REFERENCE FRAME INTEGRATION AND THE CROSSED-HANDS DEFICIT

EXPLORING REFERENCE FRAME INTEGRATION USING THE CROSSED-HANDS DEFICIT

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LAY ABSTRACT

Determining the boundary of our body requires we localize the touches to our body. When the body moves and interacts with the world this determination becomes more difficult. Integrating information from other senses can support the localization of touch, and thus knowledge of our body. For example, to locate a touch to your right hand, you must feel the touch on your right hand, but also determine where your right hand is located in space. This thesis shows that the contributions of each sense to locate a touch is consistent within an individual and remains consistent over time. Interestingly, based on the availability of each sense, we flexibly adapt their contributions to ensure that our ability to locate the touch remains unchanged. What we define as our body is constructed based on the information available in the present moment.

ABSTRACT

You can only perceive the location of a touch when you know where your hands are in space. Locating a touch to the body requires the integration of internal (somatotopic) and external (spatial) reference frames. In order to explore the relative contribution of internal versus external information, this thesis employed a crossed-hands tactile temporal order judgment (TOJ) task. This task requires participants to indicate which of two vibrations, one to each hand, occurred first. The magnitude of the deficit observed when the hands are crossed over the midline provides an index into how internal and external reference frames are integrated. This thesis first showed that the crossed-hands tactile TOJ task is a reliable measure, supporting its use as a measure of reference frame integration. Next, this thesis applied a probabilistic model to theoretically estimate the weights placed on the internal and external reference frames. We showed that a bias towards external information results in a larger external weight and vice versa for internal information. Finally, using the model we showed that the crossed-hands deficit is reduced while lying down, supporting an influence of vestibular information on the external reference frame. Taken together, this thesis highlights that we are able to flexibly adapt the weighting of different spatial representations of touch.

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TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

LIST OF TABLES

CHAPTER 2

CHAPTER 3

DECLARATION OF ACADEMIC ACHIEVEMENT

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It should be noted that because each of the empirical chapters are meant to be stand alone publications, there will be redundancy between each chapter's introduction and methodology.

CHAPTER 1: GENERAL INTRODUCTION

Accurate localization of an object often uses information from across our different sensory systems. For example, to find your dog you could *look* and see where he is located, you might *listen* for his bark, or wait to *feel* his wet nose touch your hand. Considering the sense of touch specifically, when you feel your dog's nose touch your left hand, how do you know where to move your right hand in order to pet him? The orientation of your gaze and where you guide your movements will be determined by whether the touched hand is on the left or right side of your body. In the case of both left and right sides of the body, the touch is the same, however the external location of the hands differs. This external location can only be determined when information from other senses are taken into account. Specifically, the locally-applied, skin-based, tactile information needs to be combined with the current body posture, inferred using vision and proprioception (Badde & Heed, 2016). Visual information, initially coded based on its location on the retinas, can also be coded with reference to a body part (Heed et al., 2015). Once the initial sensory information has been integrated with information about the current body posture, an object's location relative to the body can be determined. Tactile localization has an added layer of complexity because our bodies move and interact with the environment: the initial sensory location of the touch (e.g., right hand) can sometimes conflict with the body posture (e.g., right hand on left side of the body). This thesis aims to explore the multisensory contributions involved in locating a touch in space. To do so, I employed different manipulations to a crossed-hands tactile temporal order judgment (TOJ) task. This task investigated how tactile localization changes when information from vision, touch, and proprioception were placed in conflict, by crossing the hands over the body midline compared to conditions where no conflict was present (i.e., uncrossed hands).

What is a Reference Frame in the Context of Tactile Localization

Consider a situation when your dog touches your right hand when your arms are crossed, thereby positioning your right hand on the left side of your body. When indicating the location of your dog, you can describe his location using different coordinate systems—or reference frames; an internal and an external reference frame. The internal reference frame uses information obtained through skin-based, tactile receptors. Using the internal reference frame provides an accurate location of the touch to a place on the body but does not provide information about the location of that touch relative to objects external to the body. Internal coordinates would lead you to say your dog is touching your right hand. In contrast, based on external coordinates you would say that your dog is on the left side of your body (recall your hands are crossed). The external reference frame defines an object's location relative to the external world (Badde & Heed, 2016). The external reference frame integrates information available through vision and proprioception to infer the body's current posture. The external reference frame will consider an object held in the left hand as being located on either the left or right side of the body, depending on the current body posture. For example, when your arms are crossed, your left hand will be on the right side of your body. This process of translating information from an internal, skin-based, reference frame, to an external reference frame is referred to as tactile remapping (Driver & Spence, 1998).

Evidence of tactile remapping to an external reference frame was first reported in patients with hemispatial neglect (lack of awareness of objects positioned on one side of space; Aglioti et al., 1999). Typically, these individuals are able to detect a tactile stimulus applied to the ipsilesional side of their body (i.e., the same side of the body as the brain lesion), but not the contralesional side of the body (i.e., the side of the body opposite the brain lesion). Interestingly, when their hands are crossed over their body midline, a tactile stimulus presented on the ipsilesional hand, in the contralesional space, is not detected. Detection of the tactile stimulus is therefore determined by the remapped, external coordinates, of the touch. Further evidence of tactile remapping in healthy participants was obtained by having participants determine whether a touch to the unseen forearm (positioned vertically beside the face) was presented above or below a touch on the face (Azañón et al., 2010). The touches occurred at different locations/elevations on the forearm and face and the position of the forearm was moved up or down relative to the face. Accurate task performance, therefore, required integrating the location of the touch on the forearm with the current arm position, ensuring the use of the external reference frame. Participants were able to accurately judge the relative elevation of the two touches (face and arm), highlighting the ability to remap the touch to external space.

In comparison to other modalities, localizing a touch is unique because the internal and external reference frames can provide incongruent information. For this reason, the internal reference frame always remains relevant for tactile perception. Both internal and external coordinates are required for locating, interpreting, and reacting to the touch. When the information is consistent between both reference frames, it is unknown how much each is used to create the final percept. Quantifying the extent to which each reference frame contributes to tactile localization requires using situations where the information from the internal and external reference frames diverge. Take for example, a situation where someone has crossed their hands. A touch on the right hand would be interpreted by the internal reference frame as ‘right’, but when remapped to the external reference frame would be considered on the ‘left’ side of the body. Comparing performance in situations with a conflict between internal and external reference frames to situations where there is no conflict allows for an indirect measure of the weighted integration of the reference frames. If performance is worse when conflicting information is present between the reference frames, this can indicate the relative use and magnitude of the external reference frame.

One such experimental paradigm that uses a crossed-hands manipulation to better understand reference frame integration is the cross-modal cueing task. A tactile stimulus was presented to the left or right hand, at either an upper or lower location relative to gravity (Spence and Driver, 1998; Kennett et al., 2001). The goal of the task was to indicate whether the tactile stimulus was presented to the upper or lower location, irrespective of which hand was stimulated. Before the tactile stimulus, a spatially non-predictive and task-irrelevant visual cue was presented in one hemispace. When the hands were uncrossed, the visual cue facilitated elevation judgements occurring on the same side as the cue. However, in an uncrossed posture, it was not possible to determine whether the cue facilitated judgments to the same hand, or to the same hemispace (i.e., the hand occupying the same external space as the cue). Crossing the hands differentiates these two options and revealed that the cue aided judgments presented in the same hemispace as the cue; for instance, a cue on the right side of space facilitated judgements for the left hand when in a crossed posture (occupying the right side of space), showing that touch is remapped to the external reference frame.

Tactile Temporal Order Judgments

One of the most widely used experimental procedures to study reference frame integration during tactile localization is combining a tactile temporal order judgement (TOJ) task with a crossed-hands manipulation (Shore et al., 2002; Yamamoto & Kitazawa, 2001a; for a review see Badde & Heed, 2016). In this task participants are presented with two vibrations, one to each hand, and they are asked to indicate, in an unspeeded fashion, which hand received the first vibration (Figure 1). Typically, participants perform this task with their eyes open and responses are provided using buttons placed underneath the stimulated fingers. The task is performed with the two vibrations separated by a variable amount of time, or Stimulus Onset Asynchrony (SOA). Performance is worse when the two vibrations are presented in close succession, than when there is a longer time difference between the vibrations. Critically, a crossed-hands deficit occurs, whereby worse performance is observed when the task is completed with the hands crossed over the body midline compared to when the hands are uncrossed (Azañón & Soto-Faraco, 2007; Azañón et al., 2015; Azañón et al., 2016; Badde et al., 2015a; 2015b; Cadieux et al., 2010; Cadieux & Shore, 2013; Craig & Belser, 2006; Crollen et al., 2019; Kóbor et al., 2006; Pagel et al., 2009; Roberts & Humphreys, 2008; Röder et al., 2004; Schicke & Röder, 2006; Shore et al., 2002; Unwalla et al., 2020; Wada et al., 2014; Yamamoto & Kitazawa, 2001a; 2001b). When the hands are uncrossed, the internal and external reference frames provide congruent information (e.g., right hand, right hemispace). When the hands are crossed over the midline, the two reference frames conflict (e.g., right hand, left hemispace). This crossed-hands deficit is thought to be caused by a conflict in the left–right coding between the internal and external reference frames. It should be noted that such a task can easily be accomplished using only the internal, skin-based, reference frame as hand posture is not required to make temporal order judgments. However, if participants were actually implementing this strategy of just using the internal, skin-based reference frame, then crossing the hands should not influence task performance. The fact that a crossed posture significantly impairs performance on temporal order judgements of locally applied tactile stimulation, has been taken as evidence that tactile remapping is an automatic process (Azañón & Soto-Faraco, 2008; Badde et al., 2015a).

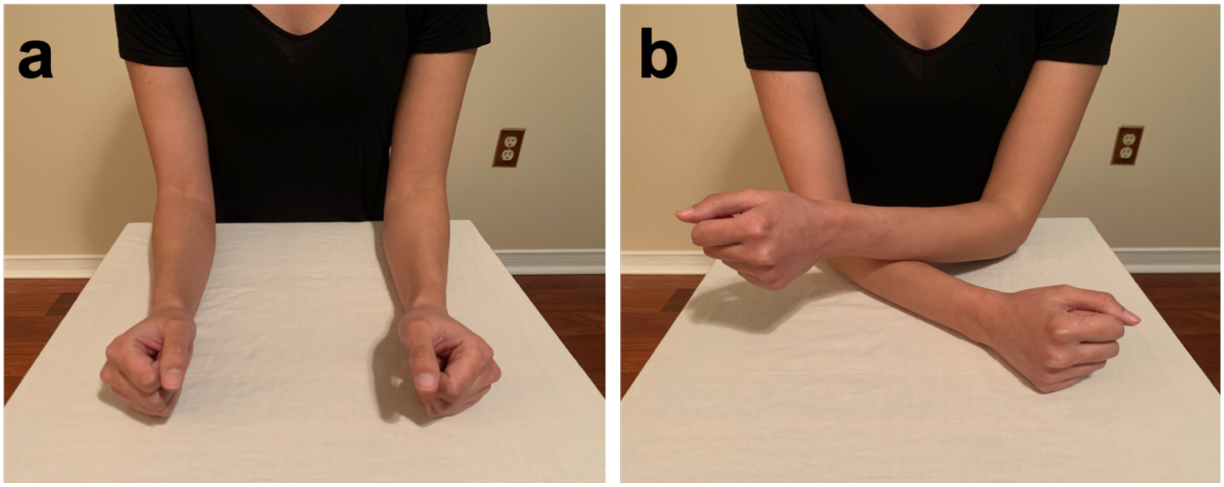

Figure 1: (a) Typical uncrossed hand postures used in the crossed-hands tactile TOJ task, and (b) typical crossed posture. Note, there will be subtle differences in the posture across studies, including the finger that receives the stimulus and provides the response.

Even after the tactile stimulus has been remapped to an external reference frame, the internal coordinates for the touch are still available. Many theories have been put forward to explain how these reference frames interact to determine the stimulus location. There are three main theories explaining the deficit: the non-integration model, the conflict model, and the integration model. All theories agree that the touch must be transformed from internal coordinates to external ones. The theories differ based on how information from each reference frame is subsequently used. Non-integration models posit that localizing a touch only uses information from the external reference frame (Yamamoto & Kitazawa, 2001a). Judgements about the relative temporal order of the two stimuli cannot occur until each touch has been remapped into external coordinates. The deficit then arises because crossing the hands impedes the ability to remap the tactile stimulus from the internal to the external reference frame.

In contrast, the conflict model and the integration models suggest that the touch is automatically remapped from the internal to the external reference frame. The conflict model posits that the opposing locations provided by each reference frame causes a conflict, which must be resolved before the touch can be located (Shore et al., 2002). The integration model builds upon the conflict model by suggesting the conflict is not of a fixed magnitude, but instead changed based on the differential weights applied to two reference frames (Badde et al., 2015a). The integration model uses the principles of optimal integration to explain how the internal and external reference frames are combined to locate a touch. Information from each sensory modality is integrated together in a statistically optimal manner with a greater weight placed on sensory information, or in this case the reference frame, that is considered more reliable when creating the final percept. Both reference frames are combined using a weighted average, where the weight placed on each reference frame is determined by the reliability of each estimate (Ernst & Bülthoff, 2004). As one reference frame is made less reliable, for example, through the introduction of noise (i.e., degrading visual inputs by blindfolding), that reference frame will be given less weight in the combined average. Given that both internal and external information are available at the time of response, this weighted average can sometimes lead to erroneous localization in the crossed-hands posture.

Measuring the Crossed-Hands Deficit

All previous experiments that have used temporal order judgments in the crossed-hand deficit paradigm have required participants to identify the hand that received the first vibration. Responses are typically summarized based on the proportion of ‘right-first’ responses as a function of stimulus onset asynchrony (SOA; the time difference between the two vibrations).

Several different SOAs are tested during an experiment, typically ranging from 15–200 ms (e.g., Shore et al., 2002), but can sometimes be up to 3000 ms (e.g., Yamamoto and Kitazawa, 2001a; Heed et al., 2012).

Many different measures have been used to quantify the size of the crossed-hands deficit. One method compares the slope of the crossed and uncrossed psychometric functions (Shore et al., 2002). The slope indicates how precise the participant was at differentiating the temporal order of the two vibrations. In order to fit a straight line to the psychometric curve, the proportion of right-first responses are converted into a z-score, and the slope is computed from this straight line. The crossed-hands deficit is reflected in a shallower slope in the crossed compared to uncrossed posture, indicating generally lower precision at differentiating the temporal order. Similar methods can also be used to calculate the just noticeable difference (JND), which indicates the time difference needed between the two vibrations to accurately determine their temporal order. A larger JND is typically observed in the crossed compared to uncrossed posture, indicating less precision in identifying the relative temporal order of the tactile stimuli. These analysis techniques are only valid for short SOAs because the psychometric function in the uncrossed posture asymptotes at longer SOAs. The inclusion of long SOAs would result in insensitive slope and JND measurements (Heed and Azañón, 2014). There is some debate regarding what is considered a long SOA, with some experiments defining long SOAs as greater than 100 ms (Badde et al., 2014; Badde et al., 2015a; 2015b; Crollen et al., 2019; Roder et al., 2004), while others suggest SOAs greater than 200 ms (Shore et al., 2002); all seem to agree that SOAs longer than 200 ms should be excluded.

Another analysis technique for the tactile TOJ task is to calculate the proportion correct difference (PCD) score (Cadieux et al., 2010). The proportion of right-first responses is first converted into the proportion of correct responses at each SOA. This accuracy score is then summed across all SOAs, and the difference between crossed and uncrossed accuracy is calculated. A larger PCD score signifies a larger crossed-hands deficit. The PCD score provides one number that summarizes crossed and uncrossed performance, making it easy to compare the size of the deficit across different manipulations. An advantage of this measure is that it assumes no underlying distribution to the data, and is therefore useful when few SOAs are tested, as curves cannot be estimated (Heed & Azañón, 2014). There are, however, also disadvantages with the PCD. For instance, while most manipulations influence performance in the crossed condition, there are some manipulations (e.g., Badde et al., 2014) that influence uncrossed performance as well. Because the PCD measure collapses across both crossed and uncrossed responses it cannot be used to differentiate whether a change in performance is due to modulations in the crossed or uncrossed performance.

Another analysis technique that is sometimes used is the “flip” model. This model was created by Yamamoto and Kitazawa (2001a) when they discovered that some of their participants showed lower than chance performance at the short SOAs. This results in an N-shaped, rather than S-shaped, response curve. The implementation of this model requires fitting multiple parameters, which necessitates that a large number of SOAs be tested (Heed & Azañón, 2014). Furthermore, the “flip” is typically observed at shorter SOAs, requiring multiple short SOAs be tested. The studies included in this thesis used only a few SOAs, and even fewer short SOAs. As such, this analysis technique was not employed in this thesis.

More recently, a probabilistic model has been put forward to directly measure the weight placed on the internal and external reference frames (Badde et al., 2015a). The aim of the model is to select an internal and external weight pair that best captures the participants’ crossed and uncrossed performance using Bayesian maximum likelihoods. Based off the integration model for the deficit, the model presumes that the crossed-hands deficit arises from a conflict in integrating internal and external reference frames. As such, the model estimates performance differences between crossed and uncrossed postures as a weighted average of the two reference frames. Therefore, the model determines an internal and external weight pair that best estimates the slope of the crossed and uncrossed psychometric curves. The sum of the internal and external weight determines the slope of the uncrossed curve, as the reference frames provide congruent information. In the crossed posture, the slope is calculated as the difference between the weights, as the reference frames are in conflict; the more weight an individual places on the external reference frame, the shallower the slope.

Individual Differences in Reference Frame Integration

There is large inter-individual variability observed in crossed-hands tactile TOJ performance (Cadieux et al., 2010). Some participants show near perfect TOJ performance when their hands are crossed, others perform close to chance, and some have worse than chance performance in the crossed posture. Some variability is also observed in uncrossed performance, but not to the same degree as in crossed performance. To date, few sources of these individual differences in tactile TOJ performance have been identified. Sex at birth is one factor that has been associated with tactile TOJ performance in some studies (Cadieux et al., 2010), with males generally presenting with smaller crossed-hands deficits than females. One of the main theories to explain this sex effect is that females rely more on the external reference frame than the internal reference frame compared to males.

