards an internal reference frame, participants were still required to remap stimuli presented to their hands to their feet in order to make accurate responses. It is possible that this remapping still requires the use of an external reference frame as in Experiment 1. We examine this possible explanation of the previous null results in Experiment 3.

3.5 Experiment 3

In this experiment, we modified the response demands to a more direct measure using buttons mounted under the vibrators on which the participants placed their thumbs (cf. Shore, et al., 2002). They pressed down on the vibrator that was perceived to be stimulated first. Participants responded using the thumb that was vibrated. In this case, no remapping was necessary. For simplicity and since no difference was seen in the first three experiments, the eyes open–lights off condition was dropped from this experiment.

3.5.1 Methods

Participants.

40 participants (20 males) were recruited from the McMaster University undergraduate psychology subject pool[3]. Participants received one extra course credit as compensation for their participation in the experiment. All participants were right handed except for 6 who were left handed as reported by a handedness questionnaire and all provided informed consent prior to participation. Participants had an average age of 19.1. All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment.

Apparatus and Stimuli

The tactile stimulators were mounted on top of response buttons, and the entire assembly was enclosed in a small wooden box with a Plexiglas top. A hole 2 cm in diameter was cut into the Plexiglas so that the participant could place their thumb in contact with the vibrating surface and push down on the vibrator to respond. Participants made responses by pushing down on whichever button vibrated first. A new program was written in Matlab to control the vibrators. All other aspects of stimulus delivery were the same as Experiment 1.

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[3] Experiments 1 and 2 had unbalanced numbers of men and women; both experiments were conducted prior to the publication of Cadieux et al. (2010), which revealed a significant sex-difference in the crossed-hands deficit. Experiment 3 has an equal number of males and females.

Procedure

This was similar to Experiment 1 with the following exceptions. Only 2 visual conditions were used: eyes open with the light on and eyes closed (blindfolded) with the lights off. We returned to a between-participant manipulation. Participants performed 5 blocks in one posture (arms crossed or uncrossed) followed by 5 blocks in the opposite posture; the initial starting position was counterbalanced across participants.

Analysis

The analysis was identical to Experiment 1

3.5.2 Results

A between–participants univariate ANOVA with covariates of visual condition and sex was conducted on the PCD scores (Fig. 4). The crossed-hands deficit was smaller in the blindfolding condition (mean = 0.94) compared to the eyes open condition (mean = 1.87; $F(1,37) = 8.84$, $p = 0.005$). Males and females did not differ in the size of their deficit ($F(1,37) = 0.01$, $p = 0.97$). Two one sample t-tests determined that PCD scores (means: eyes open/lights on = 1.87; eyes closed/lights off = 0.94) differed significantly from zero ($t(19) = 7.16$, $p < 0.001$; $t(19) = 5.82$, $p < 0.001$), indicating a crossed hands deficit was observed in all visual conditions.

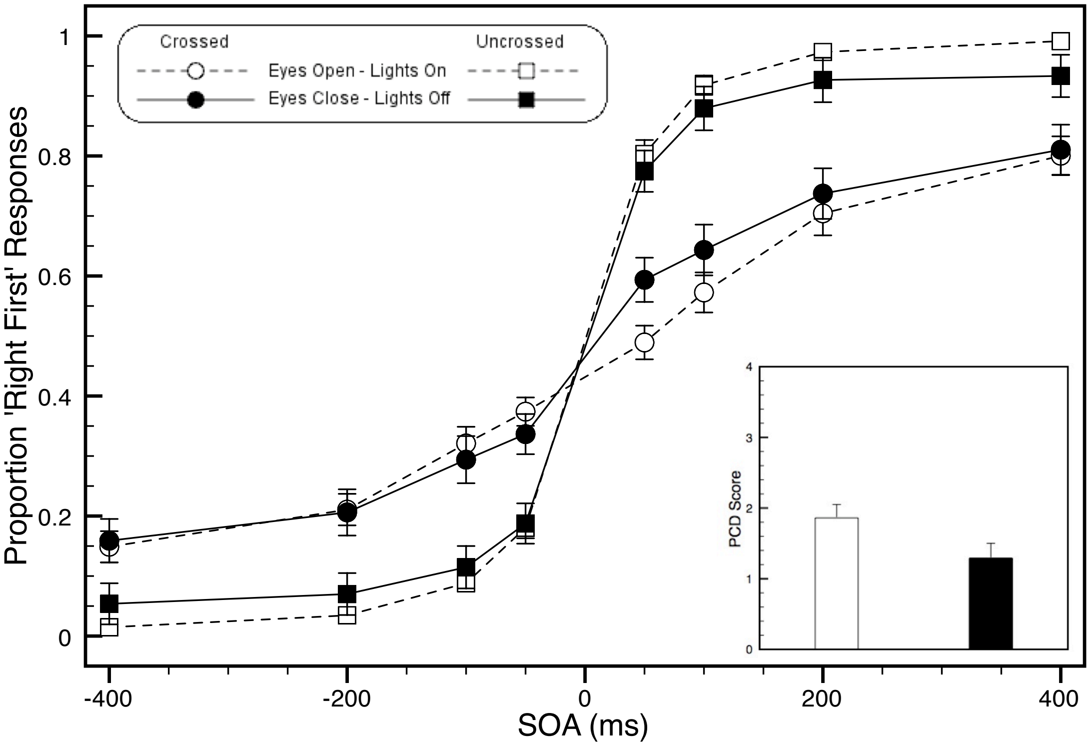

Figure 3.4 Data from Experiment 3: a between-participant manipulation of visual conditions with "which hand" responses. The average proportion of 'right first' responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean corrected for a within-participant design. The average PCD score for each visual condition is represented in the inset bar graph. The crossed-hands deficit was reduced in the eyes closed–lights off condition.

3.5.3 Discussion

Blindfolded participants produced a smaller crossed-hands deficit than those who could see their hands. This reduction in the size of the crossed-hands deficit provides support for the conflict resolution account of the deficit (cf. Shore et al., 2002). We observed no effect of sex in this experiment, which appears to be in contrast to previous work with this task (Cadieux et al., 2010; see General Discussion).

3.6 General Discussion

The present study examined the impact of visual information on the crossed-hands tactile TOJ deficit. In Experiments 1 and 2 participants were unaffected by the manipulation of visual condition: the lighting condition (on or off) and eye condition (open or closed) did not affect PCD scores. In Experiment 3, participants who were blindfolded produced a reduced crossed-hands deficit (Figure 5). The critical difference between the first two experiments, and Experiment 3 was a change in the response demands; the first two experiments required representation in the external reference frame in order to respond, whereas, little or no remapping was required from an internal reference to an external one for the last experiment.

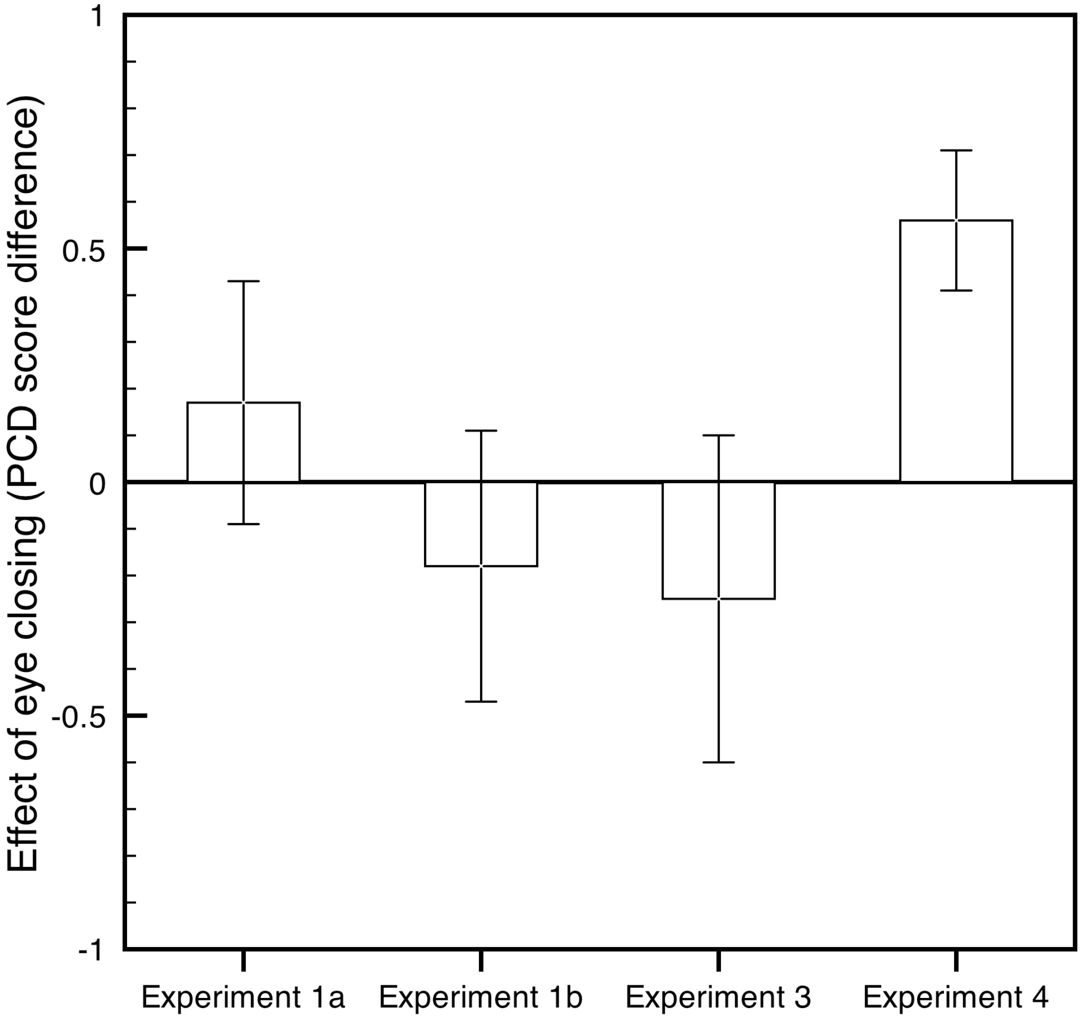

Figure 3.5 An across–experiment comparison. The PCD score difference from the eyes open–lights on condition and the eyes closed–lights off condition was calculated. This difference represents the effect of the visual condition on the crossed hands deficit.