Certain psychiatric conditions have also been proposed to change the relative weights placed on each reference frame. Children with autism have a smaller crossed-hands deficit than age-matched controls, suggesting a less developed external reference frame (Wada et al., 2014). Individuals who measure high in schizotypy have a larger crossed-hands deficit than those who measure moderate or low in schizotypy (Ferri et al., 2016), suggesting that those with high schizotypy weigh external, spatial, information more than internal, somatosensory, information. This idea that high schizotpy individuals emphasize external compared to internal information is consistent with findings of studies using the rubber hand illusion (RHI; Botvinick & Cohen, 1998). The RHI paradigm introduces a conflict between vision, proprioception, and touch, by viewing a fake, rubber hand being stroked while simultaneously feeling the stroking on one's own, real, hidden, hand. The illusion occurs when the congruent visual and tactile information (viewing stroking on the rubber hand and feeling stroking on the real hand) overrides proprioceptive information of the location of the real hand (Makin et al., 2008), causing the illusory impression that the rubber hand is one's own. The strength of the illusion is measured by the extent to which an individual's judgement of the location of their real hand is shifted towards the location of the rubber hand. A stronger illusion is thought to indicate a greater reliance on visual compared to proprioceptive information. When the illusion is induced on individuals with schizophrenia, a stronger RHI is measured than among healthy controls (Thakkar et al., 2011). This might suggest greater reliance on external, visual, information. Similarly, individuals with an eating disorder also show a stronger RHI than healthy controls (Eshkevari et al., 2012; 2014). While the RHI is not a direct measure of tactile localization, both the RHI and tactile TOJ task do share some basic elements in common. In both the RHI and tactile TOJ task, visual information seems to be weighted more heavily than tactile or proprioceptive information. In the

RHI, the visual information of the fake hand leads to mislocalization of the real hand; in the crossed-hands deficit, visual information indicating the hemispace of the hand is given more weight than tactile information, resulting in mislocalization of the touch. Given the similarities between these two tasks, it is possible that groups that have a stronger RHI will also show a larger crossed-hands deficit, but this has yet to be tested.

Given the variability observed in the magnitude of the crossed-hands deficit across individuals, it is likely that individual differences exist in reference frame integration. However, it is also possible that this variability reflects within-participant variability across trials. In order to determine this, the reliability of measures of the crossed-hands deficit must be evaluated within an individual participant across trials. To date, no study has looked at whether the magnitude of the crossed-hands deficit is consistent within or between experimental sessions. Ensuring the reliability of the crossed-hands deficit is an important first step in making sure that the between-participant (inter-individual) variables observed are not an artifact of an inconsistent measure.

Factors Influencing the Magnitude of the Crossed-Hands Deficit

It is clear that there are certain individual differences that are capable of altering the weights placed on the internal and external reference frames. These weights can also be systematically changed within an individual in response to many different factors. In the next few sections, I will discuss some of the factors that have been shown to influence reference frame integration in the context of a tactile TOJ task.

Hand Position

For both crossed and uncrossed postures, as the hands are placed farther apart, it becomes easier to judge which hand received the first vibration (Shore et al., 2005; Gallace & Spence, 2005; Roberts et al., 2003). As the hands move farther apart, the precision of left–right judgments improves, facilitating the integration of the different cues. The crossed-hands deficit has also been observed when the vibrations are presented, not to the hand directly, but at the end of hand-held sticks (Yamamoto & Kitazawa, 2001b). Impaired performance not only occurred when the hands were crossed, but even if the hands were uncrossed and the hand-held sticks were crossed. This means that the deficit occurred when the ends of the hand-held sticks occupied the opposite hemispace as the hand. Accuracy recovered to the level of uncrossed performance when both the hands and sticks were crossed, such that the ends of the sticks were back in their uncrossed hemispace.

A similar effect can be observed by double crossing the hands (Figure 2; Heed et al., 2012). Here a crossed-hands deficit was observed when either the arms were crossed, or when the arms were uncrossed but the stimulated fingers were crossed over the midline. Similar to crossing the sticks, double crossing occurs by crossing the arms and also crossing the stimulated fingers, such that the fingers were placed in their original hemispace. This double crossing led to a reduction in the size of the deficit compared to conditions where either the arms or fingers were crossed. Both the conflict and integration models for the deficit agree that double crossing should improve performance, as the reference frames provide congruent information, allowing integration to proceed without conflict. This suggests that remapping to the external reference frame only takes into account the final position of the hands, and therefore only the location of the touch on the body matters for reference frame integration.

Figure 2: Hand and finger placement in Heed et al. (2012). Stimulation was provided to the little finger. (a) hands were placed in an uncrossed posture, (b) hands were placed in a crossed posture, and (c) double crossed posture where the hands were crossed over the midline, and the stimulated fingers were crossed back to their original hemispace.

Vision

While both reference frames are integrated to locate a touch, many factors affect how each reference frame is weighted to determine the tactile location. Removing visual information influences the relative weights placed on the internal and external reference frames. Blindfolding participants significantly reduces the magnitude of the crossed-hands deficit compared to non-blindfolded participants (Cadieux & Shore, 2013). These manipulations impede the ability to visually locate the hands in external space, reducing the reliability of the external reference frame. As a result, less weight is placed on the external reference frame, thereby leading to a reduced deficit. The accuracy benefit obtained by temporarily removing visual information through blindfolding resulted in a similar magnitude deficit to that seen in late-blind individuals (Röder et al., 2004). Despite the improved performance, a crossed-hands deficit was still observed in the absence of visual inputs. It is likely that participants are still relying on some external information, perhaps a degraded visual representation of their surroundings based on visual imagery. Only congenitally blind participants show no difference between crossed and uncrossed performance (Crollen et al., 2019; Röder et al., 2004).

Not only does removing visual information altogether affect crossed-hands performance, but providing visual information of uncrossed fake hands can also reduce the size of the crossed-hands deficit. For instance, in a study by Azañón and Soto-Faraco (2007) participants were asked to view crossed and uncrossed rubber hands while performing a tactile TOJ task with their own, concealed, hands crossed. Simply viewing uncrossed rubber hands resulted in a smaller crossed-hands deficit than viewing crossed rubber hands. Similar to the double crossing of the hands, the view of the fake rubber hands resulted in the two reference frames agreeing on the location of the touch, allowing integration to proceed without conflict.

Task Instructions

Even simple changes to the task instructions can affect the magnitude of the crossed-hands deficit. In a typical tactile TOJ task participants are asked to indicate which of two vibrations, one on each hand, occurred first (i.e., relative *temporal* order judgment). In contrast, for the first touch localization (FTL) task, participants must indicate the location of the first of two vibrations (i.e., relative *spatial* judgment; Badde et al., 2015a). Despite the identical stimulation and method of responding, the FTL task results in more accurate tactile localization compared to the TOJ task when the hands were crossed, and therefore a smaller crossed-hands deficit (Badde et al., 2015a). Modelling revealed that this change in the deficit was the result of a larger internal weight and smaller external weight in the FTL task compared to the TOJ task (Badde et al., 2015a).

Task instructions can be used to bias perception to one reference frame or another by implementing response demands that emphasize a particular coordinate system (Cadieux & Shore, 2013; Crollen et al., 2019). For example, by switching from a hand button response to a foot pedal response when making temporal order judgments about hand-applied tactile stimuli, two different response demands could be employed. Specifically, in order to introduce an anatomical response demand participants are asked to respond with the foot corresponding with the *hand* that vibrated first. This response demand places the emphasis on the internal reference frame by preserving the left–right coding between the vibration and response. In contrast, in order to introduce a spatiotopic response demand participants are asked to press the foot pedal corresponding with the *hemispace* that received the first vibration. A spatiotopic response biases perception toward the external reference frame by requiring that responses be remapped from the hand surface to the corresponding hemispace. The use of an anatomical response demand results in a smaller deficit than the spatiotopic response demand (Crollen et al., 2019).

Small changes to the task instructions can alter the magnitude of the crossed-hands deficit. At present, the effect that task instructions have on the underlying reference frame weights has not been investigated. With the probabilistic model outlined above, it is now possible to theoretically measure the weights applied to each reference frame. By applying this probabilistic model we can theoretically determine whether task instructions bias the weights systematically towards either the internal or external reference frame.

The Direction of Upright

Another factor that might influence the weight placed on each reference frame is the perceived direction of upright. Many cues are integrated to determine the subjective vertical. One such cue is visual information obtained through the polarity of objects (Jenkin et al., 2004; Mamassian & Goutcher, 2001; Ramachandran, 1998). Other cues to upright are gravitational information, obtained through the vestibular system; and body cues, such as proprioception, and the pressure or distribution of fluids in the body (de Winkel et al., 2018; Dyde et al., 2006). Lying down results in a misalignment between the body upright, and the direction of upright indicated by visual and vestibular cues.

Evidence for this misalignment can be seen when comparing tasks requiring estimates of subjective visual vertical (SVV) to tasks requiring estimates of perceptual upright (PU) while participants are upright and lying on their side (Dyde et al., 2006). The SVV task requires participants to indicate when a line appears to be aligned with the direction of gravity. The PU task, on the other hand, asks individuals to judge whether a letter is a ‘p’ or a ‘d’. Given that the characters p and d are identical apart from their rotated 180 degree orientation, the perceived letter is an indirect measure of their perception of upright. Body, visual, and gravitational cues are all used to perform both the SVV and PU tasks, however, the weight placed on each cue differs based on the task. When sitting, the SVV and the PU provide consistent perceptions for upright, as all cues indicate the same direction of upright. When lying down, body-based cues predict a different direction of upright from the direction of upright predicted by visual and gravitational cues. As a result, the perceived direction of upright as measured through the PU and SVV diverge—the PU estimate remains aligned with the body, but the SVV stays aligned with the direction of gravity (Dyde et al., 2006).

Knowledge of the subjective vertical may be used to inform the external reference frames. The misalignment between the body, visual, and vestibular cues for upright might impact the relative weights placed on each reference frame. If so, then lying down may reduce the reliability of the external reference frame and thus, less weight may be placed on external information, which could decrease the magnitude of the crossed-hands deficit. To the best of my knowledge, no published study has explicitly tested whether lying down influences tactile localization. As such, it remains unknown exactly what impact this would have on reference frame integration and the crossed-hands deficit.

Objectives of the Current Thesis

The crossed-hands tactile TOJ task is one of the most commonly used tasks to measure reference frame integration during tactile localization. While previous studies have observed variability across participants and different population types, it is not yet known whether the effect itself is consistent and reliable within individuals. This is important to ensure that any between-individual difference, or differences observed within particular populations, can be replicated and is not simply a spurious effect. Therefore, the first goal of this thesis was to determine whether the crossed-hands tactile TOJ task is reliable within individuals over trials and over time (Chapter 2). Chapter 2 determined whether performance on the crossed-hands tactile TOJ task was consistent within individuals using two strategies. First, to determine consistency of the effect in the same person over time, I measured participants' performance during two separate sessions, one week apart. Second, to determine the consistency of the effect in the same person within a single study session, I conducted a split-half reliability analysis on data from 23 previous experiments conducted in the Multisensory Perception Laboratory.

Many factors have been identified that alter the weighted integration of the internal and external reference frames. For example, previous research has demonstrated that task instructions that bias perception towards either the internal (anatomical response) or external (spatiotopic response) reference frame alter the magnitude of the crossed-hands deficit. For example, an anatomical response results in a smaller deficit than a spatiotopic response. However, it is unknown exactly how the underlying reference frame *weights* are influenced by these task instructions. Therefore, in Chapter 3, I first replicated the task instruction manipulation to confirm that a larger crossed-hands deficit would be observed for the spatiotopic response demand compared to the anatomical response demand. Next, in order to evaluate the weight placed on each reference frame as a result of changes to the task instructions, I applied the probabilistic model outlined by Badde et al. (2015). This model determined the internal and external weight pair that best accounted for participants' crossed and uncrossed performance. I hypothesized that the model would support the inferences made based on the behavioural data; specifically, that a spatiotopic response demand would lead to a greater weighting of the external reference frame compared to a anatomical response demand.

Chapter 4 explored a possible new influence on the magnitude of the crossed-hands deficit; specifically, body position relative to gravitational upright. While it has been previously shown that perceptual upright is influenced by the position of the body relative to gravity (e.g., sitting upright vs. lying on the side), nothing is currently known about how these differences in the subjective vertical might affect the crossed-hands deficit. I investigated whether lying down on the side would influence the magnitude of the crossed-hands deficit. First, the influence of body position was investigated in the presence of visual information. Then, visual information was removed through the use of a blindfold to separate visual cues from body-based and gravity-based cues for upright. To further examine how body position influenced the integration of internal and external reference frames, the aforementioned probabilistic model of reference frame integration was applied to calculate their relative weights.

Overall, this thesis had three main objectives. Objective 1 was to determine the *reliability* of the tactile TOJ task to confirm its utility for measuring reference frame integration within and between individuals (Chapter 2). Objective 2 was to investigate how a bias introduced towards the internal or external reference frame during a tactile TOJ task influences the *relative weights* placed on each reference frame (Chapter 3). Objective 3 was to explore whether *body position* affects the integration of reference frames during tactile localization (Chapter 4).

CHAPTER 2: RELIABILITY OF THE CROSSED-HANDS DEFICIT IN TACTILE TEMPORAL ORDER JUDGEMENTS

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Abstract

Crossing the hands over the midline impairs performance on a tactile temporal order judgement (TOJ) task, resulting in the crossed-hands deficit. This deficit results from a conflict between two reference frames — one internal (somatotopic) and the other external (spatial) — for coding stimulus location. The substantial individual differences observed in the crossed-hands deficit highlight the differential reliance on these reference frames. For example, women have been reported to place a greater emphasis on the external reference frame than men, resulting in a larger crossed-hands deficit for women. It has also been speculated that individuals with an eating disorder place a greater weight on the external reference frame. Further exploration of individual differences in reference frame weighing using a tactile TOJ task requires that the reliability of the task be established. In Experiment 1, we investigated the reliability of the tactile TOJ task across two sessions separated by one week and found high reliability in the magnitude of the crossed-hands deficit. In Experiment 2, we report the split-half reliability across multiple experiments (both published and unpublished). Overall, tactile TOJ reliability was high. Experiments with small to moderate crossed-hands deficits showed good reliability; those with larger deficits showed even higher reliability. Researchers should try to

maximize the size of the effect when interested in individual differences in the use of the internal and external reference frames.

Introduction

Localizing a touch in space requires the integration of two reference frames. These reference frames serve as coordinate systems for coding the location of tactile stimuli. The internal reference frame consists predominantly of somatosensory information coded relative to the body surface — this code indicates where on the skin, regardless of the position of the limb, a tactile stimulus was applied. In contrast, the external reference frame consists predominantly of spatial information, indicating where the touch would occur if the body were in its default (uncrossed) posture. In order to compute the location of a tactile stimulus, the spatial position of the relevant body part must be integrated with the location on the skin surface. To perceive and act towards the stimulus location, the observer must integrate these two reference frames. The two reference frames typically work in concert; however, when the hands are crossed over the body midline, conflict and confusion can arise (Azañón *et al*., 2016; Badde *et al*., 2015; Crollen *et al*., 2017, 2019; Kóbor *et al*., 2006; Röder *et al*., 2004; Shore *et al*., 2002; Yamamoto and Kitazawa, 2001). The deficit occurs when participants report the relative order of two taps, one to each hand. This tactile temporal order judgement (TOJ) task produces high error rates when the hands are crossed compared to when the hands are uncrossed (see review by Heed and Azañón, 2014). Theoretical explanations of the deficit focus on the conflict between the internal and external reference frames (Badde *et al*., 2015; Shore *et al*., 2002). In support of this account, degrading the external reference frame, for example by placing the hands behind the back (Kóbor *et al*., 2006), or blindfolding the participant (Cadieux and Shore, 2013), reduces the deficit; being born blind eliminates it (Röder *et al*., 2004). The finding of drastic individual differences in the size of the deficit (Cadieux *et al*., 2010), and the suggestion that clinical eating disorders involve a misbalance between these two reference frames (Riva, 2012), raise the question of the within-individual reliability of this deficit. As such, the present paper focuses on assessing the reliability of the crossed-hands deficit using the tactile TOJ task.

Sex at birth provides an example of an individual difference affecting performance in the crossed-hands deficit: female participants generally produced a larger deficit than male participants (Cadieux *et al*., 2010). In this regard, the deficit may be related to other spatial effects that show a similar individual difference. One clearly related effect concerns the increased probability of making left-from-right errors (Gormley *et al*., 2008; Hannay *et al*., 1990; Harris and Gitterman, 1978; Ofte and Hugdahl, 2002; Wolf, 1973). Other spatial tasks that show a sex difference include mental rotation (Linn and Petersen, 1985; Parsons *et al*., 2004; Voyer *et al*., 1995; although see Neubauer *et al*., 2010), maze navigation (Grön *et al*., 2000; Shore *et al*., 2001), path integration (Chaudhury *et al*., 2004), and the Rod-and-Frame test (Barnett-Cowan *et al*., 2010; Bogo *et al*., 1970; Cadieux *et al*., 2010; Hyde *et al*., 1975; Linn and Petersen, 1985). Accounts of these effects have considered both differential levels of sex-hormones (Collaer and Hines, 1995; Gouchie and Kimura, 1991; Moffat and Hampson, 1996; Resnick *et al*., 1986) and expression of specific sex-linked genes as potential causes (Bock and Kolakowski, 1973; Garron, 1970; Hartlage, 1970; Stafford, 1961). The greater use of the external reference frame by female observers forms one common theme in the literature. However, these average differences across sex are dwarfed by the individual differences observed within each sex (see Fig. 2 of Cadieux *et al*., 2010). Extreme reliance on the external reference frame may be linked to at least one clinical disorder.

The bodily experience of an individual with an eating disorder (ED) often differs from that of a healthy individual. ED patients may have a heightened sensitivity to visual capture, leading to either excessively attending to visual information over somatosensory information, or overall reduced somatosensory processing (Eshkevari *et al*., 2012). Individuals with EDs are hypothesized to be locked in an allocentric representation of their body, due to an inability to update this representation with ongoing egocentric inputs (Riva, 2012). An allocentric representation aligns with an external reference frame, whereas an egocentric one aligns with an internal reference frame. By disrupting how the body is experienced and remembered, individuals may be unable to use perception-based signals to update their representations (Riva, 2012). This ‘allocentric lock’ thus primes the brain to make incorrect body-related perception judgements (Riva and Gaudio, 2012). The crossed-hands deficit may provide a good tool to understand this perceptual bias, but only if it is a reliable measure.

The crossed-hands deficit, with its large individual differences, presents an opportunity to investigate how individuals rely on their internal and external reference frames. Understanding these differences will support a greater understanding of related clinical disorders. In order to use any measure to explore individual differences, we must be sure that the measure is reliable (i.e., it produces the same index of the individual across repeated measures). The present study evaluated the reliability of the crossed-hands deficit across two sessions separated by a week (Experiment 1). We also assessed the split-half reliability from within a single session by reanalyzing previously collected data from the Multisensory Perception Laboratory at McMaster University (Experiment 2). Given that the crossed-hands deficit is attributed to reference frame conflict and that relative reference frame use remains consistent over time, we expected to find high reliability in both experiments.

Experiment 1

Methods

Participants

Twenty participants (10 males), average age 18.8 years old, were recruited from McMaster University using an online recruitment tool; all participants were enrolled in a psychology course at the university. All but two participants were right-handed as reported by a handedness questionnaire. Participants received course credit as compensation for their participation. All had normal or corrected-to-normal vision and were naïve to the purpose of the experiment. Participants provided written informed consent prior to participation.

Apparatus and Stimuli

Participants sat at a table (height of 73.7 cm) with their hands placed 18 cm apart. Stimulation and responses were delivered and collected from a small wooden box with a Plexiglas top and an enclosed vibrator (Oticon-A bone conduction vibrator; [100 Ohm; Oticon, Copenhagen, Denmark] width: 1.6 cm, length: 2.4 cm). A 2-cm-diameter hole was cut in the Plexiglas top for participants to place their thumb on the vibrator. The vibrators were driven by an amplified 250 Hz sine wave, set by the experimenter to be comfortable and clearly suprathreshold. Mounted beneath the vibrators were response buttons. All stimulation was controlled by a set of reed-relays connected to the parallel port of a DELL (Round Rock, TX, USA) Dimension 8250 running Windows XP software. Matlab (MathWorks, Natick, MA, USA) was used to administer the stimulation and collect responses. Participants wore headphones playing white noise during the experiment to mask the sounds produced by the tactile vibrators.

Procedure

Participants held one wooden cube in each hand, with their thumbs in contact with the vibrators. Participants first completed two practice blocks, each with 16 trials. The first block was completed with their hands uncrossed, and the other with their hands crossed over the midline, with their right hand resting on top. The experimenter was in the room during the practice trials to provide feedback and answer any questions. The participant then completed 12 experimental blocks of 64 trials each. The experimenter started each block of trials and then left the room, coming in after each block to check on the participant and start the next block. Hand position alternated between crossed and uncrossed each block. The starting hand position was counterbalanced across participants.

Each trial began 800 ms after the participant's previous response. Each trial consisted of two 20 ms vibrations, one to each thumb, separated by one of four fixed stimulus onset asynchronies (SOAs): ±400, ±200, ±100, ±50 ms, where negative SOAs indicated the vibration was to the left hand first. This resulted in 48 trials for each session per SOA for each hand posture. Participants reported which hand was vibrated first by pressing down on the corresponding vibrator after the second vibration occurred. If no response was made within three and a half seconds of the second vibration, the trial timed out. To alert the participant that they missed a trial, both buttons vibrated three times, and participants were required to press both buttons and release for the experiment to continue. Time-out trials and trials with premature responses (i.e., responses made in less than 100 ms) were removed from all analyses. This resulted in the removal of 76 trials across all participants and sessions.

Participants returned one week later to complete the experiment a second time. Experimenters provided shortened verbal instructions and ran two blocks of practice trials, one in each hand posture. Participants then completed 12 blocks, alternating posture every block. This time, participants began the experiment with the opposite initial hand posture they adopted the previous week (i.e., if they initially adopted an uncrossed posture on Day 1, they would first adopt a crossed posture on Day 2).

Analysis

The magnitude of the crossed-hands deficit was evaluated using the proportion correct difference (PCD) score (see Cadieux *et al*., 2010; Heed and Azañón, 2014). To calculate the PCD score, we took the difference in performance between the crossed and uncrossed postures at each SOA and added these values together. To determine whether the size of the deficit was consistent across days, a 2 × 2 analysis of variance (ANOVA) was conducted on the PCD scores with test session (Day 1 *vs*. Day 2) as a within-subject factor and sex (male *vs*. female) as a between-subject factor. One-sample t-tests were conducted on each test session's PCD score to evaluate whether it differed significantly from zero, indicating the presence of a crossed-hands deficit. For the ANOVA, effect-size was computed as η^2; for the t-tests, it was computed as Cohen's d.

To measure reliability of the crossed-hands deficit, a Pearson correlation was calculated between the PCD score on Day 1 and the PCD score on Day 2.

Results and Discussion

The crossed-hands deficit, as indexed by the PCD score (see Figs. 1 and 2), was significantly different from zero on both days (Day 1: M = 1.26, *SD* = 0.77, $t_{(19)} = 7.35$, $p < 0.001$, d = 1.64; Day 2: M = 1.23, *SD* = 0.78; $t_{(19)} = 7.03$, $p < 0.001$, d = 1.57) and did not significantly differ across the two days ($F_{(1,19)} = 0.13$, p = 0.73, $\eta_g^2 < 0.001$). The factor sex was significant ($F_{(1,19)} = 4.82$, p = 0.04, $\eta_g^2 = 0.2$), with females having an overall larger PCD score than males. Sex did not interact with day of testing ($F_{(1,19)} = 0.07$, p = 0.79, $\eta_g^2 < 0.001$).

The crossed-hands deficit, as indexed by the PCD score, was highly correlated across Day 1 and Day 2 (r = 0.86, $p < 0.001$; see Fig. 3) indicating a highly reliable task (this remains true even when the one female with a high PCD score was removed). This reliability remained even when computed separately for females (r = 0.87, p = 0.002) and males (r = 0.72, p = 0.01).

Using PCD as a measure of the crossed-hands tactile TOJ deficit, we saw no significant change in performance across two testing sessions separated by a week. This was true for both males and females. The findings of this experiment support our initial hypothesis that performance on a tactile TOJ task provides a reliable measure of the crossed-hands deficit: individuals apparently rely on their internal and external reference frames consistently across time.

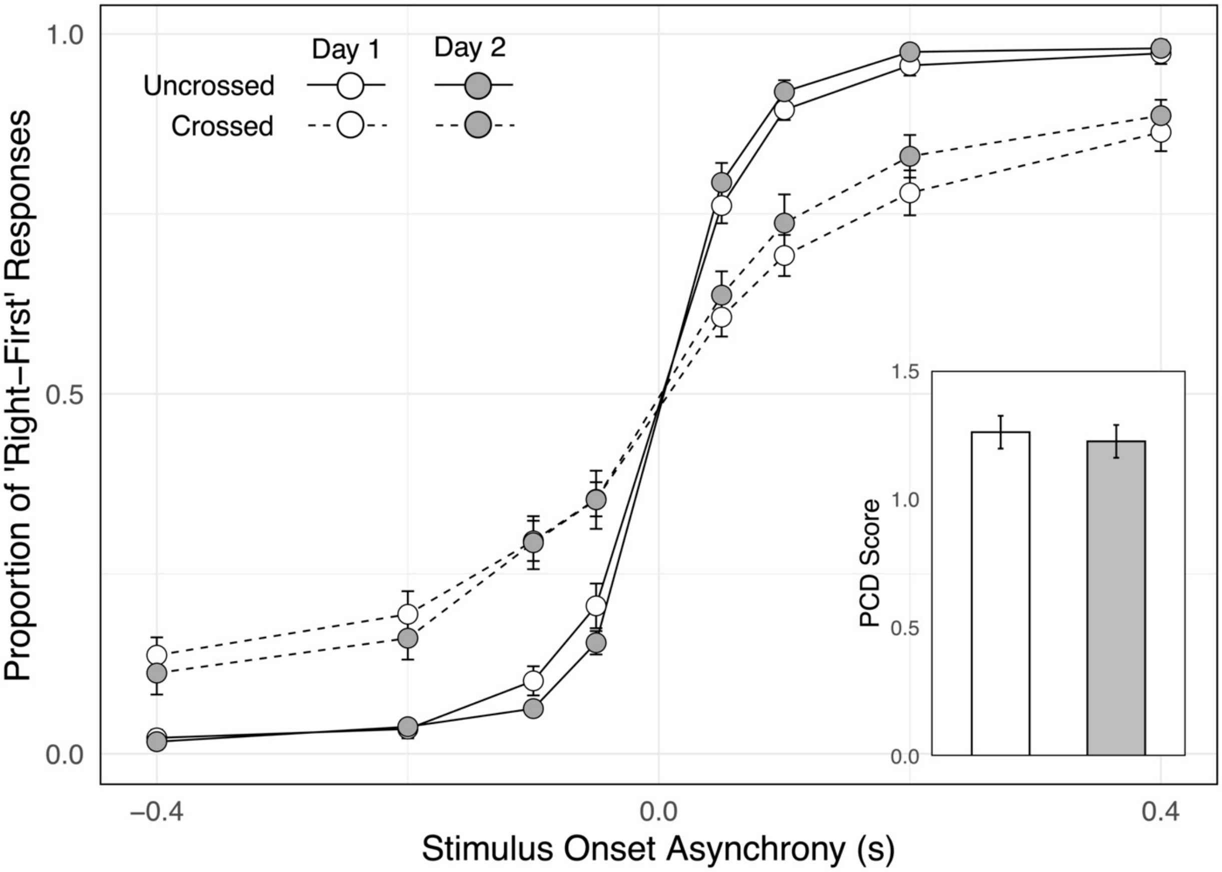

Figure 1: Proportion of right-first responses across stimulus onset asynchrony (SOA) from 20 participants (10 males) for both the crossed and uncrossed hand postures. Bar graph represents the average proportion correct difference (PCD) score for each session. Error bars represent standard error corrected for a within-subject design (Cousineau, 2005; Morey, 2008).

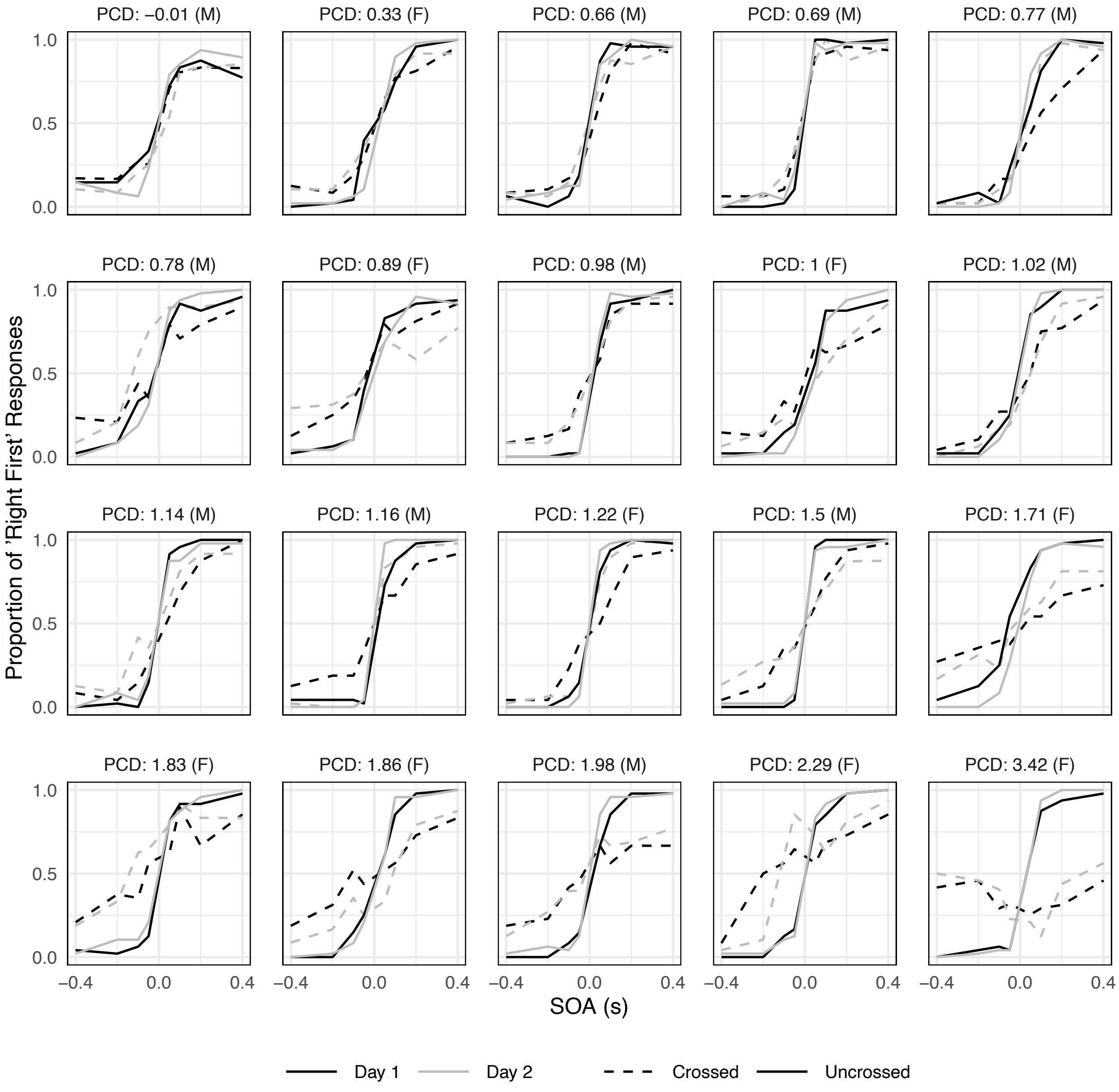

Figure 2: Individual data from 20 participants (10 males) arranged by proportion correct difference (PCD) score on Day 1.

The present findings contrast slightly with the results from Craig and Belser (2006), where a large practice effect was observed. There are some key differences between the two studies that may explain the magnitude difference of the practice effect. The current experiment only contained two sessions, where no feedback was provided. Craig and Belser's participants completed 12 sessions and provided feedback after each trial, allowing more time for improvement. Furthermore, in the present study participants altered their hand posture from uncrossed to crossed every 64 trials, rather than once halfway through the session. This constant posture alteration can impede learning the task (Azañón *et al.*, 2015). More research is required to fully understand when practice will lead to improved crossed-hands tactile TOJ performance.

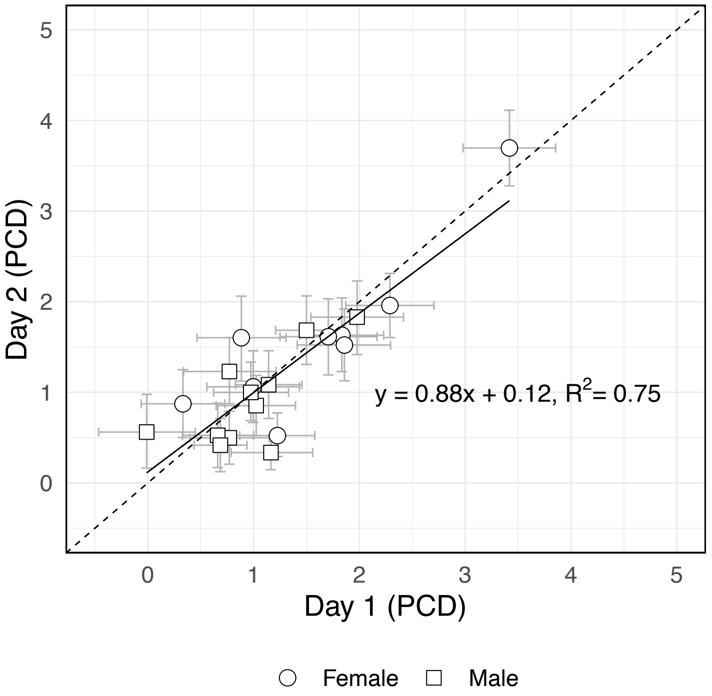

Figure 3: Scatterplot depicting proportion correct difference (PCD) scores on Day 1 *vs*. Day 2. Each point represents a bootstrap of the participants data with 95% confidence intervals as the error bars. A significant correlation was observed between scores across sessions.

Experiment 2

To determine whether the crossed-hands deficit remains consistent within a single session, we measured the split-half correlation within many unique experiments conducted in the

Multisensory Perception Laboratory. This analysis was repeated 5000 times with randomly sampled, equally large subgroups (Imbault *et al*., 2018; MacLeod *et al*., 2010). The experiments differed in terms of the posture of the participant, the placement of the hands, and the method of response collection.

Methods

Participants and Procedure

The stimuli, apparatus, and general instructions were the same as in Experiment 1, except that some experiments had only six SOAs. In this case the SOAs of ±100 were removed. Across the 23 experiments, multiple manipulations were used, which each required specific instructions; however, all involved the completion of a tactile TOJ task while the hands were crossed and uncrossed and thus had the same general instructions as Experiment 1. When the participants were seated upright the right hand was resting on top, and when the participants were lying down the left hand was placed above the right. For some of the experiments (Experiments 18–23), participants responded with foot pedals. In some conditions of these experiments, the response demands followed an internal mapping (i.e., lift your right foot when your right hand is stimulated first regardless of posture), whereas others relied on an external mapping (i.e., lift the toe directly under the finger vibrated first). Two experiments collected data from female participants only, and one experiment only used male participants.

Experiments

1. Test–Retest: 20 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses across two different sessions, completed one week

apart. In total eight SOAs were tested, each repeated 48 times per condition. These data are the data from Experiment 1 in this paper.

2. Test–Retest Replication: 54 participants (24 males) completed the same experiment as Experiment 1, except fewer trials were completed each day. In total eight SOAs were tested, each repeated 16 times per condition. This was done to determine whether high reliability could be measured with fewer trials. This was completed as part of a larger experiment looking at the correlation between the crossed-hands deficit, heartbeat perception, and the rubber hand illusion.
3. Body Image Correlation with Hand Buttons: 19 participants (all females) completed a tactile TOJ task with their hands crossed and uncrossed using hand button responses. Before the tactile TOJ task, participants were asked to complete a few questionnaires relating to their perception of their own body, and their mental health. Participants were tested using six SOAs, each repeated 60 times per condition.
4. Sex Difference: 49 participants (25 males) performed a tactile TOJ task with their hands crossed and uncrossed using hand button responses. Participants were tested using eight SOAs, each repeated 40 times per condition. This was part of a larger experiment to investigate sex differences in the crossed-hands deficit (data published in Cadieux *et al.*, 2010).
5. Pseudoneglect: 16 participants (six males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses. Half the time, participants were lying on their left side, and the other half of the time, participants were lying on their right side. Participants were tested using eight SOAs, each repeated 24 times per condition. Participants

also completed a modified line bisection task to explore the association between the crossed-hands deficit and pseudoneglect.

6. Posture (Up *vs*. Back): 20 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses. Half of the time, participants were upright with their hands resting on the table, and the other half of the time, participants were lying on their back with their hands placed away from the body (elbows bent 90 degrees, to mimic sitting at a table). Participants were tested using eight SOAs, each repeated 24 times per condition.
7. Posture (Up *vs*. Back) 2: 25 participants (12 males) completed a tactile TOJ task with their hands crossed and uncrossed using hand button responses. For half of the experiment, participants were upright with their hands resting on the table, and for the other half, participants were lying on their back with their hands at their side. Participants were tested using eight SOAs, each repeated 24 times per condition.
8. Posture (Up *vs*. Back) 3: 19 participants (nine males) completed a tactile TOJ task with their hands crossed and uncrossed using hand button responses. Participants were upright for half of the experiment, and for the other half, were lying on their back. When participants had their hands uncrossed the hands were resting at their side, and when the participant crossed their hands, the hands were placed on their chest. Participants were tested using eight SOAs, each repeated 24 times per condition.
9. Posture (Up *vs*. Side): 20 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses. Half of the time the participants were upright with their hands resting on the table, and for the other half, the participants were lying on their side with their hands placed away from the body (elbows bent 90 degrees, to

mimic sitting at a table). Participants were tested using eight SOAs, each repeated 24 times per condition (published abstract Cadieux *et al*., 2015).

10. Posture (Up *vs*. Side) Blindfold: 20 participants (10 males) completed the same experiment as in Experiment 9, except participants wore a blindfold throughout the whole experiment (published abstract Cadieux *et al*., 2015).
11. Virtual Reality: 21 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses while lying on their side with their hands placed away from the body (elbows bent 90 degrees, to mimic sitting at a table). For the duration of the experiment, the participants wore a virtual-reality headset that presented images of rooms either aligned with the participant's body or with gravity. Participants were tested using eight SOAs, each repeated 24 times per condition.
12. Vestibular Stimulation: 42 participants (20 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses. For half the experiment, the participants were given galvanic vestibular stimulation in order to assess the role of the vestibular system on tactile processing. Participants were tested using eight SOAs, each repeated 24 times per condition.
13. Posture (Back *vs*. Side) Hands Near: 42 participants (21 males) performed a tactile TOJ task using hand button responses with their hands crossed and uncrossed on their chest. For half the experiment, participants were lying on their back and for the other half participants were lying on their side. Participants were tested using eight SOAs, each repeated 24 times per condition.