The primary goal of manipulating visual input was to contrast two proposals for the cause of the deficit. The reduced deficit seen in Experiment 3 supports the role of reference frame conflict (Shore et al., 2002) as opposed to increased processing time to remap stimuli in the crossed-hands posture (Yamamoto & Kitazawa, 2001). Degrading or eliminating the representation of the external environment reduced the crossed-hands deficit when response demands were centered on the internal reference frame. The direction of the effect is interpreted to support the claim that information from both the internal and external reference frames are integrated at the time of response selection. Further, without a representation of external space, these responses are biased towards the internal reference frame, thus reducing the conflict and decreasing the deficit. If, as Yamamoto and Kitazawa (2001) proposed, the deficit was driven by the time necessary to remap stimuli from internal to external space, the deficit should have increased.

Other lines of evidence support the conflict model. As mentioned in the Introduction, when the hands are crossed behind the back the TOJ deficit is reduced (Kobor et al., 2006). In both conditions of that study (i.e., hands in front of the body or behind the body), the eyes were closed; thus, it cannot be a lack of visual information *per se* that causes these results. Rather, it is more likely that the fidelity of the external reference frame behind the back is less reliable, which again forces observers to rely more heavily on the internal reference frame, which is unaffected by hand crossing.

Changes in response demands also provide evidence for the conflict model. When observers were forced to make responses using at external reference frame, the crossed-hands deficit was increased (Shore et al., 2006 in prep). In the present study, a comparison of Experiments 1b and 2 provides a replication of this result. In Experiment 1b observers reported which side of space was stimulated first (i.e., lift the left toe when the right hand was stimulated first in the crossed-hands posture) while in Experiment 2 they reported which hand was stimulated first (i.e., lift the left toe when the left hand was stimulated first regardless of posture). This somewhat subtle manipulation had a profound effect on the PCD scores: the deficit was more than double in Experiments 1b (side of body; 2.76) than in Experiment 2 (which hand; 1.32; $t(45) = 3.38$, $p=0.002$). This radical difference again supports the conflict model over the increased time for the crossed-hands posture model: if responses were made based on the external reference frame alone (Yamamoto & Kitazawa, 2001), performance should be improved by having observers respond in an external reference frame, and should be hindered when they must recode their response into an internal reference frame. On the other hand, bolstering the reliance on the internal reference frame should reduce the relative conflict between the two and thus reduce the deficit. It is interesting to note that Kobor et al. (2006) appears to have used a “which hand” response demand when testing the effect of crossing behind the back; if they had used a "which side of space" response demand the deficit would have been larger overall. But, we do not know if there would have been a difference between front space and rear space with this response demand—that is, requiring observers to respond in an external reference frame may have forced them to represent the stimuli in that frame, and thus eliminated the difference that they found. Response demands appears to be a powerful manipulation to explore the causes of this deficit.

With regards to the lack of a sex-effect in Experiment 3, Cadieux et al. (2010) proposed that the sex-difference was caused by men being better able to resolve a reference frame conflict driven by external information. This was seen in two tasks used in that study, the rod-and-frame test and the vibrotactile TOJ. In the rod-and-frame test, participants have to ignore a visual tiled square while making judgments about the tilt of a line presented at its center. Men were better able to ignore the frame, resulting in a smaller frame effect. The vibrotactile TOJ task required side of body responses, forcing participants to use the external reference frame. For men, but not for women, performance on these two tasks was correlated such that those individuals with a larger frame effect also had a larger crossed hands deficit. In the current experiment, all effort where taken to reduce the use of the external reference frame, and thus a 'which hand' response demand was used. It is possible that this change in response demands is responsible for the lack of a differences. This hypothesis cannot be tested with the current data given the unbalanced groups in the first two experiments. However, post-hoc test on Experiment 1, in which an external response demand was used, does reveal a sex-effect in Experiment 1b. Males had a lower PCD score (mean = 1.81) than females (mean = 3.07) (F(1,31) = 4.48, p = 0.04). A future study should directly address the effect of response demands on the crossed-hands deficit sex-difference.

The present study provides several tools to further explore the causes of the crossed-hands deficit in tactile TOJs. Other manipulations of the external reference frame may provide further insights into how these stimuli are coded on the body and in space. Here we have used vision; however, manipulating one's sense gravity could also prove interesting. For instanced, a microgravity environment causes participants to be more body centric (Jenkin et al., 2005). In other words, responses are biased towards the internal reference frame. If the crossed-hands deficit is caused by a conflict between reference frames, as proposed here, then the deficit should decrease in microgravity. A similar logic could be applied to manipulations of body posture (cf. Dyde, Jenkin & Harris, 2006): when participants adopt a supine posture they are less influenced by gravity and thus rely more on body-based cues to the subjective visual vertical. Finally, finding correlates with other spatial tasks involving reference frames translation could also help provide evidence for an underlying mechanism. Tasks such as mental rotation and navigation that use multiple reference frames would be ideal for such studies.

To conclude, the crossed-hands deficit appears to be driven by a conflict between the internal and external reference frames (Shore et al., 2002) and not an increase in the time to translate from one frame to the other (Yamamoto & Kitazawa, 2001). The logic of this conclusion rests on the assumption that degrading an external reference frame should bias observers to use an internal reference frame more heavily. Response demands played an important role in this study since simply removing vision of the limbs was not enough to reduce the conflict; response selection needed to be aligned with the internal reference frame.

3.7 Acknowledgments

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Chapter 4: Supine body position and the crossed hands deficit

4.1 Abstract

Performance on tactile TOJs is impaired when the hands are crossed over the midline. The cause of this effect appears tied to a conflict between internal and external reference frames. In two experiments we measured the effect of body position (upright vs. supine) and hands posture (near vs. far from the body) on the crossed-hand deficit. In Experiment 1, the deficit was smaller in supine than upright body position. However, the hands were placed in front of participants in the upright position and close to the body in the supine position. Experiment 2 revealed that the difference in hand posture rather than the difference in body position was the driving factor in the result observed in Experiment 1. Specifically, cross-hands performance for the upright body position was better with the hands close to the body than with the hands far from the body, suggesting that hands close to the body induces a more internal reference frame.

4.2 Introduction

The integration of multiple sensory modalities influences perception and cognitive processing of stimuli. The coherent percept of a unified stimulus stems from information from different sensory sources. This consolidation of information can be influenced by different factors including the temporal and spatial relations of stimuli. With tactile stimuli, the placement of the hands can have a drastic influence on perception. For example, performance on tactile temporal order judgments (TOJs) is impaired when observers place their hands in a crossed posture (Drew 1896, Yamamoto & Kitazawa 2001, Shore et al. 2002, Roder et al 2004, Wada et al 2004, Kobor et al 2006, Holmes et al 2006, Craig & Belser 2006, Azañón & Soto-Faraco 2007, Robers & Humphreys 2008 Cadieux et al 2010; Heed et al., 2012). This phenomenon is referred to as the crossed-hands deficit. The present study explores the impact of gravity and body position on the magnitude of this deficit.

Two theories have been proposed to explain the crossed-hands deficit. Both suggest an interaction between an internal and an external reference frame (Yamamoto & Kitazawa, 2001; Shore et al., 2002). Yamamoto and Kitazawa (2001) submit that the first stimulus presented to the hands (internal) in a TOJ task must be localized in space (external) before the onset of the second stimulus. The deficit arises when the second stimulus is presented before the remapping of the first stimulus has been completed. Under this hypothesis, responses are made based on the external reference frame only. Shore et al. (2002) propose that stimuli are quickly transformed from the internal reference frame to the external; however, both internal and external reference frames remain active. During response selection, information from both reference frames is processed, and it is the conflict between these two reference frames that causes the deficit. In essence, the difference between these two theories stem from the stage of processing—early or late—that produces the profound deficit.

Degrading the representation of information in the external reference frame provides one way to contrast these two models. If stimuli must be localized in external space prior to judging their order (Yamamoto & Kitazawa, 2001) then the deficit should be increased by manipulations that degrade the representation of this external reference frame. On the other hand, if the deficit arises from a conflict between the two reference frames (Shore et al., 2002), then degrading the external reference frame should decrease the conflict, and thus the size of the deficit. The removal of visual input provides one way to examine degradation of the external frame. With this method, recent work from our lab (Cadieux & Shore, accepted), has provided some evidence for a conflict model of crossed-hands processing.

The present study was designed as an extension of the results from visual deprivation (Cadieux & Shore, accepted). Here we degraded the external reference frame by manipulating the influence of gravity—observers either sat up or lay down while completing the TOJ task with hands crossed or uncrossed.

4.2.1 The crossed-hands deficit

A change in posture can influence the temporal processing of tactile stimuli presented to the hands. With uncrossed hands, increasing the physical (Shore et al., 2005) or perceived (Gallace & Spence, 2005) distance between the hands can enhance temporal accuracy. With the hands crossed, performance is generally very poor; however, crossing the hands behind the observer's back (Kobor et al., 2006) improves performance. Also, substituting the hands for rubber hands (Botvinick & Cohen, 1998; Favani et al., 2000; Azañón & Soto-Faraco, 2007) can refine performance – accuracy with actual crossed hands was improved with the sight of uncrossed rubber hands (Azañón & Soto-Faraco, 2007). In line with the conflict model of the crossed-hands deficit, different degrees of the deficit can be produced by influencing the amount of conflict present with respect to the hands and fingers (Heed et al., 2012). An intermediate deficit is observed when the hands but not fingers or the fingers but not hands are crossed when compared to a full crossed posture. Thus, reducing the level of conflict between the internal and external reference frames appears to reduce the deficit.

Early visual experience plays a key role in the development of the crossed-hands deficit. While late-blind and sighted individuals show a deficit, congenitally blind individuals are unaffected (Roder et al., 2004). The use of the visual external reference frame seems to be acquired early in life and depends on visual experience for its development and function. While young children (age 5) are more reliant on tactile information, the bias shifts towards visual information around age 8 (Gori et al., 2008). Children older than five years of age show the crossed-hands deficit, whereas younger children do not (Pagel et al. 2009). If the deficit were caused by a delay in the transfer of information from the internal to the external frame, performance should improve through development, as it would be easier to transfer information to a fully developed frame of reference. However, this is not the case. The deficit does not occur until this reference frame is developed.