14. Posture (Back *vs*. Side) Hands Far: 28 participants (13 males) completed the same experiment as in Experiment 13, except their hands were placed away from the body (elbows bent 90 degrees, to mimic sitting at a table).
15. Hand Position and Posture: 63 participants (33 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses. For half of the experiment, the participants' hands were placed away from the body (elbows bent 90 degrees, to mimic sitting at a table), and for the other half, hands were on the participant's chest. Some participants (a) were upright for the duration of the experiment, while others (b) were lying on their side for the duration of the experiment; the rest (c) were lying on their back for the duration of the experiment. Participants were tested using eight SOAs, each repeated 24 times per condition.
16. Hand Position and Posture Replication: 29 participants (all males) completed the same experiment as in Experiment 15, except that when the participants' hands were placed on their chest, a pillow was placed between the person's hand and chest to reduce the sensation of vibrations felt on the body.
17. Hand Position Replication: 20 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed with hand button responses while sitting upright. For half the experiment, the participants placed their hands on the table in front of them, and for the other half, the participants placed their hands on their chest. Participants were tested using eight SOAs, each repeated 24 times per condition.
18. Response Demands (Internal *vs*. External): 20 participants (10 males) performed a tactile TOJ task with their hands crossed and uncrossed. For half the experiment, participants used an internal foot pedal response, and for the other half, they used an external foot pedal

response (see Cadieux and Shore (2013) for details of this response type). Participants were tested using six SOAs, each repeated 30 times per condition.

19. Body Image Correlation with Foot Pedals: 44 participants (all females) performed a tactile TOJ task with their hands crossed and uncrossed. For half the experiment, participants used an internal foot pedal response, and for the other half, they used an external foot pedal response. Participants were tested using six SOAs, each repeated 30 times per condition. Participants also completed the rubber hand illusion task, as well as questionnaires related to their body image and mental health.
20. Response Demands (Internal *vs*. External *vs*. Hands): 41 participants (14 males) performed a tactile TOJ task with their hands crossed and uncrossed under three different response demands: hand button responses, internal foot pedal response, or an external foot pedal response. Participants were tested using six SOAs, each repeated 30 times per condition.
21. Response Demands (Internal *vs*. External) and Posture: 40 participants (20 males) performed a tactile TOJ task with their hands crossed and uncrossed. For half the experiment, participants used an external foot pedal response and for the other half they used an internal foot pedal response. Half the participants were (a) lying on their side for the duration of the experiment, and the other half were (b) on their back. Hands were placed away from the body (elbows bent 90 degrees, to mimic sitting at a table). Participants were tested using six SOAs, each repeated 30 times per condition.
22. Response Demands (Internal *vs*. Hands) and Posture: 41 participants (21 males) completed the same experiment as in Experiment 21, except the external foot pedal response was replaced with a hand button response.

23. Posture (Up *vs*. Back *vs*. Side) Foot Pedals: 30 participants (15 males) performed a tactile TOJ task with their hands crossed and uncrossed while using an external foot pedal response. All participants completed the task while upright, on their back, and on their side. Hands were placed on the table while upright, and away from the body (elbows bent 90 degrees, to mimic sitting at a table) when lying down. Participants were tested using six SOAs, each repeated 30 times per condition.

Analysis

The magnitude of the crossed-hands deficit was measured using a PCD score, as in Experiment 1.

Split-half reliability was calculated separately for males and females based on previous findings that males generally show a smaller crossed-hands deficit (Cadieux *et al*., 2010; Experiment 1). For both males and females, we separately calculated split-half estimates for each condition within an experiment, using a modified version of the split-half procedure outlined by MacLeod *et al*., (2010). The number of conditions per experiment ranged from 1 to 6. After grouping the raw data based on condition, hand posture, and SOA, we randomly split the participants' responses into two groups. We then used these split halves to calculate two PCD scores for each participant per condition. Then for each condition, a Pearson correlation was calculated between the two PCD scores across all participants. This process was repeated 5000 times, creating 5000 correlations per condition. Our estimate of the split-half reliability for each condition was found by taking the mean of the 5000 correlations. A 95% confidence interval was obtained by removing the lowest and highest 2.5 percent of correlations. To extrapolate the test–retest reliabilities from these split-half reliabilities, the Spearman–Brown Prophecy Formula, twice the correlation divided by one plus the correlation, was applied to the correlations for each experiment separately, to equate sample length to that of the original data (Spearman, 1910). These values are reported in Table 1.

To help explain the reliability output, we correlated the reliability scores with the measure of the crossed-hands deficit, the PCD score. The size of the PCD score, being a sum of the difference in performance at each SOA, is affected by the number of SOAs and by the chosen SOAs in the experiment. Given that the same SOAs were used across all experiments, some just having two fewer SOAs, this factor will not influence the size of the PCD score. In order to correct for the number of SOAs we divided the PCD score by the number of SOAs in the experiment. The interquartile range rule was applied to each measure to exclude outliers from the correlation.

To further explore the presence of a sex difference in the crossed-hands deficit, independent-sample t-tests were conducted on each study to compare the overall performance of males and females. All statistical analyses were conducted in RStudio version 1.2.5 (RStudio, Boston, MA, USA).

Results and Discussion

Split-half reliability for females ranged from −0.23 to 0.96 and for males ranged from −0.32 to 0.97 (see Fig. 4 for a histogram of reliability; see Fig. 5 for the reliability breakdown by Experiment). Overall reliability for females and males across all experiments was calculated by weighting the experiment reliability by the number of participants in that experiment. This resulted in an overall reliability of 0.78 for females and 0.67 for males. The crossed-hands deficit, as measured through PCD scores, is highly reliable within a one-hour experiment session for males and females. These findings support our initial hypothesis that performance on a tactile TOJ task should remain stable within a session, as individuals should not change the way they rely on each reference frame.

Table 1: Summary of the participants and procedure used in each experiment. Split-half and Spearman–Brown reliabilities are presented separately for each sex and condition.

Experiment	Posture	Response demand	*n*	SOAs	Nr. of conditions	SOA reps/ condition	Additional notes	Sex	Split-half results	Spearman–Brown correction
1. Test–retest	Upright	Hand buttons	20	±400, ±200, ±100, ±50	4	48	Experiment 1	F	Day 1: ρ=0.91 [0.79, 0.98]	Day 1: ρ=0.95 [0.88, 0.99]
									Day 2: ρ=0.92 [0.82, 0.98]	Day 2: ρ=0.96 [0.90, 0.99]
								M	Day 1: ρ=0.78 [0.57, 0.93]	Day 1: ρ=0.87 [0.73, 0.96]
									Day 2: ρ=0.81 [0.62, 0.94]	Day 2: ρ=0.89 [0.77, 0.97]
2. Test–retest replication	Upright	Hand buttons	54	±400, ±200, ±100, ±50	4	16		F	Day 1: ρ=0.85 [0.77, 0.92]	Day 1: ρ=0.92 [0.87, 0.96]
									Day 2: ρ=0.86 [0.78, 0.92]	Day 2: ρ=0.93 [0.88, 0.96]
								M	Day 1: ρ=0.66 [0.47, 0.81]	Day 1: ρ=0.79 [0.64, 0.90]
									Day 2: ρ=0.64 [0.45, 0.81]	Day 2: ρ=0.78 [0.62, 0.90]
3. Body image correlation with hand buttons	Upright	Hand buttons	19	±400, ±200, ±50	2	60		F	Hands: ρ=0.64 [0.41, 0.82]	Hands: ρ=0.78 [0.58, 0.90]
4. Sex difference	Upright	Hand buttons	49	±400, ±200, ±100, ±50	2	40		F	Hands: ρ=0.93 [0.89, 0.96]	Hands: ρ=0.96 [0.94, 0.98]
								M	Hands: ρ=0.91 [0.85, 0.95]	Hands: ρ=0.95 [0.92, 0.98]
5.	Side	Hand buttons	16	±400, ±200,	4	24	This experiment	F	Left side: ρ=0.70 [0.40, 0.91]	Left side: ρ=0.82 [0.57, 0.96]

Pseudoneglect				±100, ±50			explored whether the side that participants lie on makes a difference to their deficit, and correlated the deficit with a line bisection task		Right side: ρ=0.56 [0.15, 0.86]	Right side: ρ=0.70 [0.26, 0.93]
								M	Left side: ρ=0.82 [0.54, 0.97]	Left side: ρ=0.89 [0.70, 0.99]
									Right side: ρ=0.77 [0.41, 0.97]	Right side: ρ=0.86 [0.58, 0.99]
6. Posture (up *vs*. back)	Upright and back	Hand buttons	20	±400, ±200, ±100, ±50	4	24		F	Upright: ρ=0.83 [0.64, 0.95]	Upright: ρ=0.90 [0.78, 0.97]
									Back: ρ=0.83 [0.64, 0.95]	Back: ρ=0.90 [0.78, 0.97]
								M	Upright: ρ=0.84 [0.68, 0.96]	Upright: ρ=0.91 [0.81, 0.98]
									Back: ρ=0.72 [0.43, 0.92]	Back: ρ=0.83 [0.60, 0.96]
7. Posture (up *vs*. back) 2	Upright and back	Hand buttons	25	±400, ±200, ±100, ±50	4	24	Hands were resting at participants' side when lying on back	F	Upright: ρ=0.90 [0.80, 0.97]	Upright: ρ=0.95 [0.89, 0.98]
									Back: ρ=0.81 [0.63, 0.93]	Back: ρ=0.89 [0.77, 0.96]
								M	Upright: ρ=0.71 [0.47, 0.90]	Upright: ρ=0.83 [0.64, 0.95]
									Back: ρ=0.82 [0.65, 0.94]	Back: ρ=0.90 [0.79, 0.97]
8. Posture (up *vs*. back) 3	Upright and back	Hand buttons	19	±400, ±200, ±100, ±50	4	24	Hands were resting at side when uncrossed, and on chest when crossed during the back condition	F	Upright: ρ=0.85 [0.67, 0.96]	Upright: ρ=0.92 [0.81, 0.98]
									Back: ρ=0.81 [0.59, 0.95]	Back: ρ=0.89 [0.74, 0.97]
								M	Upright: ρ=0.73 [0.47, 0.92]	Upright: ρ=0.84 [0.64, 0.96]
									Back: ρ=0.79 [0.58, 0.94]	Back: ρ=0.88 [0.73, 0.97]
9. Posture (up	Upright and	Hand buttons	20	±400, ±200,	4	24	This data is presented	F	Upright: ρ=0.92 [0.82, 0.98]	Upright: ρ=0.96 [0.90, 0.99]

vs. side)	side			±100, ±50			in more detail in Chapter 4	 M	Side: ρ=0.91 [0.81, 0.98] Upright: ρ=0.88 [0.74, 0.97] Side: ρ=−0.10 [−0.56, 0.47]	Side: ρ=0.95 [0.90, 0.99] Upright: ρ=0.93 [0.85, 0.98] Side: ρ=−0.15 [−0.72, 0.64]
10. Posture (up *vs*. side) blindfold	Upright and side	Hand buttons	20	±400, ±200, ±100, ±50	4	24	All participants wore a blindfold for the duration of the experiment This data is presented in more detail in Chapter 4	F M	Upright: ρ=0.53 [0.13, 0.85] Side: ρ=−0.23 [−0.67, 0.36] Upright: ρ=0.89 [0.77, 0.97] Side: ρ=0.22 [−0.29, 0.72]	Upright: ρ=0.67 [0.23, 0.92] Side: ρ=−0.32 [−0.80, 0.53] Upright: ρ=0.94 [0.87, 0.98] Side: ρ=0.30 [−0.45, 0.84]
11. Virtual reality	Side	Hand buttons	21	±400, ±200, ±100, ±50	4	24	All participants wore a virtual-reality headset for the duration of the experiment	F M	Person: ρ=0.26 [−0.19, 0.70] Room: ρ=0.1 [−0.36, 0.60] Person: ρ=0.24 [−0.23, 0.71] Room: ρ=0.09 [−0.38, 0.61]	Person: ρ=0.37 [−0.32, 0.83] Room: ρ=0.15 [−0.53, 0.75] Person: ρ=0.34 [−0.37, 0.83] Room: ρ=0.13 [−0.55, 0.76]
12. Vestibular stimulation	Upright	Hand buttons	42	±400, ±200, ±100, ±50	4	24	All participants received galvanic vestibular stimulation for half the experiment.	F M	No vestibular: ρ=0.87 [0.78, 0.94] Vestibular: ρ=0.84 [0.74, 0.92] No vestibular: ρ=0.74 [0.57, 0.88] Vestibular: ρ=0.74 [0.56, 0.88]	No vestibular: ρ=0.93 [0.88, 0.97] Vestibular: ρ=0.92 [0.85, 0.96] No vestibular: ρ=0.85 [0.73, 0.93] Vestibular: ρ=0.85 [0.72, 0.93]
13. Posture (back *vs*. side)	Back and side	Hand buttons	42	±400, ±200, ±100, ±50	4	24	Hands were on chest	F	Back: ρ=0.74 [0.57, 0.87] Side: ρ=0.68 [0.49, 0.84]	Back: ρ=0.85 [0.72, 0.93] Side: ρ=0.81 [0.66, 0.91]

hands near								M	Back: ρ=0.51 [0.24, 0.74] Side: ρ=0.69 [0.49, 0.84]	Back: ρ=0.66 [0.38, 0.85] Side: ρ=0.81 [0.66, 0.92]
14. Posture (back *vs*. side) hands far	Back and side	Hand buttons	28	±400, ±200, ±100, ±50	4	24	Hands were perpendicular to the body	F	Back: ρ=0.83 [0.69, 0.93] Side: ρ=0.59 [0.29, 0.83]	Back: ρ=0.91 [0.812.97] Side: ρ=0.74 [0.45, 0.91]
								M	Back: ρ=0.69 [0.42, 0.89] Side: ρ=−0.04 [−0.47, 0.44]	Back: ρ=0.81 [0.60, 0.94] Side: ρ=−0.06 [−0.64, 0.61]
15. Hand position and posture	(A) Upright	Hand buttons	23	±400, ±200, ±100, ±50	4	24	Hands were perpendicular to the body, or on chest	F	Near: ρ=0.84 [0.68, 0.95] Far: ρ=0.86 [0.68, 0.95]	Near: ρ=0.91 [0.81, 0.98] Far: ρ=0.93 [0.84, 0.98]
								M	Near: ρ=0.80 [0.62, 0.93] Far: ρ=0.89 [0.79, 0.96]	Near: ρ=0.89 [0.76, 0.96] Far: ρ=0.94 [0.88, 0.98]
	(B) Side		19					F	Near: ρ=0.95 [0.89, 0.99] Far: ρ=0.72 [0.45, 0.91]	Near: ρ=0.97 [0.94, 0.99] Far: ρ=0.83 [0.62, 0.96]
								M	Near: ρ=0.79 [0.55, 0.95] Far: ρ=−0.32 [−0.74, 0.31]	Near: ρ=0.88 [0.71, 0.97] Far: ρ=−0.43 [−0.85, 0.47]
	(C) Back		21					F	Near: ρ=0.94 [0.86, 0.99] Far: ρ=0.88 [0.74, 0.97]	Near: ρ=0.97 [0.92, 0.99] Far: ρ=0.94 [0.85, 0.98]
								M	Near: ρ=0.80 [0.62, 0.93] Far: ρ=0.91 [0.82, 0.97]	Near: ρ=0.89 [0.77, 0.96] Far: ρ=0.95 [0.90, 0.99]
16. Hand position and posture	(A) Upright	Hand buttons	10	±400, ±200, ±100, ±50	4	24	Hands were perpendicular to the body, or on chest.	M	Near: ρ=0.74 [0.45, 0.93] Far: ρ=0.79 [0.55, 0.94]	Near: ρ=0.85 [0.62, 0.96] Far: ρ=0.88 [0.71, 0.97]
	(B) Side		10					M	Near: ρ=0.71 [0.44, 0.91]	Near: ρ=0.83 [0.61, 0.95]

replication	(C) Back		9				When placed on the chest, a pillow was placed between the hands and chest.	M	Far: ρ=0.54 [0.11, 0.85] Near: ρ=0.66 [0.35, 0.89] Far: ρ=0.82 [0.63, 0.95]	Far: ρ=0.68 [0.20, 0.92] Near: ρ=0.78 [0.51, 0.94] Far: ρ=0.90 [0.77, 0.97]
17. Hand position replication	Upright	Hand buttons	20	±400, ±200, ±100, ±50	4	24	Hands were perpendicular to the body, or on chest.	F	Near: ρ=0.90 [0.77, 0.97] Far: ρ=0.87 [0.74, 0.97]	Near: ρ=0.95 [0.87, 0.99] Far: ρ=0.93 [0.85, 0.98]
								M	Near: ρ=0.71 [0.42, 0.92] Far: ρ=0.47 [0.06, 0.82]	Near: ρ=0.83 [0.59, 0.96] Far: ρ=0.61 [0.12, 0.90]
18. Response demands (somatotopic *vs*. allocentric)	Upright	Foot pedals (somatotopic and allocentric response)	20	±400, ±200, ±50	4	30	This data is presented in more detail in Chapter 3	F	Allocentric: ρ=0.87 [0.74, 0.96] Somatotopic: ρ=0.72 [0.45, 0.91]	Allocentric: ρ=0.93 [0.85, 0.98] Somatotopic: ρ=0.83 [0.63, 0.95]
								M	Allocentric: ρ=0.88 [0.75, 0.97] Somatotopic: ρ=0.75 [0.51, 0.92]	Allocentric: ρ=0.94 [0.86, 0.98] Somatotopic: ρ=0.85 [0.67, 0.96]
19. Body image correlation with foot pedals	Upright	Foot pedals (somatotopic and allocentric response)	44	±400, ±200, ±50	4	30	This data is presented in more detail in Chapter 3	F	Allocentric: ρ=0.81 [0.73, 0.88] Somatotopic: ρ=0.90 [0.85, 0.94]	Allocentric: ρ=0.89 [0.84, 0.93] Somatotopic: ρ=0.95 [0.92, 0.97]
20. Response demands (somatotopic	Upright	Foot pedals (somatotopic and	41	±400, ±200, ±50	6	30		F	Allocentric: ρ=0.82 [0.72, 0.91] Hands: ρ=0.81 [0.71, 0.90] Somatotopic: ρ=0.83 [0.72, 0.91]	Allocentric: ρ=0.90 [0.83, 0.95] Hands: ρ=0.90 [0.83, 0.95] Somatotopic: ρ=0.90 [0.84, 0.95]

vs. allocentric *vs*. hands)		allocentric response and hand buttons)					M	Allocentric: ρ=0.65 [0.39, 0.86] Hands: ρ=0.70 [0.48, 0.88] Somatotopic: ρ=0.57 [0.24, 0.82]	Allocentric: ρ=0.78 [0.57, 0.92] Hands: ρ=0.82 [0.65, 0.94] Somatotopic: ρ=0.71 [0.39, 0.90]
21. Response demands (somatotopic *vs*. allocentric) and posture	(A) Side	Foot pedals (somatotopic and allocentric response)	20	±400, ±200, ±50	4	30	F	Allocentric: ρ=0.91 [0.81, 0.98] Somatotopic: ρ=0.49 [0.07, 0.38]	Allocentric: ρ=0.95 [0.89, 0.99] Somatotopic: ρ=0.63 [0.13, 0.91]
							M	Allocentric: ρ=0.97 [0.92, 0.99] Somatotopic: ρ=0.62 [0.26, 0.88]	Allocentric: ρ=0.98 [0.96, 1.00] Somatotopic: ρ=0.75 [0.41, 0.94]
	(B) Back	Foot pedals (somatotopic and allocentric response)	20				F	Allocentric: ρ=0.78 [0.57, 0.94] Somatotopic: ρ=0.71 [0.44, 0.91]	Allocentric: ρ=0.88 [0.73, 0.97] Somatotopic: ρ=0.83 [0.61, 0.96]
							M	Allocentric: ρ=0.84 [0.67, 0.95] Somatotopic: ρ=0.56 [0.19, 0.85]	Allocentric: ρ=0.91 [0.80, 0.98] Somatotopic: ρ=0.70 [0.31, 0.92]
22. Response demands (somatotopic *vs*. hands) and posture	(A) Side	Foot pedals (somatotopic response and hand buttons)	21	±400, ±200, ±50	4	30	F	Hands: ρ=0.40 [−0.01, 0.78] Somatotopic: ρ=0.48 [0.09, 0.82]	Hands: ρ=0.54 [−0.02, 0.88] Somatotopic: ρ=0.63 [0.17, 0.90]
							M	Hands: ρ=0.03 [−0.43, 0.53] Somatotopic: ρ=0.57 [0.23, 0.84]	Hands: ρ=0.04 [−0.61, 0.69] Somatotopic: ρ=0.71 [0.38, 0.92]
	(B) Back	Foot pedals (somatotopic response) and hand buttons	20				F	Hands: ρ=0.80 [0.58, 0.94] Somatotopic: ρ=0.84 [0.66, 0.96]	Hands: ρ=0.88 [0.73, 0.97] Somatotopic: ρ=0.91 [0.79, 0.98]
							M	Hands: ρ=0.86 [0.69, 0.96] Somatotopic: ρ=0.87 [0.72, 0.96]	Hands: ρ=0.92 [0.82, 0.98] Somatotopic: ρ=0.93 [0.83, 0.98]