4.2.2 The effects of body position

Body position influences both internal and external reference frames. Measuring the perception of which way is 'up' provides one way to understand reference frames relative to the body. Two different measures are used to evaluate which way is up: The subjective visual vertical (SVV) and the perceptual upright (PU) (Dyde et al., 2006). In the SVV observers judge the orientation of a line to appear vertical and aligned with the perceived direction of gravity (see Howard, 1982 for review), whereas with the PU, observers report their subjective perception, which is influenced by the orientation of objects (Dyde et al., 2006). These two measures appear to capture different contributions to our perception of which way is 'up'.

The SVV and the PU show different effects of environmental manipulations. Our perception of up is influenced by at least three reference frames: visual, body, and gravity. Gravity, like vision, is most closely tied to the external reference frame, while body position is more linked to the internal reference frame (Barnett-Cowan & Harris, 2008); the SVV relies heavily on gravity, whereas the PU is closely tied to the body (Dyde et al., 2006). When standing or sitting, the SVV and the PU are convergent; however, when in the supine position, the PU remains aligned with the body but the SVV remains stable with the direction of gravity. This creates incongruence between the two cues for 'up'. In this position, the SVV would no longer provide information congruent with the body's position. The external reference frame would be degraded with respect to the body's midline.

Degradation of one reference frame influences reliance on the other frames. During parabolic flight the effects of gravity are systematically increased and decreased. Under these conditions, the direction of 'up' is almost exclusively determined by body-based cues (Jenkin et al., 2005). Observers reported which of four shaded disks appeared to be convex as opposed to concave—a report that depends on the perceived direction of lighting, which typically comes from above (Berbaum et al., 1983; Ramachandran, 1988). Participants could base their judgments of 'up' on their body position, the direction of gravity or a visual image presented behind the shaded circles. Under high and low gravity conditions, body position was used as the main, and in the case of low gravity only, cue for 'up'. When the external reference frame was degraded by providing unfamiliar gravitation cues, judgments were biased towards the internal frame of reference.

Degradation of information in one modality can affect all types of multisensory integration. Both visual-tactile (Ernst & Banks, 2002; Gori et al., 2008) and visual-auditory (Alais & Burr, 2004; Parise, Spence, & Ernst, 2012) signals are integrated in a statistically optimal fashion. Information from different senses is combined to form a single interpretation of the stimuli. When one source becomes degraded, or less reliable, our perception is shifted towards the more dependable source of information. The same type of process should be responsible for integrating information from different frames of reference (Cadieux & Shore, accepted). We use this assumption to probe the role of external and internal reference frames in the crossed-hands deficit.

4.2.3 Scope of the present study

The present study examined the effects of body position—upright vs. supine—on the crossed-hands deficit. While in the supine position, the external reference frame should be degraded. If temporal order judgments are based on the external reference frame (cf. Yamamoto and Kitazawa, 2001), then the degradation of that reference frame should increase the deficit. That is, it should take longer to remap tactile stimuli in an external reference frame when that frame is degraded. If, on the other hand, the deficit arises due a conflict between the internal and external reference frames (cf. Shore et al., 2002), degradation of the external frame should push participants to base their judgments on the more reliable internal frame of reference, and thus reduce the size of the deficit. To be clear, participants completed a tactile temporal order judgment task with their hands crossed or uncrossed—the difference in performance between these two hand positions was taken as the size of the crossed-hands deficit. The task was completed while sitting up or lying down. Any difference in the size of the deficit while in these two positions was used to support one or the other theory—a larger deficit when lying down would support

Yamamoto and Kitazawa (2001), whereas a smaller deficit while lying down would support Shore et al. (2002).

4.3 Experiment 1

4.3.1 Methods

Participants

Twenty-two participants were recruited from the McMaster University undergraduate psychology subject pool (12 females and 10 males). Participants had a mean age of 19.9 years (19.7 for females and 20.1 for males). Two females were excluded from the experimental analysis due to previous participation in a similar experiment. Participants received compensation in the form of course credit. All participants were right-handed except for four (2 females and 2 males), as reported by a handedness questionnaire completed prior to the experiment. All participants provided written informed consent prior to the experiment and were naïve to the purpose of the study.

Apparatus and Stimuli

The experiment was conducted in a lit testing-room. For half of the experiment, participants were seated at a table (81 cm in height); for the other half, they lay on a table covered with a foam cushion. Participants held a wooden cube in each hand, with their thumbs in contact with a circular vibrator. The cubes were 4 cm in width and 8 cm in length and were separated by 25 cm. On each trial, two 10 ms vibrations were delivered to each thumb, separated by a variable stimulus onset asynchrony (SOA) of ± 400, ± 200, ± 100, ± 50 ms, where a negative SOA indicates the vibration was presented to the left hand first. In order to respond, participants pushed down on the vibrating part of the cube, which also acted as a button. All stimulation was controlled by a set of read-relays connected to the parallel port of a Windows-Based PC computer running Matlab. Throughout the duration of the experiment, participants wore headphones playing continuous white noise to prevent them from hearing any sounds produced by the equipment.

Procedure

Participants held one wooden cube in each hand with their thumbs in contact with the vibrator on the top of the cube. For each trial, participants received two vibrations, one to each thumb, separated by a variable SOA. Participants indicated on which hand they felt the vibration first by pressing down on the button of the corresponding cube. At the beginning of the experiment participants were given instructions on how to carry out the task, and completed two blocks of 16 practice trials each. Both practice blocks were completed in the upright body position, one block with arms uncrossed and the other in the arms crossed position. Hands were crossed with one arm over top of the other with arms touching; the arm placed on top was chosen by the participant, but was kept the same for the duration of the experiment. The experimenter remained in the room for the duration of the practice trials to ensure correct understanding of the procedure and to answer any questions. Once the practice trials had been completed, the experimenter left the room and the participant completed 12 blocks of 64 experimental trials. Participants completed 6 blocks in an upright body position and 6 in a supine body position, alternating crossed and uncrossed hand postures for each block of trials. The starting hand and body postures were counterbalanced across participants. In the supine body position, the hands-uncrossed trials were completed with the participants' arms resting at the sides of the body, and the hands-crossed trials were completed with the arms crossed over the chest and were in direct contact with the body.

The experimenter started blocks manually before leaving the testing room. The experimenter re-entered the room upon the end of each block to advise the participant which hand and body position to adopt, and began the next block before leaving the room. The first vibration occurred 400 ms after the start of the trial. The second vibration occurred after a temporal interval defined by randomly selecting one of a fixed set of eight SOAs. Once both vibrations had occurred, participants indicated on which hand they felt the first vibration by pressing down on the button of the corresponding cube. The next trial began 400 ms after response. If participants did not respond within three seconds of the second vibration, they received three distinct vibrations at the same time to both cubes. In this case, to move to the next trial, participants pressed down on both buttons at the same time.

Trials in which the participant did not respond within three seconds were rare (0.1% of all trials) and were not included in the analysis.

4.3.2 Analysis

The proportion correct difference (PCD) score was calculated for each participant (Cadieux et al., 2010, Heed et al., 2012). This score is computed by taking the difference, at each SOA, between performance in the crossed and uncrossed positions and summing these differences. This measure provides a single score for each participant in both the upright and supine positions. Analyses were submitted to a Greenhouse-Geisser correction when appropriate. Below we have reported the corrected p-values but the uncorrected degrees of freedom.

A paired sample t-test was calculated comparing the upright and supine positions. The upright position (mean = 1.69) had a significantly higher score then the supine position (mean = 1.08; $t_{(19)} = 4.35$, $p < 0.001$), indicating that the crossed hands deficit was lower in the supine position. Two one sample t-tests determined that PCD scores in both upright ($t_{(19)} = 8.69$, $p < 0.001$) and supine ($t_{(19)} = 6.32$, $p < 0.001$) conditions differed significantly from zero, indicating a crossed-hands deficit was observed in both body positions.

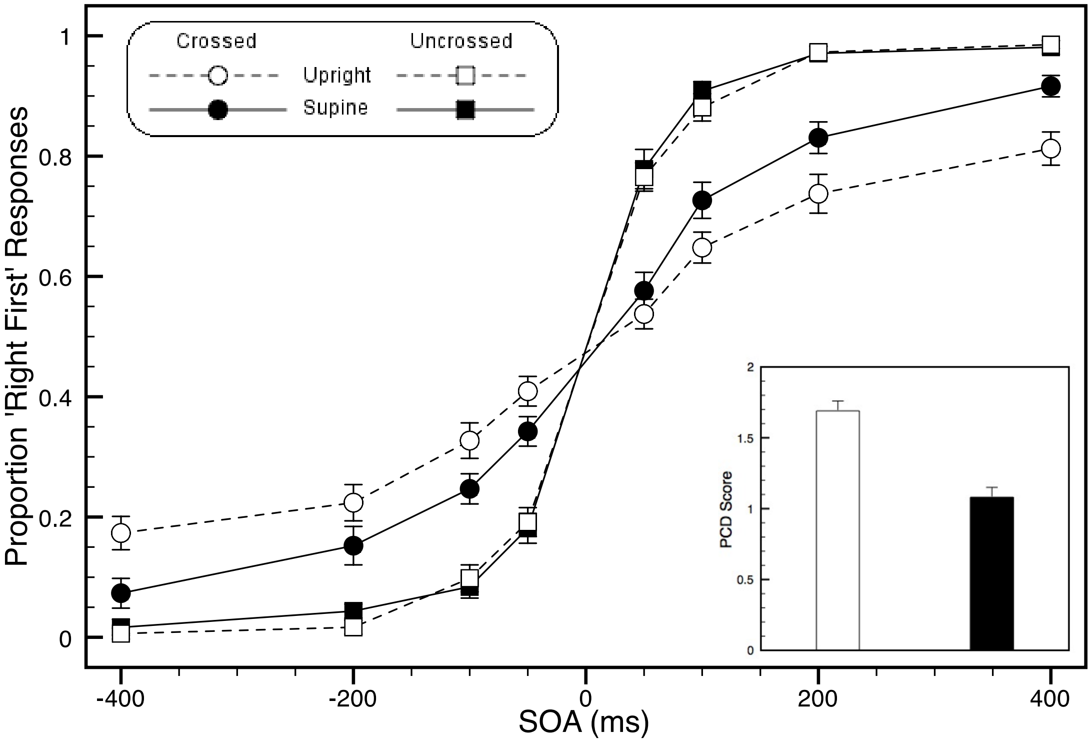

Figure 4.1 The average proportion of 'right first' responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean. The average PCD score for each position is represented in the inset bar graph. Participants were more accurate in the supine condition compared to the upright.