23. Posture (up *vs*. back *vs*. side) foot pedals	Upright and back and side	Foot pedals (allocentric response)	30	±400, ±200, ±50	6	30		F	Up: ρ=0.93 [0.87, 0.974 Side: ρ=0.96 [0.93, 0.99] Back: ρ=0.91 [0.83, 0.96]	Up: ρ=0.96 [0.93, 0.99] Side: ρ=0.98 [0.96, 0.99] Back: ρ=0.95 [0.90, 0.98]
								M	Up: ρ=0.91 [0.83, 0.97] Side: ρ=0.92 [0.85, 0.97] Back: ρ=0.91 [0.83, 0.97]	Up: ρ=0.95 [0.910.98] Side: ρ=0.96 [0.92, 0.99] Back: ρ=0.95 [0.91, 0.98]

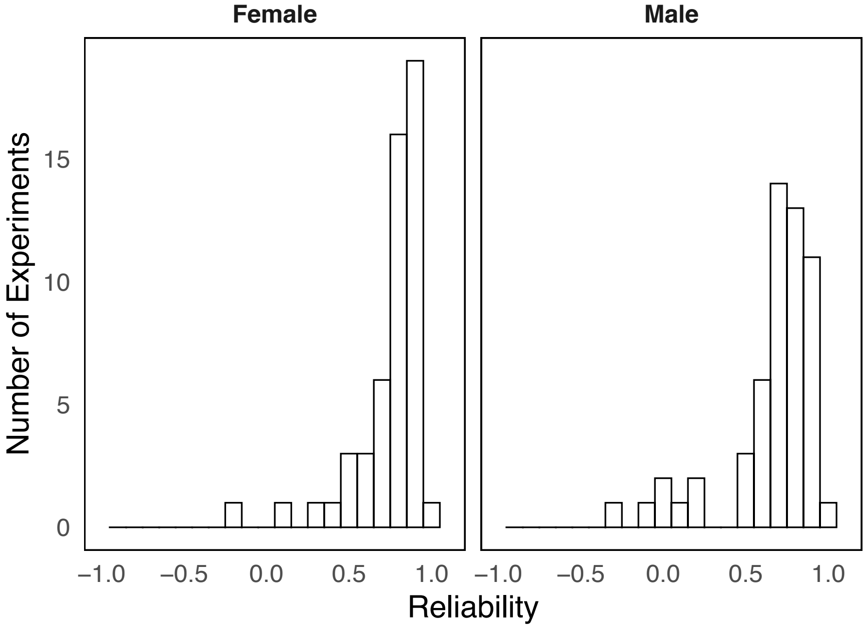

Figure 4: Histogram of reliabilities over all the experiments, separated by sex.

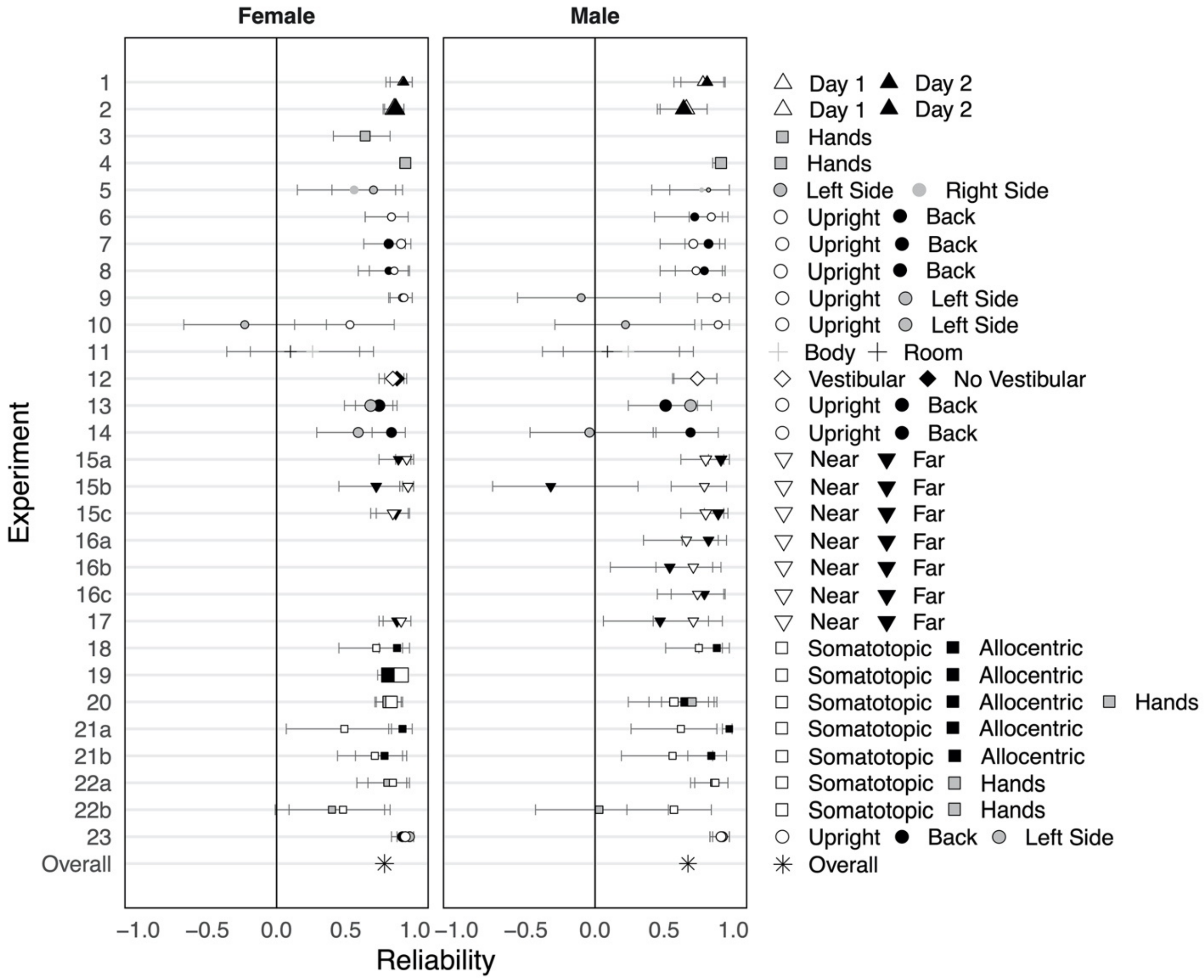

Figure 5: Split-half reliability split by sex for each condition in each experiment. The black line indicates a reliability of 0. The size of the symbol indicates the number of participants in the condition. Error bars represent 95% confidence intervals.

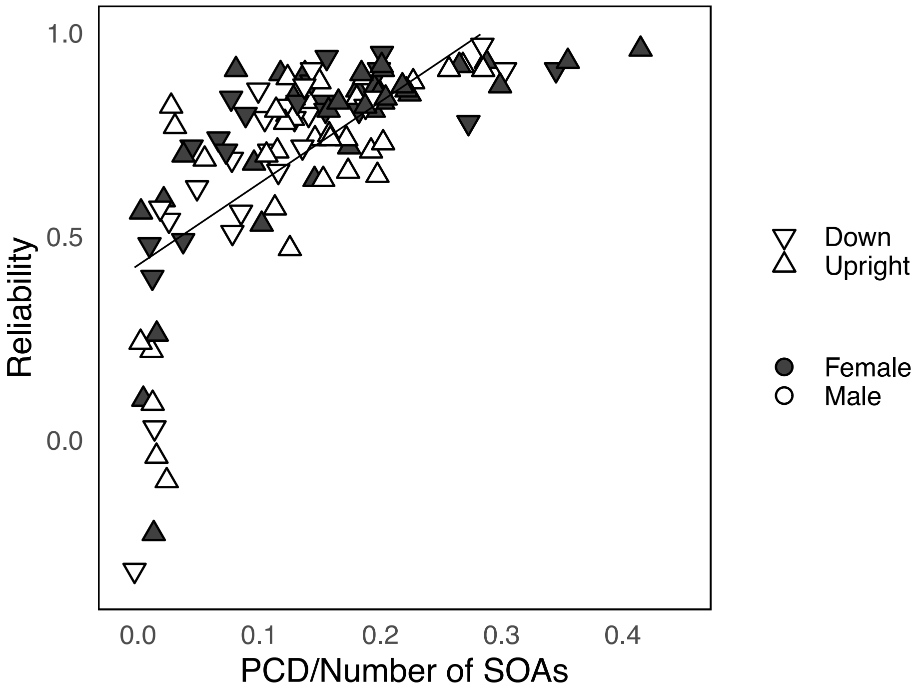

Figure 6: Scatterplot with proportion correct difference (PCD) score (scaled by the number of stimulus onset asynchronies [SOAs] in the experiment) on the x-axis and mean split-half reliability on the y-axis. Conditions where the participants were lying down on either their back or side are coded as down, while upright refers to conditions where the participants were sitting upright.

In order to better understand the variability seen in the reliability scores, we correlated the reliability scores with the PCD score. Reliability scores were positively correlated with the PCD score ($r = 0.66$, $p < 0.001$; see Fig. 6). In order to optimize internal consistency in the tactile TOJ task, one should attempt to maximize the size of the crossed-hands deficit. Under these circumstances, a consistent measure of the deficit can be obtained.

Reliability was calculated separately for males and females based on the previous finding that males have a smaller deficit than females (Cadieux *et al.*, 2010). A sex effect was found in three of the 23 studies (Posture [Up *vs*. Side]: $t_{(18)}$ = 2.14, p = 0.05, d = 0.96; Sex Difference: $t_{(47)}$ = 2.38, p = 0.02, d = 0.68; Test–Retest: $t_{(18)}$ = 2.19, p = 0.004, d = 0.99) and trended towards significance in another two (Posture [Back *vs*. Side] Hands Far: $t_{(19)}$ = 1.79, p = 0.09, d = 0.68; Test–Retest Replication: $t_{(52)}$ = 1.80, p = 0.08, d = 0.49). Each study revealing a sex difference showed larger PCD scores among females than males.

General Discussion

We measured the crossed-hands deficit using a tactile temporal order judgement task. When the hands were crossed, participants were worse at judging the temporal order of two tactile stimuli. In Experiment 1, we evaluated the test–retest reliability across two sessions separated by one week. Participants showed the same magnitude of the crossed-hands deficit when measured in two sessions, supporting the measure's reliability. In Experiment 2, we demonstrated high split-half reliability across 23 previous experiments.

The crossed-hands tactile TOJ task is a reliable method of determining an individual's reliance on their internal and external reference frame. According to the conflict model, the more an individual relies on the external reference frame, the larger the crossed-hands deficit will be (Shore *et al*., 2002). Our measure for the crossed-hands deficit, the PCD score, also increases as the size of the deficit increases. Therefore, the PCD score is a good indicator of reliance on the external reference frame. Knowing that the PCD score remains stable when measured a week apart, as well as throughout a session, provides evidence that the way individuals use and rely on these reference frames also remains stable.

In Experiment 1, we replicated the typical crossed-hands deficit in two experimental sessions. We found a larger deficit among females than males. This is consistent with previous literature on the crossed-hands deficit showing a sex effect. It was hypothesized that females show a greater deficit because they are more dependent on visual information (Cadieux *et al*., 2010). However, this sex difference is not consistently observed. Out of the 23 experiments included in the split-half analysis of Experiment 2, a sex effect was only observed in three studies and showed a trend towards significance in two other studies. Cadieux and Shore (2013) suggested that a sex effect may be more likely when the external reference frame is highlighted, such as through foot pedal responses. In contrast, we found that the majority of studies showing a significant sex difference did not contain any additional manipulations to the tactile TOJ task. These experiments had the participants sitting upright and responding with hand buttons throughout. Thus, a sex effect may only be found under these standard task instructions. Unlike foot pedal responses, which can be defined in one or the other reference frame, hand button responses use both reference frames — the internal forms the basis of the physical response, but the location of the hand in the external reference frame is computed automatically. Given the present findings, the role of response demands in observing a sex effect requires more research.

Other manipulations, by emphasizing one reference frame, may allow participants to utilize a strategy (removing some of the variability between the sexes). For instance, blindfolding participants results in less emphasis on the external reference frame (Cadieux *et al*., 2013), which may cause all participants to perform more similarly on the task. Alternatively, certain manipulations may increase the inter-participant variability within each sex. If this were the case, there might be too much noise within these conditions to measure a sex difference. However, these are unlikely to account entirely for the sex difference, as these task instructions are often used as a comparison condition in many of the studies included in this split-half analysis. In the experiments which found a sex difference there were no other conditions included, which allowed for more trials under the standard task instructions. With fewer trials, there may not be enough power to observe a subtle effect. In most of the present experiments observing a sex effect, as in Cadieux *et al*. (2010), there were no independent variables other than hand posture, which provided maximal power to measure a sex effect. Given that there are large individual differences in the crossed-hands deficit, this may have provided the power required to measure a sex difference. At present, it is still not clear what conditions consistently produce a sex effect.

In Experiment 2, we investigated the split-half reliability of the crossed-hands deficit by looking at data from 23 previous experiments. Overall, we found that individual performance on the crossed-hands deficit was reliable within an experimental session. However, there was substantial variability found in the reliability scores between experiments for both males and females. When the size of the deficit was small, there was more variability in the split-half reliability. High reliability was consistently obtained in experiments showing a moderate to high crossed-hands deficit. These experiments did not contain manipulations known to reduce the magnitude of the crossed-hands deficit (e.g., blindfolding or lying down). High reliability is not always obtained with a large effect. It is possible to have a strong effect that is not reliable (MacLeod *et al*., 2010).

Certain psychiatric conditions have been hypothesized to alter the relative weighting individuals place on their internal and external reference frame. For example, patients diagnosed with eating disorders have been hypothesized to be locked in an external reference frame, that is no longer updated by new internal information (Riva, 2012). This allocentric lock hypothesis has been supported by studies using the rubber hand illusion (Eshkevari *et al*., 2012, 2014; Mussap and Salton, 2006). In the rubber hand illusion (RHI), a rubber hand is synchronously brushed along with the real hidden hand. The individual takes ownership over the rubber hand, believing that the rubber hand is their hand (Botvinick and Cohen, 1998). When asked to judge the location of their real hand, the perceived position was shifted towards the rubber hand (Botvinick and Cohen, 1998). This occurs because congruent vision and touch on the fake hand overrides proprioception of the real hand (Makin *et al*., 2008). More simply, information in the external reference frame is relied on more than information from the internal reference frame, as in the crossed-hands deficit. Individuals with eating disorders experience a larger rubber hand illusion, showing a greater reliance on external information (Eshkevari *et al*., 2012, 2014). We hypothesize that individuals with eating disorders should therefore also show a larger crossed-hands deficit. Furthermore, the crossed-hands deficit may be a useful clinical tool to assess eating disorder recovery. Since the size of the deficit remains stable over time, any changes in the deficit can be attributed to changes in the eating disorder brought about through treatment. Other clinical disorders have also shown differences in the size of the crossed-hands deficit. High-schizotypy individuals have a larger crossed-hands deficit than those with moderate or low schizotypy (Ferri *et al*., 2016); children with autism have a smaller deficit than age-matched controls (Wada *et al*., 2014); when embodiment of an arm prosthesis occurs in amputee participants, similar crossing effects are observed as in healthy controls (Di Pino *et al*., 2020). The crossed-hands deficit could be used as a tool for these clinical disorders as well.

One possible limitation to the applicability of the tactile TOJ task is the size of the deficit. Manipulations to the basic task that degrade the external reference frame, such as lying down or blindfolding, reduce the size of the crossed-hands deficit. Under such conditions, the reliability is also reduced. Therefore, it is important to use conditions that maximize the size of the deficit when high reliability is required.

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CHAPTER 3: EXPLORING REFERENCE FRAME INTEGRATION USING RESPONSE DEMANDS IN A TACTILE TOJ TASK

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Abstract

Exploring the world through touch requires the integration of internal (e.g., anatomical) and external (e.g., spatial) reference frames—you only know what you touch when you know where your hands are in space. The deficit observed in tactile temporal order judgements when the hands are crossed over the midline provides one tool to explore this integration (Shore *et al.,* 2002; Yamamoto and Kitazawa, 2001). We used foot pedals (e.g., Crollen *et al.,* 2019) and required participants to focus on either the hand that was stimulated first (an anatomical bias condition) or the location of the hand that was stimulated first (a spatiotopic bias condition). Spatiotopic-based responses produce a larger crossed-hands deficit, presumably by focusing observers on the external reference frame. In contrast, anatomical-based responses focus the observer on the internal reference frame and produce a smaller deficit. This manipulation thus provides evidence that observers can change the relative weight given to each reference frame. We quantify this effect using a probabilistic model that produces a population estimate of the relative weight given to each reference frame. We show that a spatiotopic bias can result in either a larger external weight (Experiment 1) or a smaller internal weight (Experiment 2) and provide an explanation of when each one would occur.