4.3.3 Discussion

The crossed-hands deficit was reduced when in the supine position. Thus, degrading the external reference frame through a manipulation of body position reduced the size of the deficit. We interpret this finding as support for the hypothesis that the deficit is caused by conflicting information received from the internal and external frames of reference (Shore et al., 2002). As stated earlier, if the deficit were due to a delay in the remapping of stimuli from the uncrossed to the crossed posture alone (Yamamoto & Kitazawa, 2001) we would expect the degradation of the external reference frame, caused by the misalignment of the SVV and the body, to increase the deficit, as it would take longer to code the information in external space. However, that was not what we found here. Performance was significantly better with the degraded external reference frame; participants apparently based their responses on the internal reference frame since it was the more reliable. By ignoring the external frame, the conflict was reduced.

Before accepting this conclusion completely, we must rule out an alternative explanation of the data. While sitting up, the hands were placed away from the body on the table's surface, whereas in the supine position, the hands were placed closer to the body (at the side of the body in the uncrossed posture, and over the chest in the crossed posture). To evaluate the role of this potential confound, a second experiment was conducted in which the same arm crossing posture was adopted for both body positions: that is, participants held their hands to their side in the uncrossed posture and crossed them over their chest for the crossed posture, both while sitting up and while lying down.

4.4 Experiment 2

4.4.1 Methods

Participants

Twenty participants were recruited from the McMaster University undergraduate psychology subject pool (10 females and 10 males). Participants had a mean age of 19.9 years (19.7 for females and 20.1 for males). Participants received compensation in the form of course credit. All participants were right-handed except for four (2 females and 2 males), as indicated by a handedness questionnaire completed prior to the experiment. All participants provided written informed consent prior to the experiment and were naïve to the purpose of the study.

Apparatus and Stimuli

All equipment and stimuli were identical to Experiment 1.

Procedure

The procedure was the same as Experiment 1 except for the posture of the arms in the sitting up position. In the crossed posture, arms were crossed over the participant's chest and in the uncrossed posture they were at the participant's side. As such, the arm position was now similar in the two body position conditions.

4.4.2 Analysis

As in Experiment 1, a PCD score was calculated for each participant in both the upright and supine position. A paired sample t-test was calculated comparing these two positions. The upright position (mean = 1.21) did not have a significantly higher score then the supine position (mean = 1.25; $t_{(19)} = -0.40$, $p = 0.70$), indicating that the crossed-hands deficit did not differ for the two body positions. Two one sample t-tests determined that PCD scores in both upright ($t_{(19)} = 6.18$, $p < 0.001$) and supine ($t_{(19)} = 7.07$, $p < 0.001$) body positions differed significantly from zero, indicating a crossed-hands deficit was observed in both body positions.

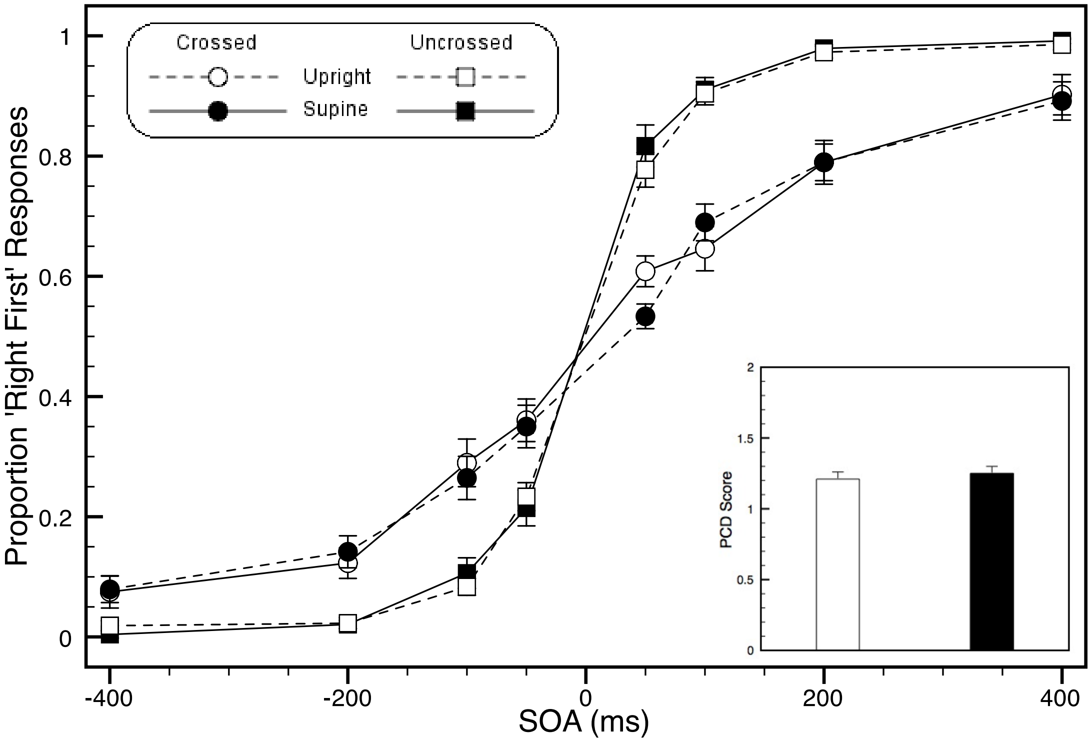

Figure 4.2 The average proportion of ‘right first’ responses was calculated for each participant at each SOA. Error bars represent the standard error of the mean. The average PCD score for each position is shown in the inset bar graph. No difference in performance was seen between the upright and supine positions.

4.4.3 Discussion

The crossed hands deficit did not differ for the two body positions. This result is in stark contrast to Experiment 1. When the hands were kept close to the body in the upright position—as they were in the supine position—performance was the same across the two body positions. The results seen in Experiment 1 were most likely due to the difference in the proximity of the hands to the body and not to the change in body position per se. To directly address this hypothesis, post hoc comparisons of the two experiments were completed.

Cross-experiment analysis

Slope measures were calculated for the crossed posture in the upright and supine body position for both experiments. PCD scores could not be used here as they capture the difference between crossed and uncrossed postures, and our focus here was the cross posture only. The slope was calculated by converting the proportion of 'right first' responses at each SOA to its standardized z-score equivalent. The slope of the best-fitting line was calculated for each observer (i.e., a probit analysis; cf. Finney 1971). A step slope would indicate good performance whereas a shallow slope represents poor performance. A 2x2 mixed measures ANOVA with the within-participant factor of body position (upright vs supine) and between-participant factor of experiment (Experiment 1 vs Experiment 2) was completed (Figure 3). Slope values were steeper in the supine (mean = 4.54) compared to upright (mean = 3.65) positions ($F(1, 38) = 24.95$, $p < 0.001$). The interaction between body position and experiment was also significant ($F(1, 38) = 14.00$, $p = 0.001$). To further evaluate these results, separate comparisons were run on the four possible slope parings. As reflected in the PCD scores, slope values were steeper in the supine (mean = 4.54) compared to the upright (mean = 2.98) position in Experiment 1. In other words, crossed performance was improved in the supine position. Slope values did not differ between upright (mean = 4.32) and supine (mean = 4.53) positions in Experiment 2 ($F(1, 19) = 1.21$, $p = 0.29$). Additionally, slope values in the upright crossed position differed across the two experiments, ($F(1, 38) = 7.87$, $p = 0.01$), with hands crossed over the chest (mean = 4.32) having a steeper slope than hands crossed in front (mean = 2.98).

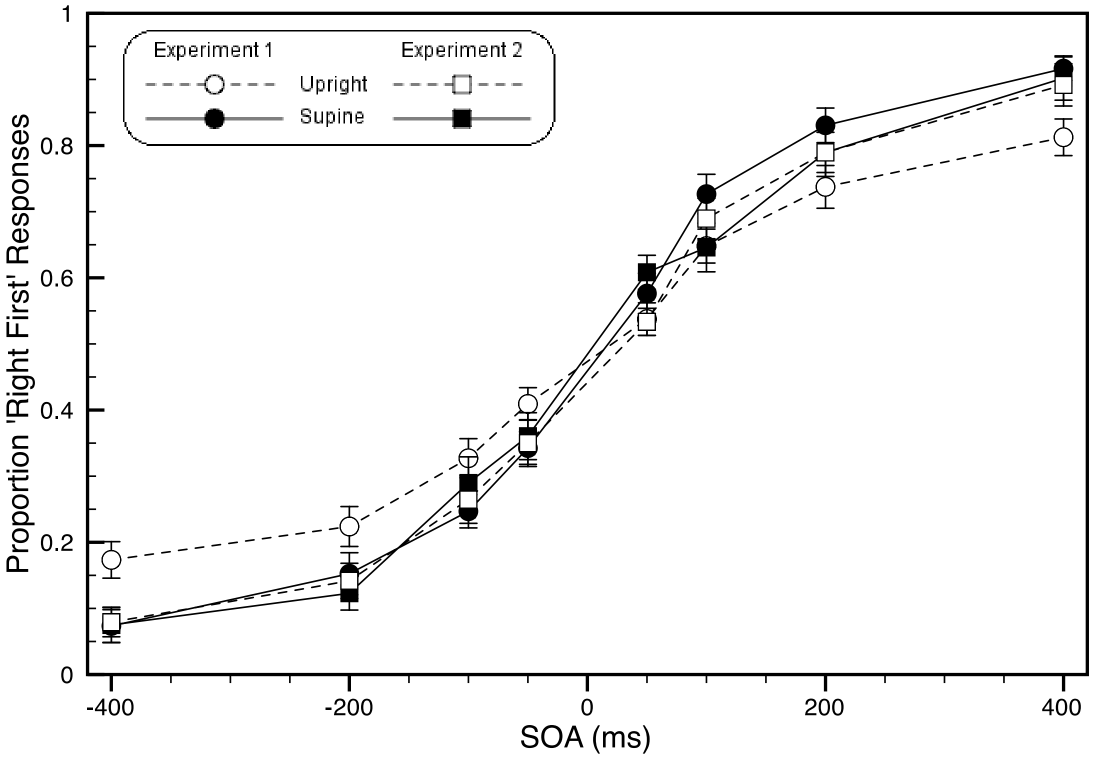

Figure 4.3 Across experiment comparison of crossed-hands only data. Participants were more accurate in the supine condition compared to the upright. The slope value in the upright position of Experiment 1 had a shallower slope than that of Experiment 2.

4.5 General Discussion

The main question of interest for these two experiments was the effect of degrading the external reference frame on the crossed-hands deficit. In Experiment 1, participants completed the TOJ task sitting up and lying down. The crossed-hands deficit was reduced in supine position. However, there was a confounding variable of how close the hands were to the body: in the supine position the hands were in contact with the body, whereas in the upright position, the hands were held in front of the body on the table surface. Experiment 2 controlled this confound by placing the hands close to the body in both body positions. No effect of body position (upright versus supine) was observed. Cross experiment analyses revealed that it was the proximity of the hands to the body that improved performance in a crossed hands posture.

When the hands were placed close to the body in the crossed position, participants received two internal reference frame cues as to their location – the stimuli on the hands themselves and the location of the hands on the chest. The tactile stimulus, the location of the hands, and the required response demands were all placed under an internal coordinate system. Given that visuotactile peripersonal space is represented using body-part-centered coordinates (see Holmes and Spence, 2004 for review), the closer proximity of the hands to the torso most likely pushed participants to adopt a more internal frame of reference. While the effect of body position was confounded in Experiment 1, the difference in hand postures across the two experiments allows us to examine the effects of adopting a more internal reference frame.

The present study supports our previous research on the cross hands deficit (Cadieux and Shore, accepted). When an internal reference frame is adopted, as occurs when the hands are placed close to the body, the crossed-hands deficit is alleviated. If stimuli had to be located in external space before they could be ordered in time (Yamamoto & Kitazawa, 2001), the deficit would have increased rather than decreased with the hands placed close to the body. Therefore, it is more likely that the crossed-hands deficit is caused by a conflict between the two reference frames (Shore et al., 2002), as adopting an internal reference frame appears to improve performance.

Although the present data provided some evidence as to the cause of the crossed-hands deficit, they did not address the original hypothesis of this study. The close proximity of the hands to the torso interfered with any possible influence of body position. To assess this issue, participants would need to have their arms away from their body while lying down. As it would be uncomfortable for them to place their hands in front while in the supine position, participants might be placed on their side instead of on their back. In this position, the direction of gravity is still misaligned with the body and participants could comfortably cross their hands in front of them (with foam support). In this position, we could examine the true effect of body position without the interference of having the hands placed close to the body.

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4.7 References

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Chapter 5: Rubber hands do not cross the midline

5.1 Abstract

The rubber hand illusion (RHI) occurs when a person misattributes a fake hand as his or her own hand. Previously, the RHI has been examined with both the rubber hand and the participant's real hand uncrossed with regards to the participant's midline. The present study examined the strength of the illusion when the real hand, the fake hand or both hands are placed across the body midline. The illusion was induced by stroking the rubber hand and the real hand simultaneously. Asynchronous brushing served as a comparable condition since the RHI is not seen under these circumstances. Participants indicated where they felt their real hand was located by marking a sheet of paper under the table on which their unseen hand was placed. A significant RHI was observed with both the hands uncrossed. In contrast, no RHI was present when either hand was crossed over the midline. Additionally, a shift in hand judgment towards the midline was observed when participants crossed their real hand. A follow-up experiment indicated that this shift is influenced by vision in an extreme crossed-hand position. These results indicate the importance of the midline in understanding representations of the body.

5.2 Introduction

Successful interaction with the world around us requires knowledge of our hands' location in space. Both proprioception and visual feedback provide relevant information to acquire this knowledge. However, the integration of these different sensory signals is not always perfect, which can result in the mislocalization of our hands, such as that seen in the rubber hand illusion (RHI) (Botvinick & Cohen, 1998; for review see Makin, Holmes, & Ehrsson, 2008). The participant's hand is hidden from view and a fake (i.e. rubber) hand is placed in a visible location near the participant's real hand. Both the real and rubber hand are brushed synchronously with paintbrushes. When participants are asked to localize their real hand, their judgments tend to drift towards the location of the rubber hand. This effect is not seen when the real hand and rubber hand are brushed asynchronously. The difference in position judgment between these two conditions provides an estimate of the RHI. The RHI results from a conflict between the visual position where the touch is <u>seen</u> and the tactile position where the touch is <u>felt</u>. The present study examined the role of the body midline in enhancing or reducing the strength of the illusion.

The RHI provides evidence of malleability in the body schema. In this case, a fake rubber hand influences the perception of our real arm. The representation of our body is not fixed but flexible and capable of being modified. The RHI can offer important insight into other research areas involving body representation such as telerobotics, eating disorders, and complications that can arise of sudden loss of limbs. These wider implications involving the adaptability of the body schema present us with even greater reason to study the RHI.

Many factors affect the strength of the RHI. For example, providing an unusual pattern of touch during the synchronous brushing phase enhances the illusion (Armel & Ramachandran, 2003). A varied touch has a less likely chance to be occurring in two places at once compared to a patterned one. Further, having a more realistic hand can also enhance the illusion when compared to a hand that is larger or extends further than the participant's actual arm (Armel & Ramachandran, 2003). Similarly, having the rubber hand in an anatomically-accurate position produces a stronger illusion (Pavani, Spence, & Driver, 2000; Costanini & Haggard 2007). The realism of the rubber hand, as well as its position relative to the body, play a significant role in the RHI. In the current study, we considered the position of the real hand relative to the body midline, which we believe can affect the spatial accuracy of limb awareness.

A mislocalization of the hands can arise when the hands are placed across the midline. When participants perform tactile temporal order judgments (TOJs) in this crossed posture, performance is drastically impaired (Drew, 1896; Yamamoto & Kitazawa, 2001; Shore, Spry, & Spence, 2002; Roder, Rosler, & Spence, 2004; Sanabria, Soto-Faraco, & Spence, 2005; Shore, Gray, Spry, & Spence, 2005; Craig & Belser, 2006; Azañón & Soto-Faraco, 2007; Cadieux, Barnett-Cowan, & Shore, 2010;). When a crossed-hands posture is adopted, participants can become less aware of the position of their hands. While executing a typical crossed-hands tactile TOJ task, participants must localize their hands in space before judging which hand was stimulated first. This is similar to the requirements of the RHI experiment. In both instances, participants are required to make judgments based on the location of their hands. For this reason, we believe the RHI illusion will also be affected by a crossed-hands posture.

In the present study, we explored the effects a crossed-hands posture would have on the RHI. Lloyd (2007) considered the consequences of crossing the rubber hand over the participant's midline while exploring the effect of distance between the real hand and the fake hand. The illusion decreased as the distance between the two increased. In that study, the position of the real hand remained constant in the congruent hemisphere throughout the experiment; whereas, in the present study, the distance between the real hand and the rubber hand remained constant while the position relative to the midline was manipulated. Specifically, a 2x2 design was employed where the two factors were position of the real hand (ipsi- or contralateral) and position of the fake hand. It was hypothesized that the illusion would be increased when the participant's real hand was crossed over their midline since they would be less able to localize their real hand and therefore be more influenced by the visible rubber hand. That is, by degrading the proprioceptive cues, a greater reliance on vision should emerge. This would be reflected in a larger drift towards the rubber hand in the synchronous brushing condition when compared to the asynchronous. However, it was also possible that the illusion would be decreased due difficulty in localizing the rubber hand as well.

5.3 Experiment 1

5.3.1 Methods

Eighteen McMaster University undergraduate students, reporting normal or corrected-to-normal vision, took part in the experiment after giving written consent. Participants all appeared healthy and showed no signs of psychiatric disorders. Participants had an average age of 18.1 and four of the participants were male. All were right-handed save two left-handed females.

A wooden occluder box, open on two opposite sides, was constructed to shield the participant's hand from view while undergoing the illusion. Paper was mounted under the box so that participants could indicate hand location using markers of different colours. The rubber hand was constructed using a yellow rubber glove stuffed with cotton batting. Two identical 65mm paintbrushes were used to brush the participant's hand and the rubber hand (Figure 1).

Participants were instructed to align the center of their body with the position marked on the center of the occluder. They then placed their right arm with their palm facing upwards into the occluder and aligned their elbow with one of two positions marked on the occluder (middle of participant's body and 24cm to the right). Participants were draped with a cloth to prevent seeing the open end of the rubber hand and to give the visual perspective that it was their hand. The experimenter then moved the participant's hand to one of the four specified positions inside the box. These positions were 12 and 34 cm from the middle of the participant's body in both directions, labeled as A, B, C and D (A = 34 cm to the right; B = 12 cm to the right; C = 12 cm to the left; D = 34 cm to the left).

During control trials participants marked the location of their right hand by using their left hand to draw either an "x" or an "o" on the paper mounted underneath the occluder. No rubber hand was present during these trials. The participant's right hand was placed inside the occluder at one of the four possible positions. They indicated their hand position using a marker that was passed to them by the experimenter. All control trials were conducted with participants' eyes closed and no brushing occurred during these trials. During experimental trials, the rubber hand was placed on top of the occluder while the participant's real hand was placed inside the occluder. They could see the rubber hand but not their own hand. The experimenter then brushed the real hand and the rubber hand either synchronously or asynchronously with the paintbrush for thirty seconds. After brushing, participants used their left hand to respond on the paper mounted under the occluder. They were told to indicate where they felt the middle of their right palm. The participant's eyes were open while making the hand position judgments.