Introduction

Locating tactile sensations requires knowing where our hands are in space. Two reference frames are used to locate a touch: the internal, anatomical, reference frame and the external, spatial, reference frame. Responding to touch involves integrating these sources of information. The relative contribution of each reference frame can be measured using a tactile temporal order judgment (TOJ) task (Azañón and Soto-Faraco, 2007; Azañón *et al.,* 2015; Azañón *et al.,* 2016; Badde *et al.,* 2015a; Cadieux *et al.,* 2010; Cadieux and Shore, 2013; Craig and Belser, 2006; Crollen *et al.,* 2017; Crollen *et al.,* 2019; Kóbor *et al.,* 2006; Pagel *et al.,* 2009; Roberts and Humphreys, 2008; Röder *et al.,* 2004; Schicke and Röder, 2006; Shore *et al.,* 2002; Wada *et al.,* 2014; Yamamoto and Kitazawa, 2001).

This unspeeded task requires participants to report which of two vibrations applied to each of their hands occurred first, with their hands uncrossed and crossed. Consistently, the crossed-hands condition produces poorer temporal order judgement performance than the uncrossed condition. All accounts of the deficit highlight the automatic transfer of information from the internal to the external reference frame (i.e., spatial remapping; see Badde and Heed, 2016 for review). Models differ with respect to how the two reference frames are treated to determine the final stimulus location. Non-integration models suggest that the touch is located based solely on the external reference frame (Yamamoto & Kitazawa, 2001). The conflict model highlights confusion caused by opposing response requirements for the two locations (i.e. internal versus external; Shore *et al.,* 2002). The integration model builds upon the conflict model by defining the conflict as differential weights placed on the two reference frames in determining the location of the final percept (Badde *et al.,* 2015a). Both the conflict and integration models predict that emphasising the external reference frame will increase the size of the deficit whereas the non-integration model makes the opposite prediction.

One way to bias perception to one reference frame or the other is to emphasize the coordinate system within which the observer must respond (Cadieux and Shore, 2013; Crollen *et al.,* 2019; Shore *et al.,* 2006). For example, by using foot pedals instead of hand buttons to respond, it is possible to place emphasis on either the internal or the external reference frame. The anatomical response demand (i.e., lift the toe corresponding to the hand that was stimulated first) preserves the left–right coding of the vibration and response, making it more internally based. In contrast, the spatiotopic response demand (i.e., lift the toe directly underneath the stimulated hand) requires remapping the response from the hand surface to the corresponding hemispace in the external reference frame. All studies using the response demand manipulation implicitly assume that a tactile stimulus must first be localized to the hand before a response can be made. Critically, response demands are presumed to affect the ability to localize the tactile stimulus on the hand. The anatomical response demand ties the response to the body (right hand, right foot) biasing the localization towards the internal reference frame which results in a smaller deficit (Cadieux and Shore, 2013; Crollen *et al.,* 2019; Shore *et al.,* 2006). In contrast, the spatiotopic response demand ties the response to the space around the body (left side of space, left foot) biasing the localization to the external reference frame, therefore increasing the deficit.

Quantifying the size of the deficit has typically used behavioural measures (such as the slope of a psychometric curve, or proportion of correct responses), and inferred the weight given to each reference frame by a change in these measures. The recent development of a probabilistic model (Badde *et al.,* 2015a) affords us the potential to quantify the response demand effect using estimated reference frame weights. Accordingly, we sought to replicate the response demand effect (larger crossed-hands deficit with a spatiotopic response demand) and apply the probabilistic model (Badde *et al.,* 2015a) that maps behaviour onto weights for the internal and external reference frames.

Measuring the crossed-hands deficit

Multiple measures of the crossed-hands deficit exist. Early work examined the difference in the slope of the psychometric curves for crossed and uncrossed postures (e.g., Shore *et al.,* 2002). The probit analysis converts the proportion of right-first responses into a z-score and then fits a straight line to the z-score across stimulus onset asynchrony (SOA). This method allows for separate analysis of the uncrossed and crossed performance, and indexes the crossed-hands deficit as the difference in the slope measures. The same analysis can be used to derive a just noticeable difference (JND). The JND is an indicator of the time difference required between the two tactile stimuli to accurately assess their temporal order. These analysis techniques have two shortcomings. First, at longer SOAs, performance reaches ceiling making the measure less sensitive at detecting performance differences. Second, in the crossed posture, the slope can approach zero or be negative, which can produce unreasonable extrapolation of the data. In terms of the response demand manipulation (Crollen *et al.,* 2019), the uncrossed posture produced similar slopes with both demands. In the crossed posture, the spatiotopic response demand produced significantly shallower slopes (i.e., worse performance) than the anatomical response demand. This larger crossed-hands deficit in the spatiotopic response condition was attributed to a greater reliance on the external reference frame when localizing the tactile stimulus, and supported the conflict model of the deficit.

Another measure, used more recently, is the proportion correct difference (PCD) score (Cadieux *et al.,* 2010). To calculate the PCD score, the difference in the proportion of correct responses between crossed and uncrossed performance is computed at each SOA, and then summed across SOA. There are several advantages of the PCD score over other measures (i.e., slope or JND). For instance, both the uncrossed and crossed-hands performance are combined into a single score that indexes the magnitude of the deficit. Additionally, the measure is model free—no assumptions are made about the underlying distribution of responses or the shape of the psychometric curves. With this measure, a larger deficit was found when participants used a spatiotopic response compared to an anatomical response (Cadieux and Shore, 2013).

These measurements (e.g., slope, JND and PCD) are mostly atheoretical. They provide a description of the data, but not how the underlying theoretically construed reference frame weights change under different task demands. Recently, a probabilistic model was developed to estimate the relative weight placed on the internal and external reference frame during a crossed-hands tactile TOJ task (Badde *et al.,* 2015a). The researchers tested two models for the crossed-hands deficit: the integration model and the non-integration model. The integration model explained the crossed-hands deficit as a difficulty integrating the internal and external reference frame in the crossed posture. In contrast, the non-integration model explained the deficit as the result of a difficulty remapping from the internal to the external reference frame. The integration model better accounted for their data. The model estimates a pair of internal and external weights that most likely created both the uncrossed and crossed psychometric curves.

The model assumes the weights are stable within an individual across time; therefore, changing hand position from uncrossed to crossed should not change the weights. Based on these two weights—an internal and an external—the model produces psychometric curves for the uncrossed and crossed postures. In the uncrossed condition, the reference frames provide congruent information, so the model takes the sum of the weights to compute the slope of the curve. In the crossed-hands condition, the two reference frames conflict, with the external reference frame providing incorrect information. As a result the model takes the difference between the weights to compute the slope of the curve; the more an individual relies on the external reference frame when resolving the conflict, the shallower the slope (i.e., the worse the performance will be). Using this model, performance in the two conditions can be fit simultaneously to the weights placed on the two reference frames. Critically, this measure is theoretical as it is based on the integration/conflict model of the deficit (Badde *et al.,* 2015a; Shore *et al.,* 2002).

Although the weights are assumed to remain constant across postural changes, task demands, including instruction, can lead to a change in the weights (Badde *et al.,* 2015a). In addition to the typical TOJ task, Badde et al. (2015a) used two other tasks. The first touch localization (FTL) task asks participants to indicate, in a speeded fashion, the hand that received the first of two vibrations and ignore the second vibration. The only difference between the TOJ and FTL task is the instruction to ignore the second vibration and respond as quickly as possible. The third task was a single touch localization (STL) task, where only one tactile stimulus was administered and participants had to indicate which hand was vibrated. Each task was completed in a crossed and an uncrossed posture. In comparison to the tactile TOJ task, both the FTL and STL showed an increased internal weight and a decreased external weight. The weights remained stable within an individual, but simply by changing the instructions provided during the tasks, the emphasis on each reference frame was altered.

Scope of the present study

The present study had two main goals. First, we wanted to confirm whether manipulating response demands would influence the magnitude of the crossed-hands deficit. Second, we applied a probabilistic model to these data to gain insight into the response demands manipulation. Each participant completed a crossed-hands tactile TOJ task under both the anatomical and spatiotopic response demand. To compare the size of the crossed-hands deficit across the two conditions an analysis was conducted on PCD scores. Based on previous studies, we predicted that the use of an anatomical response demand would result in a smaller crossed-hands deficit, whereas a spatiotopic response demand would show a larger crossed-hands deficit. This larger deficit would be revealed by a shallower slope in the crossed posture and a larger PCD score in the spatiotopic response demand, compared to the anatomical demand.

We employed probabilistic models to estimate how response demands influenced the weights placed on the internal and external reference frame. First, we used a participant-specific model. This provided an estimated internal weight and external weight for each participant in each response demand condition individually. Next, we implemented a hierarchical model that assumed participants were affected equivalently by the response demand manipulation; we used this model to estimate the internal and external weights for the population as well as weights for each participant. We predicted that the larger deficit in the spatiotopic response demand would be explained by a decrease in the internal weight, by an increase in the external weight, or by a combination of the two. All options would result in decreased accuracy in the crossed-hands posture, with minimal changes occurring to the uncrossed posture.

Experiment 1

Methods

Participants

Twenty right-handed participants (10 males; average age: 19.3 years), were recruited from the McMaster University subject pool. All had normal or corrected-to-normal vision, were naïve to the purpose of the experiment, and provided written informed consent prior to participation. All procedures were approved by the McMaster Research Ethics Board and complied with the tri-council statement on ethics (Canada).

Apparatus and Stimuli

Throughout the experiment, participants were seated at a table (height of 73.7 cm) and placed their hands 18 cm apart. Placed in each hand was a small wooden cube with a Plexiglas top; there was a 2 cm hole in the top for participants to place their thumbs on the vibrators, which were mounted under the Plexiglas. Vibrations were delivered with an Oticon-A (100 Ohm) bone conduction vibrator (width: 1.6 cm, length: 2.4 cm), that was driven by an amplified 250 Hz sine wave, set by the experimenter to be comfortable and clearly suprathreshold. Mounted beneath the vibrators were response buttons to be pressed by the thumbs on timeout trials. Two foot pedals were positioned beneath the toes of each foot to collect responses. All stimulation was controlled by a set of reed-relays connected to the parallel port of a DELL Dimension 8250 running Windows XP software. Matlab was used to administer the stimulation and collect responses. Participants wore over the ear headphones, connected to an iPod Touch, playing white noise during the experiment to mask the sounds produced by the tactile vibrators.

Procedure

Participants held one wooden cube in each hand, with their thumbs in contact with the vibrators. Each trial began 800 ms after the participant's previous response. Two 20 ms vibrations, one to each thumb, were delivered separated by one six possible stimulus onset asynchronies (SOA): ±400, ±200, ±50 ms, where negative SOAs indicate the vibration was to the left hand (anatomical instructions) or hemispace (spatiotopic instructions) first. The task required participants to determine which of two vibrations occurred first under two different response demands. Participants responded by lifting the foot associated with the appropriate response demand. In the anatomical response demand condition, participants were instructed to "lift the foot pedal corresponding with the hand that was vibrated first." If the left hand received the first vibration they should lift the left toe (same for right hand and right toe). In the spatiotopic response demand condition, participants were instructed to "lift the foot pedal directly underneath the hand that was vibrated first." If the left hemispace received the first vibration they should lift their left toe (same for right hemispace with right toe). If no response was made within three and a half seconds of the second vibration, the trial timed out. In this situation, both vibrators vibrated three times, and participants pressed down on both vibrators to activate the buttons mounted underneath. These trials and trials where participants responded in less than 100 ms were removed before analysis. This resulted in the removal of 23 trials across all participants. The next trial began as soon as the participant pressed down on both foot pedals.

Participants initially completed two practice blocks of 18 trials each. During the first practice block, their hands were uncrossed; during the second practice block, their hands were crossed over the midline. The experimenter remained in the room for the practice trials in order to provide feedback and answer any questions. Participants subsequently completed 12 experimental blocks of 60 trials. For one half of the experiment, participants used the anatomical response demand and for the other half the spatiotopic response demand. Hand position was altered every three blocks between crossed and uncrossed positions. The starting response demand and hand position were counterbalanced across participants.

Analysis

The crossed-hands deficit was assessed using PCD scores (the sum of the difference between the proportion of correct responses in the crossed and uncrossed postures at each SOA; see Cadieux *et al.,* 2010; Heed and Azañón, 2014). The PCD scores were submitted to a 2x2 ANOVA with response demand (anatomical vs. spatiotopic) as a within-subject factor and sex (male vs. female) as a between-subject factor. We tested whether the crossed-hands deficit was significantly different from zero in each response demand using one-sample *t*-tests.

The above analysis provides an index of overt behaviour. In contrast, reference frame weight represents a theoretical construct that must be inferred from the data. We first used the equations outlined by Badde et al. (2015a) to derive psychometric curves from the weights. We took a participant-specific approach by using a maximum likelihood estimation to determine the combination of internal and external weights that best accounted for each individual participant's data. An internal and external weight combination forms a hypothesis, which can be used to generate psychometric curves, p(t), the probability of a right-first response as a function of SOA (t) for the crossed and uncrossed postures (Eq. 1). Each curve was a logistic function with slope parameter, θ, calculated from a linear combination of the internal and external weights (ω). With the hands uncrossed, the external response was congruent with the internal response. When the hands were crossed, the external response was incongruent with the internal response. Thus, for the uncrossed posture, θ is the sum of the internal and external weights, whereas for the crossed posture, θ is the difference between the weights. To compute the likelihood of the hypothesis (H = $\omega_{int\,i},\ \omega_{ext\,i}$), the probability of the participant's responses at each SOA was calculated from a binomial distribution with expected value p(t). Each participant's internal and external weights were fit to the participant's uncrossed and crossed data simultaneously, reflecting the assumption that the weights do not change across these postures (see Badde *et al.,* 2015a). Using a brute force algorithm, we discretized each participant's internal and external weights into bins of 0.5 spanning the range 0 to 40, calculated the log-likelihood (Eq. 2) at each combination of internal and external weights for each participant, and read out the maximum likelihood estimate. Estimates for the weight parameters were determined separately for the spatiotopic and anatomical response demands.

Eq. 1

$$p(t) = \frac{1}{1 + e^{-\theta t}}$$

Where:
$\theta_{uncrossed} = \omega_{int} + \omega_{ext}$
$\theta_{crossed} = \omega_{int} - \omega_{ext}$
t in {±400, ±200, ±100, ±50}

Eq. 2

$$\log(p(d_{i\,rd}|\omega_{int\,i\,rd}, \omega_{ext\,i\,rd})) = \sum_{t} r_{t\,i\,rd} \cdot \log(p_{i\,rd}(t)) + l_{t\,i\,rd} \cdot \log(1 - p_{i\,rd}(t))$$

Where:
$d_{i\,rd}$ = the data from participant i for the given response demand
$\omega_{int\,i\,rd}, \omega_{ext\,i\,rd}$ = the hypothesized internal and external weight values for each response demand
$r_{t\,i\,rd}$ = number of right-first responses
$l_{t\,i\,rd}$ = number of left-first responses (i.e., the number of trials – number of right first responses)
t in {±400, ±200, ±100, ±50}

The participant-specific model assumed that participants' data were statistically independent of one another. We next implemented a hierarchical model that encoded the arguably more plausible assumption that participants had similar weights and were affected equivalently by the response demand manipulation. For this purpose, we modified the hierarchical model proposed by Badde et al. (2015a). The hierarchical model encodes the assumption that the response-demand manipulation will have the same effect on all participants. Each participant's weights in one condition (we used the anatomical response demand) were multiplied by a population task parameter to obtain the weights in the other condition (the spatiotopic response demand).

A Markov Chain Monte Carlo (MCMC) sampler using a Metropolis-Hastings algorithm, implemented in R, was used to estimate the task parameters and the population means and standard deviations for the internal and external weights (see Badde *et al.,* 2015a). We assumed that population distributions of internal and external weights were approximated by truncated Gaussian distributions (limits = 0, ∞), with unknown means and standard deviations. These population distributions served to generate priors for individual participant weights.

The MCMC procedure provides an approximation for the posterior distribution of the model parameters. This is accomplished by comparing the posterior probability of the current location in parameter space (which we refer to as a hypothesis) with the posterior probability of a proposed hypothesis. The proposed hypothesis is selected by randomly choosing a value from a gaussian distribution with a mean of the current value and a proposal standard deviation (specified before starting the simulation). If the proposed hypothesis has a higher posterior probability, then the simulation accepts the proposed hypothesis. A new proposed hypothesis is then generated from this location. If the current hypothesis has a greater probability than the proposed hypothesis, the probability of accepting the new hypothesis is computed as the ratio of the probability of the proposed hypothesis to that of the current hypothesis.

The parameter set for the hierarchical model consisted of 46 parameters, 6 population-level parameters and 40 participant-level parameters. The 6 population-level parameters were: the population mean internal and external weights ($\mu_{internal}$ and $\mu_{external}$) and standard deviations ($\sigma_{internal}$, $\sigma_{external}$) in the anatomical response demand, and an internal and external weight task context parameter ($\delta_{internal}$ and $\delta_{external}$). All population parameters had strictly positive, uniform hyperpriors. The standard deviation parameters represent the model's estimation of the spread of the individual weights. The task context parameters were multiplied to the respective anatomical response demand mean weights to obtain the spatiotopic response demand weights. Each of the 20 participants' data were fitted with two parameters: an internal and external weight ($\omega_{internal}$ and $\omega_{external}$) for the anatomical response demand. Given that the response demand manipulation was assumed to affect all participants equivalently, the weights for the spatiotopic response demand were calculated by multiplying each participants' anatomical response demand weights by the population task context parameters. For instance, if the population external task context parameter was 2, then the external weight in the spatiotopic condition for all participants would be twice as large as their external weight in the anatomical response demand. One hypothesis generated four psychometric curves for each participant—two for each response demand, and two for each hand posture.

Eq. 3

$$p(H|D)$$

$$\propto \prod_i p(d_i|\,\omega_{int\ i},\omega_{ext\ i})_i \prod_i p(\,\omega_{int\ i}\,,\omega_{ext\ i}|\mu_{int,}\mu_{ext},\delta_{int,}\delta_{ext},\sigma_{int},\sigma_{ext})p\left(\mu_{int,}\mu_{ext},\delta_{int,}\delta_{ext},\sigma_{int},\sigma_{ext}\right)$$

The posterior probability of a hypothesis, H, given the data set (D) was calculated by Bayes' formula (Eq. 3). The probability of each participant's data (d_i) given the participant's hypothesized weights was multiplied by the prior probability of those weights. The probability of each participant's data given the weights was calculated using the binomial formula as described in Eq. 2. To avoid underflow errors, Eq. 3 was evaluated by calculating the logarithms of all likelihoods and priors, and then summed across participants. The resulting log-likelihood was exponentiated prior to the probability comparison.

Five Markov chains with 250,000 samples each were run, with the first 50,000 samples removed as the burn-in period. The convergence metric, $\hat{R}$, was close to 1, indicating that the chains had converged (Brooks and Gelman, 1998). Each chain was initialized with random values for each of the 46 parameters. Future parameter values were chosen from a Gaussian distribution with a mean centred on the previous parameter value and proposal standard deviations of 0.14 for the weights, and 0.06 for the population standard deviations, and 0.01 for the task context parameter. All runs had acceptance rates between 25 and 26 percent, and $\hat{R}$ between 0.98 and 1.05 (see supplemental materials).