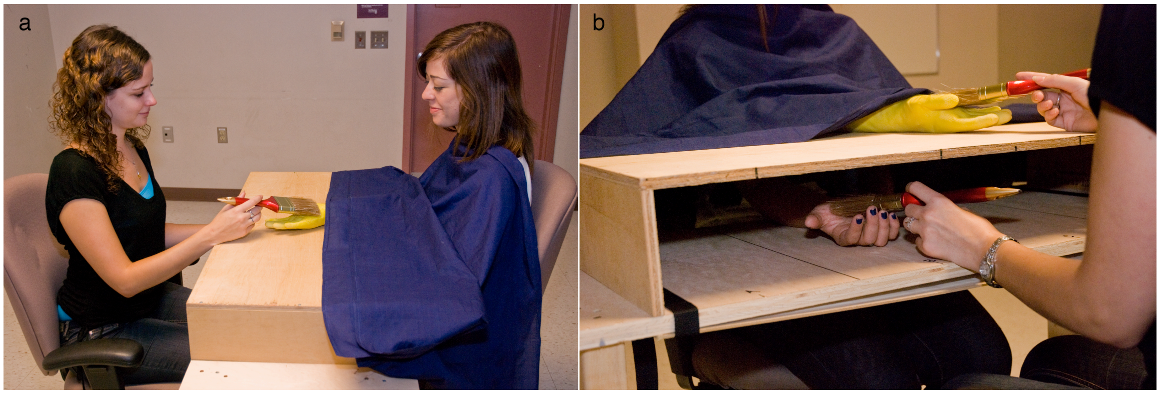

Figure 5.1 Particpant and experimenter sat across from each other. The participant's real right hand was place under the occluder and their left hand was used to make location judegements (a). During experimental trials, the experimenter brushed the participants hidden real hand and the seen rubber hand (b). During control trials, no rubber hand was present and participants were required to close their eyes.

Each participant underwent five control blocks and four experimental blocks. Control and experimental blocks alternated. Each block contained four trials. The experiment therefore consisted of a total of twenty control trials and sixteen experimental trials. The control block had one trial of each of the four possible hand positions (A, B, C, D). Each experimental block had one trial of each of the four hand positions: both hands uncrossed, hands crossed, rubber hand uncrossed with real hand crossed and rubber hand crossed with real hand uncrossed. Two of the experimental blocks were performed with synchronous brushing while the other two blocks were asynchronous. Block type and trial order were counter-balanced between participants.

Additional instructions given to participants were to relax their hand during brushing and to look at the rubber hand throughout the experiment. When participants were marking the position of their hand, they were instructed to look at the rubber hand and to respond quickly following their first instinct. They were also told to keep their hand still until after they marked the position of their hand.

The distance of each hand judgment from the center of the participant's body was measured. Hand judgments to the right of center were coded as positive and those to the left as negative (from the perspective of the participant). The participant's actual hand position was then subtracted from these measures to obtain a measure of how strongly each participant felt the illusion.

5.3.2 Results

A 2x2x2 Analysis of Variance (ANOVA) with the factors of brushing (synchronous/asynchronous), real hand position (uncrossed/crossed) and rubber hand position (uncrossed/crossed) was performed on the experimental data. The analysis revealed a main effect of the rubber hand position (F(1,17) = 24.73, p = 0.00) and an interaction between the real and rubber hand position (F(1,17) = 6.32, p = 0.02). Four planned t-tests comparing the synchronous to the asynchronous brushing on the 4 possible hand positions were performed to further evaluate the interaction (both hands uncrossed, both hands crossed, rubber hand uncrossed with real hand crossed and rubber hand crossed with real hand uncrossed). A significant difference was found when both the real hand and the rubber hand were uncrossed (t(17) = 2.22, p = 0.04), with synchronous condition having a greater drift towards the rubber hand (Figure 2). No other comparisons were significant indicating that the rubber hand illusion was not experienced in any of the other hand positions.[4]

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[4] A 2x2x2 Analysis of Variance (ANOVA) with the factors of brushing (synchronous/asynchronous), real hand position (uncrossed/crossed) and rubber hand position (uncrossed/crossed) as well as the 4 t-tests on the hand positions were performed separately on females (14 participants) and males (4 participants) to examine the possibility of sex differences that are sometimes found with crossed-hands tasks (Cadieux, Barnett-Cowan, & Shore, 2010). Female participants showed the same pattern of significant results across all tests. Males showed the same pattern in the ANOVA. To examine possible influences of left handed participants, an analysis was conduction on the 12 right-handed female participants. The same pattern of results was found in the ANOVA.

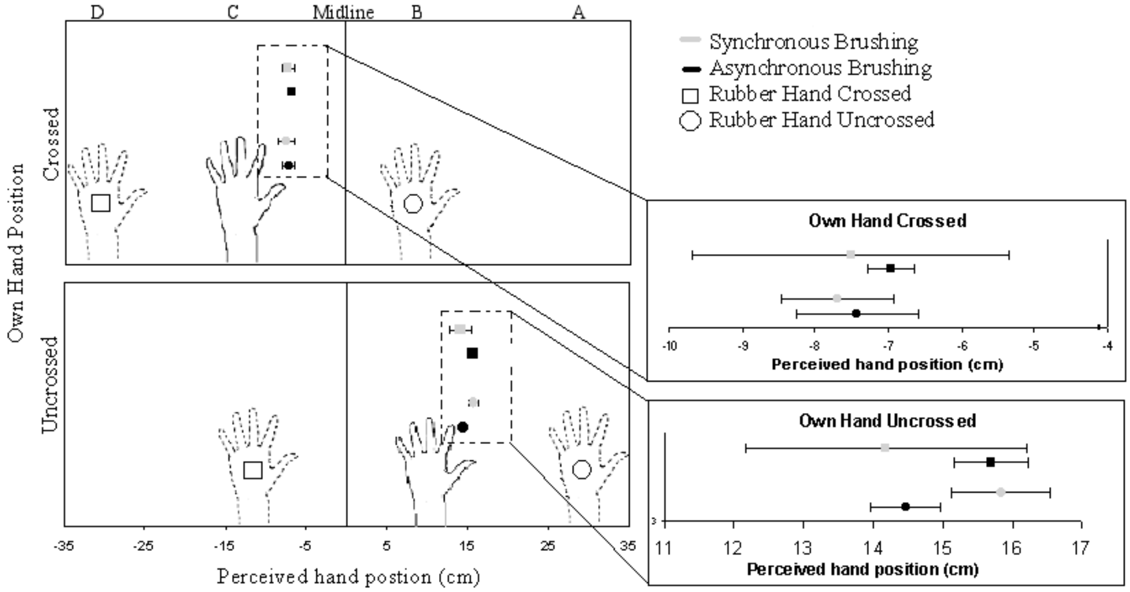

Figure 5.2 The average position of where participants judged their own hands to be in both crossed and uncrossed hand positions. The hand which is indicated with a solid outline denotes the participant's actual hand position while the dashed line indicates the position of the rubber hand. Hand positions are at -34cm, -12cm, +12cm and +34cm from the midline. Positive numbers indicate right of midline and negative numbers indicate left of midline. Error bars indicate ±1 standard error above and below the mean.

The control data were analyzed by taking of average for each of the 4 hand positions for each participant. These averages were then subtracted from the actual position of the hand. A one-way ANOVA indicated that participants were less accurate at locating their hand position when their hand was crossed as seen through the larger magnitude of error towards the midline (position C=4.6cm, position D=10.6cm) in hand judgments compared to when the hand was uncrossed (position A=1.2cm, position B=3.6cm; F=40.628; p=0.000) (Figure 2). There were also significant correlations between all the hand positions with the exception of between positions A and D (see Table 1). This demonstrates that individuals who tended to misjudge their hand position seem to make similar errors in all conditions (Figure 3). Additionally, when participants had their hands crossed, their judgments were often biased towards the midline.

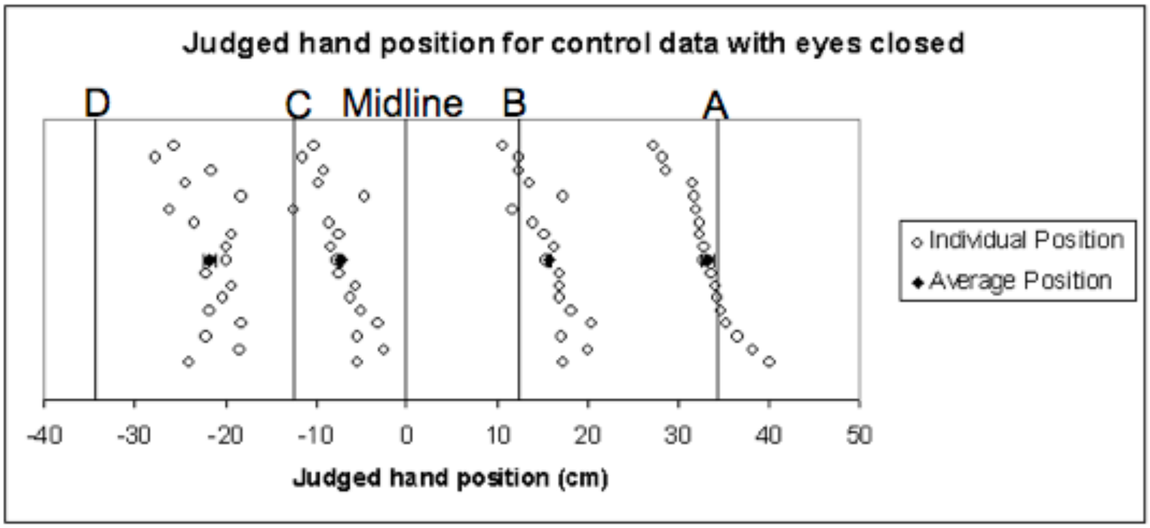

Figure 5.3 The average position each participant for the four control positions (-34cm, -12cm, +12cm and +34cm from the midline). Data are sorted by the position for each participant in position A. Position A, B, C, and D indicate the actual position of the participants hand.

Table 1. Correlations between hand position judgments for control trials at positions A, B, C and D.

	B	C	D
A	0.592*	0.626*	0.327
B		0.814*	0.584*
C			0.868*

* Significant at 0.05 level

5.3.4 Discussion

The rubber hand illusion was present only when both the participant's own hand and the rubber hand were uncrossed. This is a replication of the traditional rubber hand illusion. However, once either the participant's own hand or the rubber hand was crossed, the illusion was no longer present. When the participant's own hand was crossed, they biased their judgments towards the midline as can be seen in the control condition. We were unable to verify if this bias also exists in the experimental condition due the influences of the brushing and rubber hand. It is suspected that this bias occurred because participants were unable to locate their hand when it was crossed and they reverted towards the center of their body. Originally, it was predicted that participants would feel a stronger illusion when their hand was crossed compared to uncrossed; however, this was not the case, since participants felt no illusion when their hand was crossed. Furthermore, there was no RHI when the rubber hand was crossed and the real hand was uncrossed. Participants biasing responses towards the midline cannot explain these results, since control data for this hand position is relatively accurate. We believe that when the hands are on opposite sides of the midline the discrepancy between the two positions becomes too large to experience the illusion.

A bias towards the midline when the real hand is crossed was seen during the control trials. When the participant's own hand was crossed there was more variation in the hand judgments and participants biased their hand judgments towards the center. Additionally, there was individual variation between the participants. This variation was consistent with participants making similar errors in their hand judgments in all control positions as indicated by the correlation data.

Crossing the hands may disrupt multisensory integration when space is involved. This is consistent with the model presented by Makin, Holmes and Ehrsson (2008). They propose that the RHI is caused by the binding of visual information from the fake with the proprioceptive/touch information from the real hand. This information is best integrated when the fake hand is in anatomical alignment with the participant's shoulder position. In the current experiment, anatomical incorrectness cannot account for all the instances in which the RHI was not present. Specifically, when the fake and real hands are the positions closest the midline, the shoulder position was aligned with both positions. However, it is hypothesized that when a hand is crossed over the midline, the multisensory integration of information related to the hand is impaired (Shore, Spry, & Spence, 2002; Spence, Kingstone, Shore, & Gazzaniga, 2001). Specifically, Spence et al. (2001) showed a weaker congruency effect when hands are crossed, demonstrating a reduction in multisensory integration when the hand crossed the midline. This conforms to the predictions of the model in that accurate integration of multisensory information is what drives the RHI. When the real hand, the rubber hand or both are crossed, the visual information from the rubber hand cannot be integrated with the proprioceptive information provided by the real hand, thus resulting in a failure to produce the RHI.

5.4 Experiment 2

A second experiment, manipulating visual and tactile conditions, was conducted to expand upon the control data. Participants were required to locate their hand under different visual and tactile conditions. The participant's hand was either visible or occluded, and it was either brushed or not brushed. These four conditions allowed us to examine the individual effects of vision and touch on hand localization.

We also compared two different measures of hand position commonly used in rubber hand illusion experiments: Participants either directly pointed to their hand, as in the first experiment, or used a ruler to indicated the position of their hand. The main difference between the two measures is the active versus passive task requirements. Both procedures have been used to measure the RHI yet they have not been, to the best of our knowledge, directly compared.

5.4.1 Methods

Ten McMaster University students, reporting normal or corrected-to-normal vision, took part in the experiment after given written consent. Participants had an average age of 19.9 years and six of the participants were male. All participants were right-handed save one left-handed female.

The experimental setup was identical to the first experiment except a ruler was mounted to the top of the occluder box. It was located on the side furthest from the participant. The same four hand positions were used in both the pointing and ruler trials. As in the first experiment, only the participant's right hand was used and they were instructed to indicate the location of the middle of their palm.

Each participant underwent four blocks with the pointing task and four blocks with the ruler task. Each condition had a single block of the four different visual/tactile conditions: visual brushed hand, visual unbrushed hand, occluded brushed hand, and occluded unbrushed hand. For the visual conditions participants were instructed to place their hand on top of the occluder box. An adjustable chair was provided so that the body position was not awkward or different then in the occluded trials. Each block contained three trials at each of the four possible hand locations. The experiment therefore consisted of ninety-six trials. Condition, block type, and trial order were counter-balanced between participants.

The procedure for the pointing blocks was similar to that of the control blocks in the first experiment. Participants indicated their hand position on paper mounted under the occluder box using coloured markers. In the ruler condition, participants indicated their hand position verbally, in centimeters, using the mounted ruler. Before each block, the ruler was moved a random number of centimeters (1-12 cm) to insure participants could not repeat the same measurement on each trial of the same hand position.

5.3.2 Results

Average hand positions were calculated for each of the eight conditions. A 2x2x2x4 ANOVA with the factors of measurement type (pointing/ruler), visual condition (visual/occluded), tactile condition (brushing/no brushing), and hand position (A, B, C, D) was performed on the data. The analysis revealed a main effect of hand position (F(3,27) = 1419.22, p = 0.00) driven by the large differences in the four hand positions as well as a three-way interaction between measurement type, visual condition, and hand position (F(3,27) = 63.65, p = 0.03). A possible trend was also revealed in a marginally significant interaction between visual condition and hand position (F(3,27) = 57.42, p = 0.06). To further investigate these interactions, separate ANOVAs were run on each of the four hand positions. In position D, a main effect of visual condition was revealed (F(1,9) = 41.64, p = 0.00). In the occluded condition (mean = -22.8 cm), participants drifted towards the midline when compared to the visual condition (mean = -30.5 cm, Figure 4). No other comparisons were significant.

5.3.3 Discussion

No difference in hand localization was found between the brushing and no brushing conditions. Participants' ability to locate their hand was not influence by the tactile stimulation. Vision of the hand does play a role in hand localization, but only in the most extreme crossed posture. When the hand was unseen, there was a drift towards the midline of almost 8 cm. This difference was not seen in the most extreme uncrossed posture. It appears that vision of the hand is only necessary to properly locate the hand in the crossed posture.

We found no difference between the two measures of hand position. Actively pointing to the hand did not differ from making a passive judgment about its location. However, we cannot be sure these findings would transfer to a RHI experiment. The influence of the rubber hand and the synchronous brushing may contribute in ways not taken into account during this experiment. Nevertheless, these findings imply that experiments using a pointing method can be directly compared to those using a ruler method.

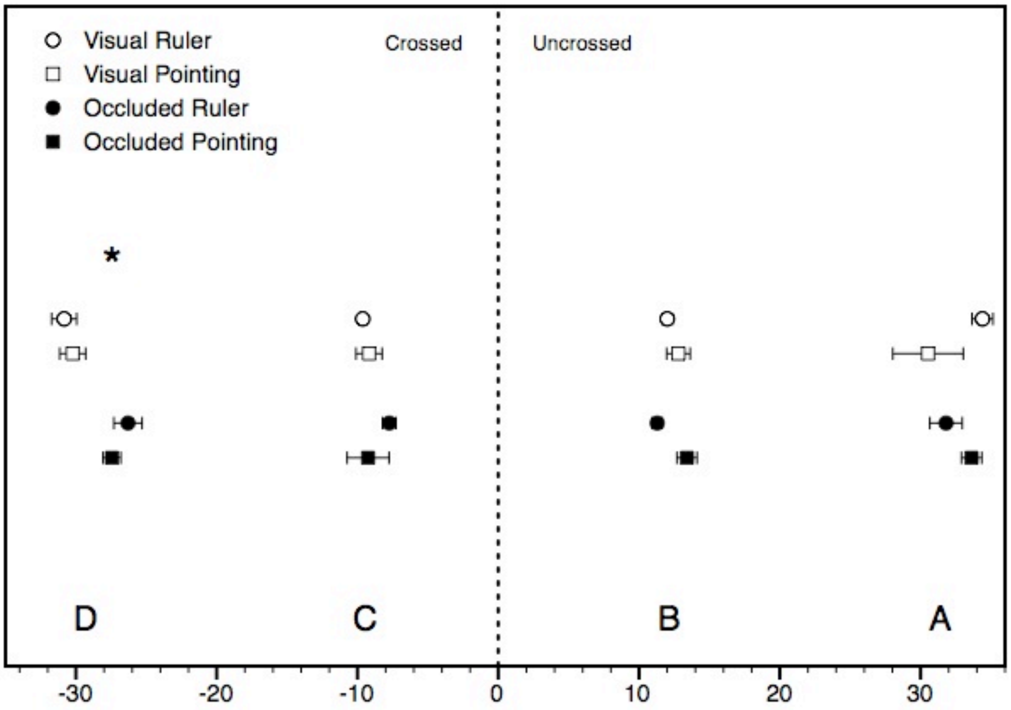

Figure 5.4 The average position each participant for the four hand positions. In position D, particpants drifted towards the midline in the occluded condition when compared to the visual condition

5.4 General Discussion

Our primary goal was to examine the effects of the midline on the rubber hand illusion. Secondary goals included exploring hand localization in general and possible differences between passive and active measures of localization. The RHI was present only when both the participant's own hand and the rubber hand were uncrossed. However, if the participant's hand or the rubber hand was crossed, the illusion was did not occur. Hand localization in general was not influenced by tactile stimulation. There was no difference in localization between the brushing and no brushing conditions. Vision of the hand improved localization only in the extreme crossed posture, where blindfolding caused a significant drift towards the midline of the body. No difference was found between the active and passive measures, providing evidence that they are comparable measure for assessing the RHI.

There are several limitations to the current study. Due to the length of time required for a single trial, we were restricted to a small number of trials per participant. In the first experiment, we also used an unrealistic looking rubber hand and limited our brushing to 30 seconds per trial. However, the rubber hand illusion has been shown to take only 11 seconds to occur (Ehrsson, Spence, & Passingham, 2004), therefore, our brushing should be adequate. We also did not ask participants to complete a subjective questionnaire, again due to time constraints. Nevertheless, we feel we provided a satisfactory environment to reliably produce the RHI. Also, the generality of our conclusions are moderated on the fact that there are sizeable individual differences in crossed-hands tasks, shown by the large variance in the crossed synchronous brushing condition (Cadieux, Barnett-Cowan, & Shore, 2010). This variance could be caused by differences in participants' abilities to integrate multisensory information across the midline. Further research should be done to examine these effects in depth with regard to the RHI.

Crossing both the participant's hand, the rubber hand or both can influence the RHI. Only when the real hand and the rubber hand are uncrossed is the illusion experienced. Additionally, vision is crucial for accurate localization of the hand in an extreme crossed posture. These results provide further evidence that adopting a crossed-hands posture decreases your ability to accurately locate your hands in space. In the case of the RHI, it would appear that participants must first know the location of their real hand before they can mislocalize it to the position of the rubber hand.