A posterior predictive model check was conducted to evaluate the goodness of fit of the model (Gelman *et al.,* 2020). During one Markov chain, simulated data were created for the chosen hypothesis on each MCMC trial using the hypothesized participant weights and population task parameters. Using the simulated data, we looked at two measures of goodness of fit: the average PCD score (in the anatomical response demand, spatiotopic response demand, and the difference between the spatiotopic and anatomical response demands), and the correlation between the PCD scores in the anatomical and spatiotopic response demands. The average PCD score would determine whether the model provided a good fit for the overall data; the correlation between conditions would be an indicator of the model's fit for individual participants. The response demands manipulation is expected to bias all participants' weights to either the internal or the external reference frame. For this reason, we might expect a systematic difference in participants' anatomical and spatiotopic response demand PCD scores. This should result in a correlation between the scores from the two response demands. Indeed, this is built into the model by having the weights for every participant in the anatomical response demand altered by the same magnitude when calculating the weights for the spatiotopic response demand. The PPMC on the correlation would therefore test whether the model and the observed data agree on this relation between participants.

Results

PCD Scores

PCD scores were calculated separately for each participant in both the anatomical and spatiotopic response demand trials (see Fig. 1). PCD scores were significantly smaller (i.e., a smaller crossed-hands deficit) using the anatomical response demand than the spatiotopic response demand (Anatomical: M = 1.00, SD = 0.51; Spatiotopic: M = 1.58, SD = 0.84; $F_{(1,18)} = 8.57, p = .009, \eta_g^2 = .16$). There was no significant difference in performance between males and females (Male: M = 1.15, SD = .69; Female: M = 1.42, SD = .79; $F_{(1,18)} = 1.24, p = .281, \eta_g^2 = .04$), and no significant interaction between response demand and sex ($F_{(1,18)} = .70, p = .42, \eta_g^2 = .02$). One-sample *t*-tests confirmed the presence of a crossed-hands deficit for both the anatomical ($t_{(19)} = 8.67$, $p < .001$, $d = 1.94$) and spatiotopic ($t_{(19)} = 8.44$, $p < .001$, $d = 1.89$)

response demand. Given the lack of a sex difference in this data set, all further analyses will not include sex as a factor.

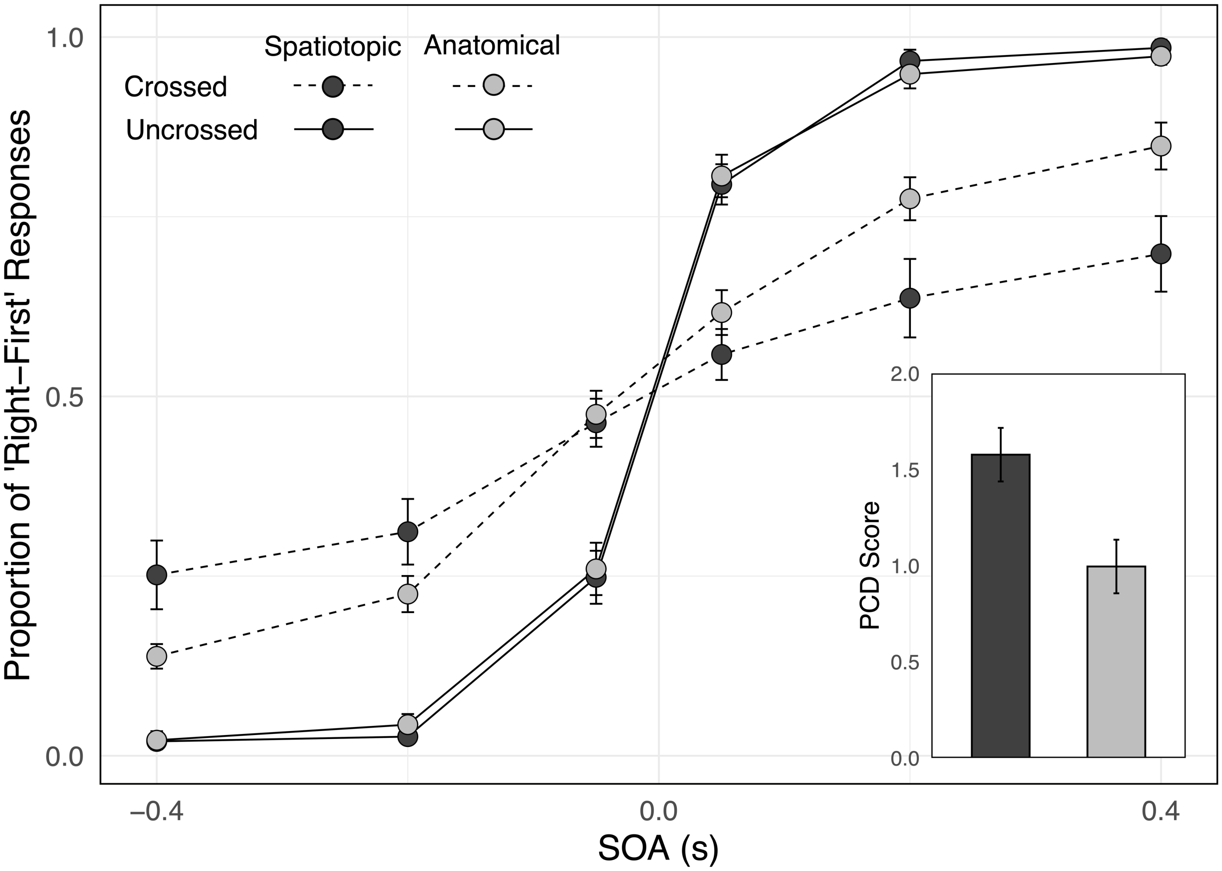

Figure 1: Proportion of right (hand for the anatomical condition, hemispace for the spatiotopic condition) first responses across stimulus onset asynchrony (SOA) from twenty participants (10 males) for both the crossed and uncrossed hand postures under both response demand conditions. Inset bar graph represents the average PCD score for each response demand. Error bars represent standard error corrected for a within-subject design (Cousineau, 2005; Morey, 2008).

Participant-Specific Model

We computed the maximum likelihood weight pair for each participant by calculating the probability of the data given each hypothesized weight pair (see Fig. 2 for the joint likelihoods of all tested weight pairs, see Fig. 3A for maximum likelihood weight pair). Based on these weights, we calculated each participant's expected data (Fig. 4). The expected data fit well with the participants' data ($R^2 = 0.93$, $p < .001$), suggesting the internal and external weight combination successfully captures each participant's crossed and uncrossed performance. Based on the most likely weights, we computed an expected PCD score for each individual, which were highly correlated with their actual PCD scores (Fig. 3B; $r = .97$, $p < .001$). Finally, we computed an average internal and external weight for the different response demand conditions (Fig. 3C). Overall there was a higher weight placed on the internal reference frame ($F_{(1,18)} = 71.3$, $p < .001$, $\eta_g^2 = .1$), and no significant difference in the overall weight value between the response demands ($F_{(1,18)} = .39$, $p = .54$, $\eta_g^2 = .003$). There was an interaction between the reference frame and response demand, ($F_{(1,18)} = 6.23$, $p = .02$, $\eta_g^2 = .006$) such that the anatomical response demand appeared to place less weight on the external reference frame ($t_{(19)} = 1.53$, $p = .14$, $d = -.05$) than did the spatiotopic response demand, while the internal weights between the two response demands was not significantly different ($t_{(19)} = -0.30$, $p = .77$, $d = .28$).

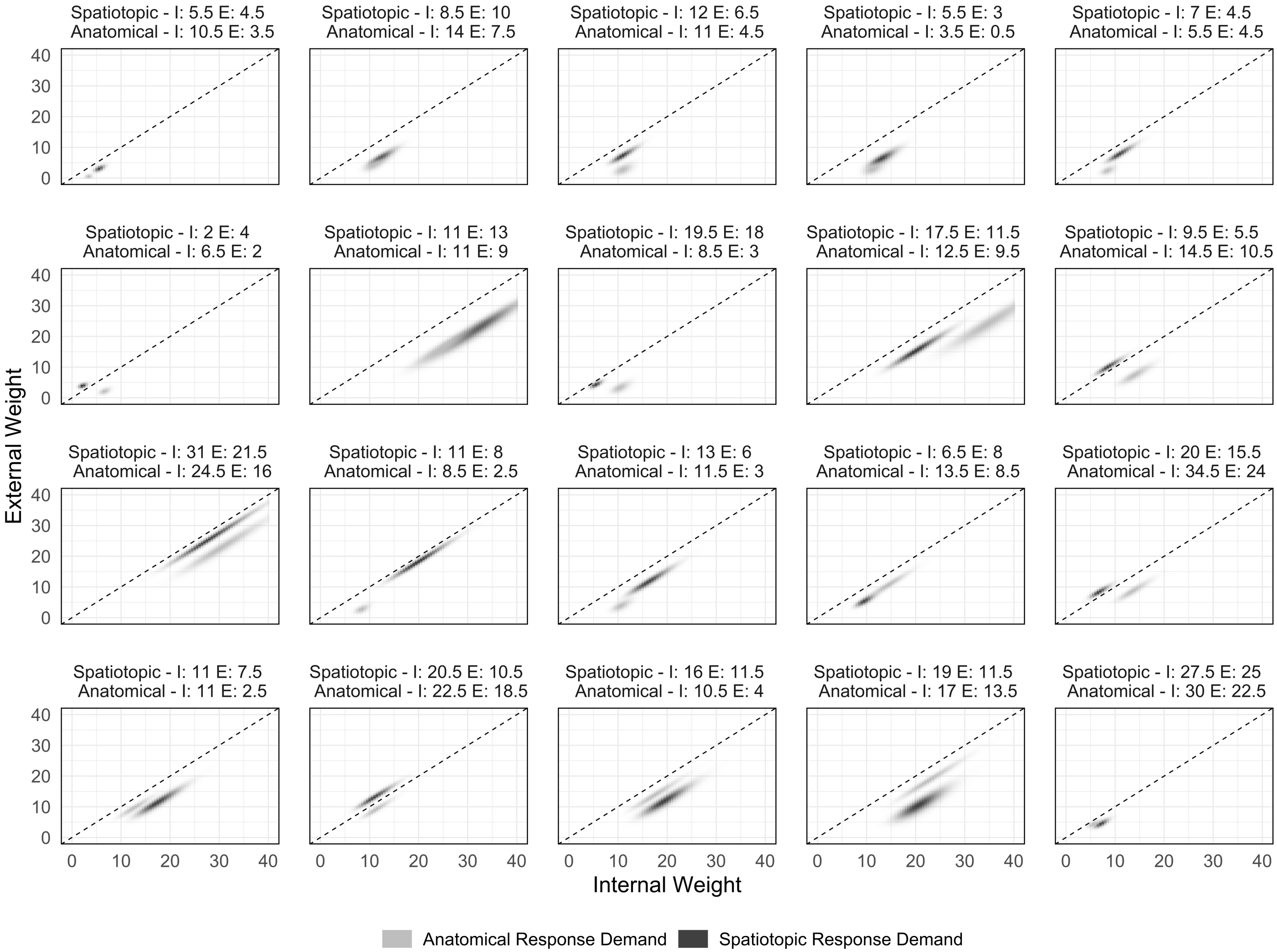

Figure 2: Joint likelihood distributions for the internal and external weights for each participant. The darker the point the greater the likelihood of the weight pair.

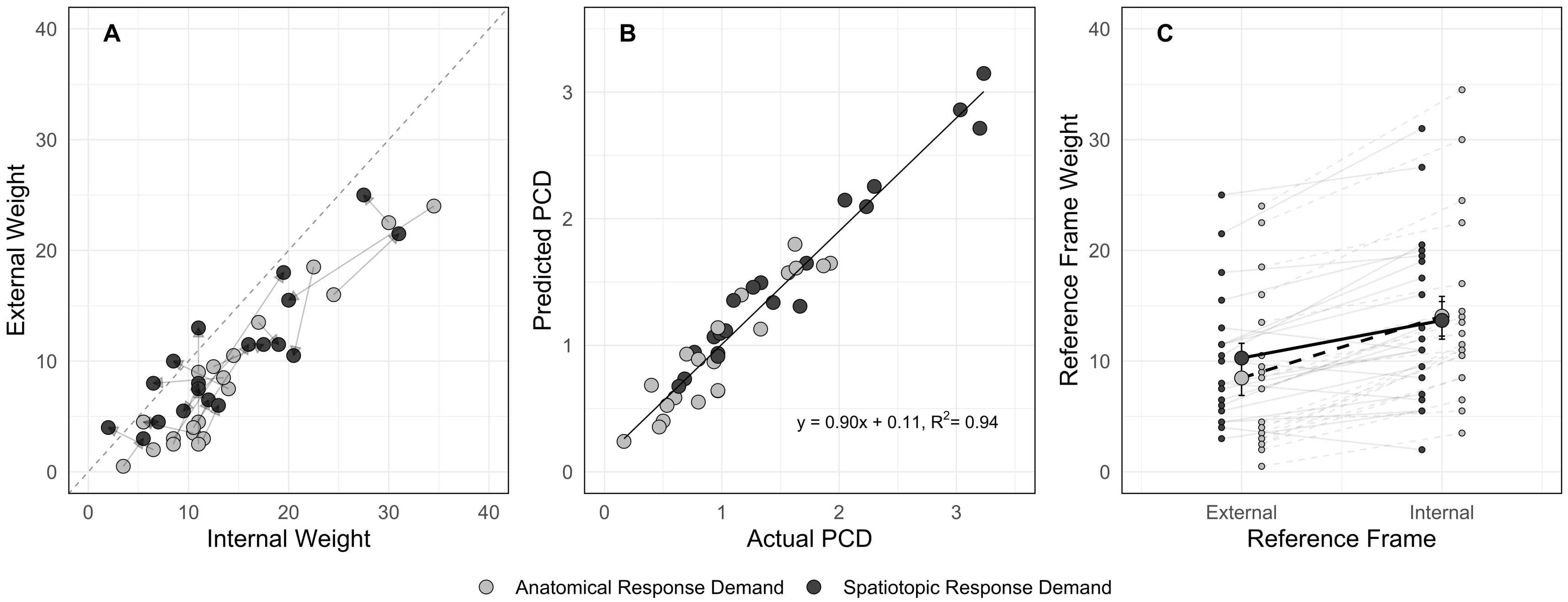

Figure 3: (A) The combination of internal and external weights that best fit the data, for each of the response demands, for each participant (connected by a line). (B) Comparison of the PCD score obtained from the participants' raw data to the PCD score calculated from their most likely weights. (C) Overall internal and external weight in each response demand. This was found by taking the average of each participants' weights. Error bars represent standard error of the mean corrected for within-subject comparisons. The smaller circles represent the weights from individual participants.

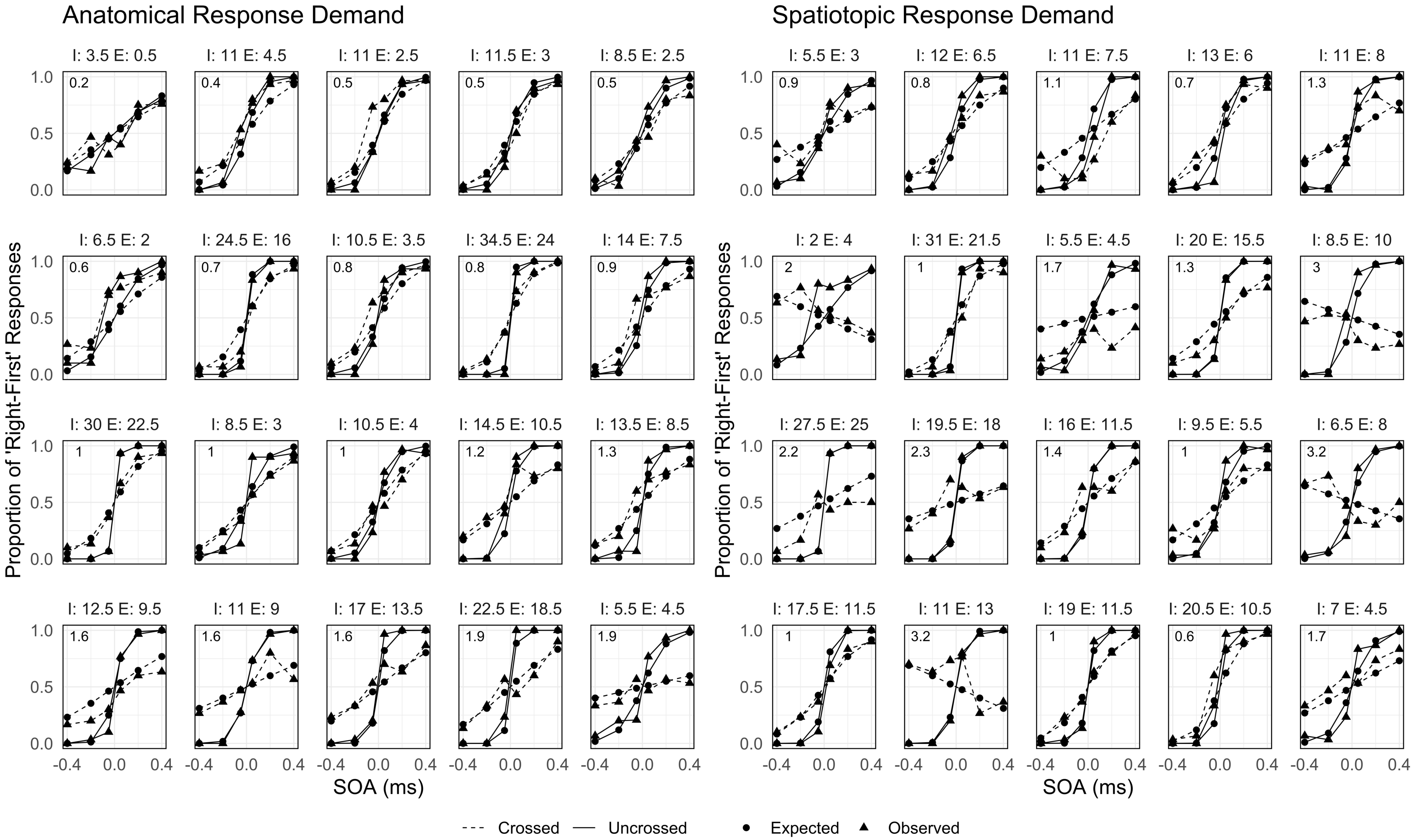

Figure 4: Individual participant performance. The triangles represent the participants observed data, and the circles represent the expected performance calculated from their most likely weights. The numbers on top of each figure represent the participant's maximum likelihood estimated internal and external weights. The number in the top left of each figure is the participant's actual PCD score. The graphs are sorted by PCD score in the anatomical condition.