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6.0 General Discussion

6.1 Thesis summary

In Chapter 2 the relation between the crossed-hands deficit and the rod and frame test (RFT) was examine. I also took a closer look at the crossed-hands deficit in general, exploring both individual differences and the possibility of sex effects. The crossed-hands deficit was correlated with the RFT, however, only for male participants. Men also had a lower crossed-hands deficit and showed a smaller performance range compared to women. This chapter provides significant insight into how men and women differ in their manipulation of reference frames. Specifically, a difference in the process that transfers information between the internal and external reference frame was postulated. Men appear to have a single method to translate information (reflected in this chapter by the correlation between the two tasks), whereas women use different methods across tasks to achieve the same goals, albeit with lesser success.

Chapter 3 expanded on the crossed-hands deficit, exploring the underlying cause of the effect. In particular, two theories of the deficit were compared. The first stipulates that the deficit is caused by a time delay in transferring information from the internal to external reference frames when the hands are crossed (Yamamoto & Kitazawa, 2001). The deficit occurs when the second stimulus of the TOJ is presented before the first has been mapped into external space. In contrast, the second theory proposes that the stimuli are quickly transferred to the external reference frame but that both frames remain active at the moment of response selection (Shore et al., 2002). It is the conflicting information from these two reference frames that cause the deficit. The external reference frame was degraded by restricting visual information through blindfolding. The time delay theory predicted an increase in the size of the deficit whereas the conflict theory predicted a reduced deficit. Across several experiments—differing primarily in the required response demands—it was found that when under internal response requirements, the deficit was reduced when blindfolded. When forced to use external response coordinates the deficit was not reduced. In other words, when participants were biased towards the internal reference frame through blindfolding and this reference frame matched the response demands, the deficit was reduced. This result provides support for a conflict model of crossed-hands effects.

Chapter 4 built on the findings from Chapter 3. I again attempted to degrade the external reference frame – this time manipulating body posture. In the supine position, reference frames for the direction of 'up' are misaligned: our body (head) is pointing in one direction whereas gravity is pointing in another, providing us with conflicting information about the external world. In the first experiment, participants had a reduced deficit in the supine compared to upright position. However, the hands were placed closer to the body in the supine position than in the upright. In the second experiment we controlled for this difference by placing the hands close to the body in both positions. There was no difference between the two body positions in Experiment 2. The deficit in both body positions in this second experiment was comparable to the supine position of Experiment 1. In other words, it was the proximity of the hands to the body and not the body position itself that reduced the deficit in Experiment 1. The original intention of the chapter was to examine the influence of degrading the external reference frame to provide further evidence for a conflict model of crossed-hands effects. While we did not accomplish this objective here, the difference between hands near and far from the body still provide some insight into the crossed-hands deficit. In this chapter, it was proposed that placing the hands close to the body strengthened the internal reference frame. Participants were provided with two internal cues for the position of their hands: the vibrations on the hands themselves and the touch of the hands to the chest. Strengthening the internal reference frame had a similar effect to degrading the external reference frame. In both cases, the internal reference frame appeared to become the more reliable of the two. This interpretation could explain why the deficit was reduced. Although the issues raised in this chapter require further study to confirm the claims, the present results do provide some evidence for the conflict model.

In the final data chapter, the task was switched completely. The rubber hand illusion (RHI) was used to examine the importance of the body's midline in multisensory integration. The RHI did not cross the midline. When the real hand, rubber hand, or both were crossed, the illusion did not occur. This was attributed to a failure in multisensory integration. For the illusion to occur, tactile information from the real hand must be integrated with the visual information from the rubber hand. It was proposed that when the hands are crossed, this integration was impaired, which results in a failure to produce the illusion. Although this chapter does not address the crossed-hands deficit directly, it does provide evidence for reduced integration when the hands are crossed over the midline.

6.2 Implications and Significance

The primary goal of this thesis was to address the underlying cause of the crossed-hands deficit. Although much research has examined this crossed-hands effect, its root cause has not been addressed directly. Secondary goals included comparing the crossed-hands deficit to the putatively related RFT, examining both individual and sex differences within the task, analyzing the effects of vision and body position on the deficit, and finally considering how multisensory integration is affected across the midline.

The main goal was addressed predominantly in Chapters 3 and 4. Both chapters provide evidence for a conflict model of crossed-hands effects over a time-delay model. Chapter 3 compared the viability of two models by degrading the external reference frame, whereas Chapter 4 did so by strengthening the internal reference frame. The results from both chapters favoured the conflict model, and fill a significant hole in the crossed-hands literature. To the best of my knowledge, these are the first studies to directly address the core cause of the crossed-hands deficit.

In light of these findings, several crossed-hands effects can be further clarified, such as the development of the deficit in childhood (Pagel et al., 2009). Young children show a large bias towards a tactile reference frame (internal), which shifts to a more visual reference frame (external) in later childhood (Gori et al., 2008). The development of this external reference fame and the crossed-hands deficit co-occur. The deficit is not present when the bias is towards the internal reference frame but develops with the growth of the external frame. When the visual reference frame is prevented from development at all – as is the case with the congenitally blind – the deficit also fails to develop (Roder et al., 2004). Only late-blind individuals show a deficit. It is the development of a second conflicting frame that causes the impairment. When this reference frame is under-developed or prevented from development entirely, the conflict does not occur and the deficit is reduced. When the level of conflict is decreased the deficit is also reduced. An intermediate deficit is produced when the hands but not fingers, or the fingers but not hands, are crossed (Heed et al., 2012). In both cases, there is less conflict by not crossing the whole hand over the midline.

The secondary goals have been addressed in the chapter summaries at the beginning of this discussion. Taken together, they help to provide a better picture of visual-tactile integration. The wide range of individual differences indicates a spectrum in our ability to integrate and interpret visuotactile information. This range also varies across men and women and may indicate a general reference frame bias specific to each sex. The integration of information from different sources can be manipulated, biasing observers to adopt an internal or external reference frame. This in turn changes how we perceive stimuli in space. The midline of our body appears to play a key role in this process. Integration is impaired when we attempt to combine information across the midline.

The representation of our body and external space is malleable. The position of our hands drastically influences how we perceive stimuli presented to our fingers. When our hands are crossed we receive different information from internal and external reference frames and the integration of these two sources of information is also impaired. The exploration of the crossed-hands deficit and the rubber hand illusion presented in this thesis has contributed to our understanding of how multisensory information is processed and integrated into a single perception of our hands.

6.3 Limitations and Future directions

In empirical work presented in Chapter 3, there was an uneven sex ratio in the first three experiments. Given the sex differences found in Chapter 2, this factor may confound some of the conclusions from those experiments. Although Chapter 3 was presented here as the second data chapter, much of the data were collected prior to the first data chapter. Once the sex effect was discovered, it was ensured that all subsequent experiments involving the crossed-hand vibrotactile TOJ task contained even numbers of males and females. This matching of the number of male and female participants can be seen in the final experiment of Chapter 3 and all of Chapter 4. We also ensured to look for potential sex differences, which is reflected in statistical foot notes in most chapters.

Chapter 4 requires two follow up experiments to clarify the current findings, as well as to address the original hypothesis of the study. The first experiment would need to directly address the difference between placing the hands near and far from the body in the crossed position using a within-subjects design. While some cross-experiment analysis was completed in this chapter, the large amount of individual differences (as reflected in the findings of Chapter 2) would make a direct comparison more valid. The second experiment would require participants to cross their hands away from their body while lying down. The best position for this would be on their side as opposed to on their back. In a side lying position, foam supports could be more easily be used to ensure a comfortable position . Additionally, in the side position, the misalignment of the SVV and the PU is increased (Dyde, Jenkin, and Harris, 2006). This should in turn further decrease the reliability of the external reference frame. In hindsight, this is the best position to examine our hypothesis. The increase degradation of the external reference frame and the consistent distance of the hands in both the upright and lying down position, make this the idea position.

In both Chapters 3 and 4, participants were pushed to adopt a more internal reference. The next step would be to bias participants towards the external reference frame. If the crossed-hands deficit is caused by a conflict between reference frames—as was proposed here—a shift towards the external reference frame should still result in a reduced deficit; it should not matter which reference frame is being prioritized. When one reference frame is made more reliable than the other, it should reduce the level of conflict. However, it is much easier to degrade the external reference frame than the internal. One possible solution is to push the participant to adopt the external reference frame by having it provide more information. In other words, don't degrade but enhance. This would likely work best under the context of the experiments presented in Chapter 3. In this chapter a wide range of response demands were used. A reduced deficit was seen when both the response demands (internal) matched with the reference frame bias (internal). If participants were pushed to adopt a more external reference frame we would expect to see a reduction in the deficit when matching external response demands were used. One way to accomplish this objective might be to provide an external congruent light stimulus that matches with the side of space being stimulated. If blindfolding improved performance with internal response demands, increasing visual information with external response demands should have a similar effect.

Following up on Chapter 2, the vibrotactile TOJ task should be compared to other reference frame tasks. As mentioned in the Introduction, both navigation and mental rotation show a dependence on reference frame manipulation. Given that the frame effect (RFT) and the PCD score (crossed-hands deficit) may share a common underlying mechanism, expansion on this idea is crucial for the greater understanding of reference frame interaction. Mental rotation (Shepard and Metzler, 1971) in particular provides an interesting framework on which to base an experiment. The two types of mental rotation—block (external) and body (internal)—would allow for the comparison of the different response demands presented in Chapter 3.

6.4 Conclusions

Temporal order judgments are severely impaired when the hands are crossed over the midline (Azañón & Soto-Faraco 2007; Cadieux et al 2010; Craig & Belser 2006; Drew 1896; Heed et al., 2012; Holmes et al 2006; Kobor et al 2006; Roberts & Humphreys 2008; Roder et al 2004; Shore et al. 2002; Wada et al 2004; Wada et al., 2012; Yamamoto & Kitazawa 2001). This crossed-hands deficit appears to be driven by a conflict of information from the internal and external reference frames. This conflict is reflected in poorer multisensory integration when the midline of the body is crossed. Surprisingly, the level of impairment seen in these studies does not result in large difficulties in our daily lives. We adapt by not placing items across the midline, such as the wine glass at the dinner table or the buttons on a pilot's console. We generally avoid crossing our arms. Taken together, the data presented in this thesis provide us with a greater understanding of how we process and integrate conflicting multisensory information, particularly when the midline of the body is crossed.

6.5 References

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