Hierarchical Model

The population internal and external weights were calculated for the anatomical response demand by taking the mean values across all 5 Markov chains. The weights in the spatiotopic response demand were calculated by taking the weights in the anatomical response demand on each trial, and multiplying it by that trial's task parameter, then averaging across the 5 Markov chains (Fig. 5C). This resulted in an internal population weight of 11.05 [95 CI: 7.89, 13.73] with a population standard deviation of 5.85. The external population weight was 4.87 [95 CI: 1.43, 7.16] with a population standard deviation of 4.16 for the anatomical condition. The population internal task parameter was 1.12 [95 CI: 1.03, 1.23] and external task parameter was 1.62 [95 CI: 1.42, 1.87], resulting in an internal weight of 12.40 and external weight of 7.87 for the spatiotopic response demand. The confidence intervals for the task parameters did not include 1, indicating an increase in both reference frame weights in the spatiotopic condition.

For each participant, we estimated the internal and external weights for each condition by taking posterior means—i.e., the average value of each weight parameter across the Markov chains (Fig. 5A). Using the posterior mean weight, we computed expected data for each participant (Fig. 6). The expected data provided a good fit for the participants' data ($R^2 = 0.9$, $p < .001$). The expected PCD scores were correlated with the participants' actual PCD scores ($r = .85$, $p < .001$; Fig. 5B). When compared to the weights obtained from the participant-specific approach (Fig. 7) these weights showed a strong correlation for the internal weight ($r = .89$, $p < .001$) and external weight ($r = .77$, $p < .001$).

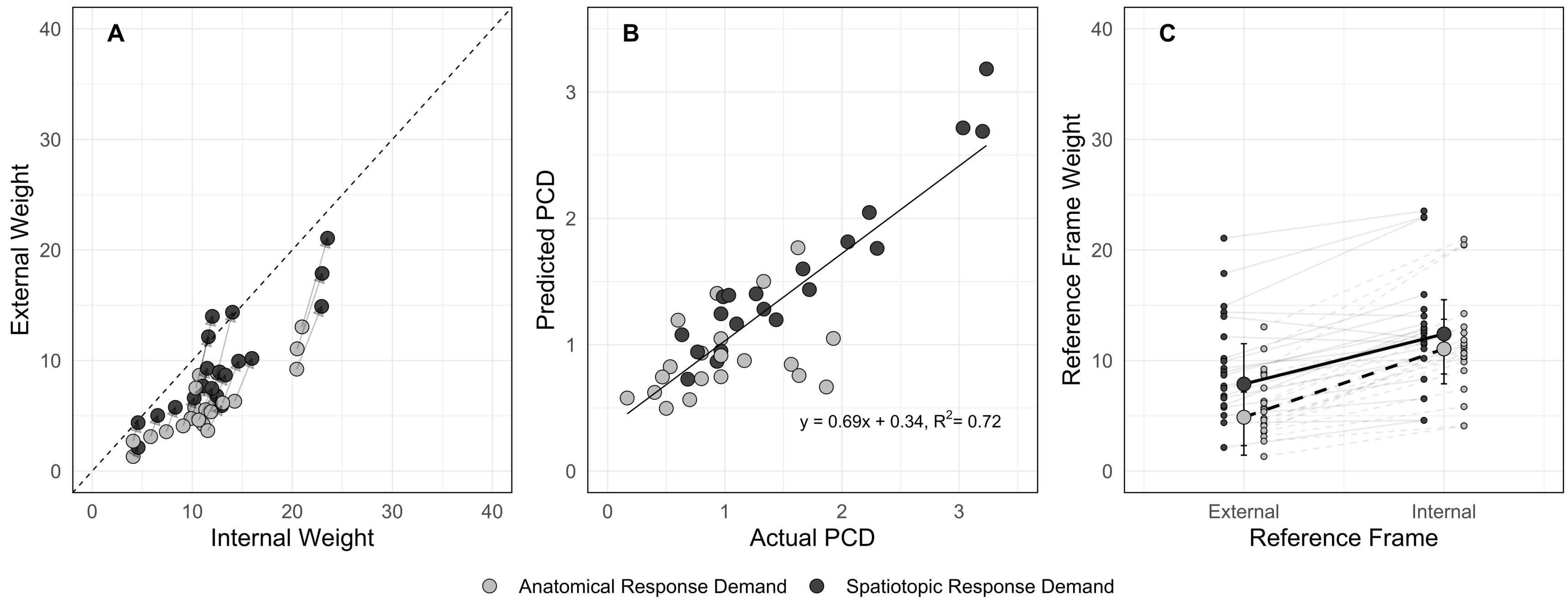

Figure 5: (A) Most likely weight for each participant in each response demand. The arrow connects the weights for each participant. (B) Comparison of the PCD score obtained from the participants' raw data to the PCD score calculated from the most likely weights. (C) Overall population internal and external weight in each response demand. Error bars represent 95 percent credible intervals. The small circles represent individual participant weights.

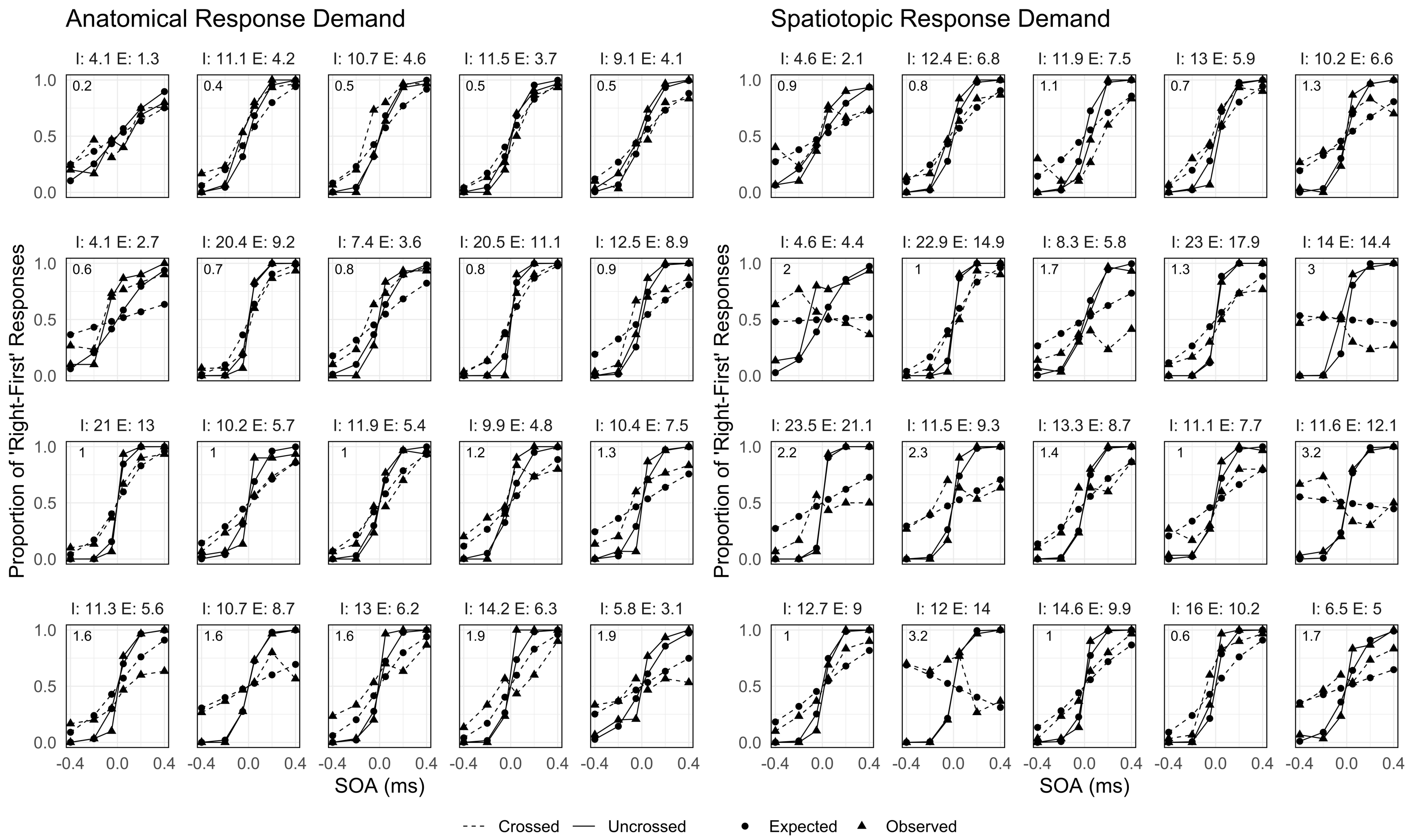

Figure 6: Individual participant performance. The triangles represent the participants' observed data, and the circles represent the expected performance calculated from their most likely weights in the hierarchical model. The numbers on top of each figure represent the participant's maximum likelihood estimated internal and external weights. The number in the top left of each figure is the participant's actual PCD score. The graphs are organized by PCD score in the anatomical condition.

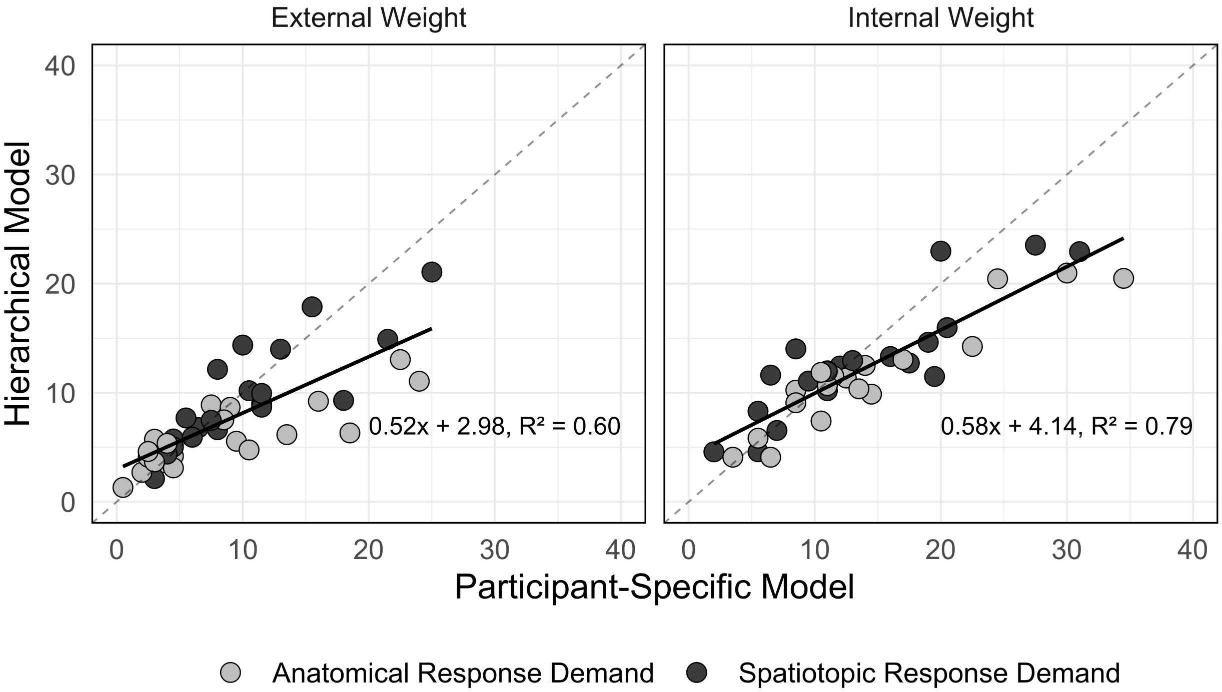

Figure 7: Comparison of the weights obtained from the participant-specific model and the hierarchical model. There was a strong correlation obtained for both the internal weight and external weight.

A posterior predictive model check (PPMC; Fig. 8) revealed that the mean from the posterior PPMC distribution matched closely with the average PCD score for each condition, meaning the model successfully captures the average PCD scores of the participants for each condition. However, the model does not reproduce the correlation between PCD scores from the two response conditions. The posterior mean of the PPMC distribution suggests a strong positive correlation between the anatomical and spatiotopic conditions (*r* = .76); however, this correlation is not observed in the raw data (*r* = .215, *p* = .36).

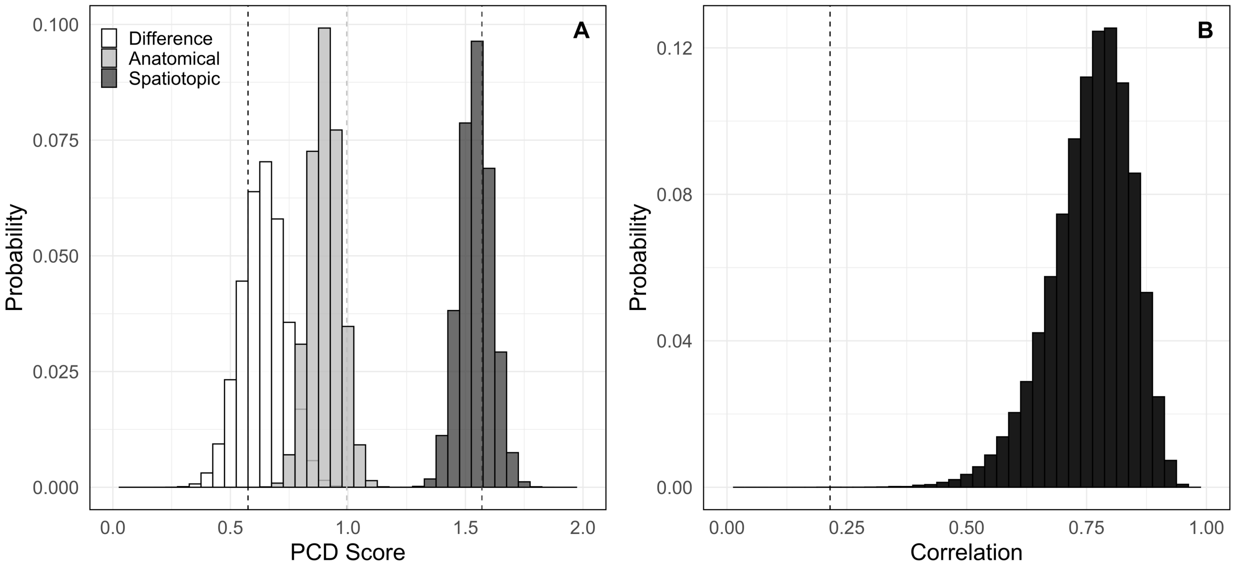

Figure 8: (A) Posterior predictive distributions of PCD scores for the anatomical and spatiotopic conditions, and the difference between the spatiotopic and anatomical conditions. (B) Posterior predictive distribution of the correlation between the anatomical and spatiotopic PCD scores. The vertical dotted lines represent the observed values from the raw data from Experiment 1.

Discussion

Overall, we observed a larger crossed-hands deficit when using a spatiotopic response demand compared to an anatomical response demand. This was evident from the proportion of right-first responses, where the crossed-hands condition showed closer to chance performance under the spatiotopic response demand. Larger PCD scores were also observed in the spatiotopic response condition. Both behavioural analyses support our initial hypothesis of a larger deficit when the external reference frame was emphasised.

A probabilistic model was used to estimate the weights placed on the internal and external reference frame in each response demand. Using a participant-specific approach, we determined the internal and external weights for individual participants. Overall, a spatiotopic response demand resulted in a greater external weight and a slightly lower internal weight than the anatomical response demand. A hierarchical model showed that, at the population level, the internal weight increased slightly with the response demand manipulation, while the external weight was 1.5 times greater in the spatiotopic response demand. This was similar to the changes observed in the participant-specific approach. The hierarchical model more accurately reflects the true relation between the conditions, as the population parameter estimates are based on more information than just an average of the participant values.

The participant-specific model used a maximum likelihood technique to determine the probability of the data given all combinations of internal and external weight pairs. By looking at the weight pairs with higher likelihoods, it is evident that the difference between the internal and external weights remains constant. Given that the crossed-hands curve is estimated as the difference between the weights, the crossed posture seems to constrain the weights that are plausible. In contrast the uncrossed posture is fitted based on the sum of the weights. This posture typically results in steeper slopes, resulting in many sums that can give rise to similar psychometric functions.

The hierarchical model provided a good fit for the participants' data, but not as good a fit as the participant specific model. This is expected of a hierarchical model, because in such a model the population parameters relate the participants to one another, refining the inference about each participant based on the data from all the others. Consequently, the inference regarding the true parameter values of each participant depends on more information than merely the data from that one participant. The hierarchical model assumed that the response demands manipulation would affect each participant to the same degree. Therefore, the participants' weights in the anatomical response demand were multiplied by the corresponding population task parameter to obtain their weights for the spatiotopic response demand. Provided that this model's structure realistically reflects the effect of the response demand manipulation, parameter estimates from the hierarchical model will be more robust than the participant-specific estimation against noise in the individual participant's data.

Posterior predictive model checks revealed the average PCD score of the model was similar to the average PCD score from the observed data. This would suggest that the hierarchical model structure realistically captures that aspect of the observed data. In contrast, PPMC applied to the correlation between the anatomical and spatiotopic response demand PCD scores reveals a poor fit with the observed data. In the observed data there is a small positive (non-significant) correlation between the two response conditions, while the hierarchical model consistently predicts a moderate to strong positive correlation. The strong correlation in the hierarchical model is likely a biproduct of the population task parameter. Given that the weights for every participant in the spatiotopic response demand are multiplied by the same values, this is perhaps predicting a cleaner relation between the two response conditions than actually exists. Because the external task parameter is greater than the internal task parameter, the model requires there to be a larger crossing effect in the spatiotopic response demand than the anatomical response demand. While this is the case for the majority of participants, five participants showed the opposite effect. It is likely that these few participants are driving the low correlation in the observed data. To test this, we checked the magnitude of the correlation with these few participants removed ($r = 0.84$, $p < .001$), and it is similar to the correlation predicted by the PPMC. It is possible that these participants are performing the task using a different strategy, and these participants might be better fitted with a different model. Future studies could explore additional model variants that can accommodate individual differences in the relation between response conditions.

Experiment 2

Next, we wanted to replicate the model results using a different data set. This data set was chosen because of its larger size and more homogeneous sample (only right-handed females). The identical task to that used in Experiment 1 was completed as part of a larger experiment investigating the relation between body image, the rubber hand illusion, and the crossed-hands deficit. For the purpose of this paper, we will only be focusing on the crossed-hands tactile TOJ portion.

Methods

Participants

Forty-seven right-handed, female participants (average age: 18.4 years), were recruited from the McMaster University subject pool. Four participants were removed for not following the task instructions. All had normal or corrected-to-normal vision, were naïve to the experiment, and gave written informed consent before participation. All procedures were approved by the McMaster Research Ethics Board and complied with the tri-council statement on ethics (Canada).

Apparatus and Stimuli

Apparatus and stimuli were identical to Experiment 1.

Procedure

The procedure was identical to Experiment 1, except 2 additional SOAs were tested (±100ms). A total of 222 time-out and premature trials were removed.

Analysis

The analyses were identical to Experiment 1, except the ANOVA on PCD score did not include the between-subject factor of sex.

Results

PCD Scores

PCD scores were calculated separately for each participant in both the anatomical and spatiotopic response demand (see Fig. 9). PCD scores were significantly smaller in the anatomical response demand than the spatiotopic response demand (Anatomical: M = 1.00, SD = 0.89; Spatiotopic: M = 1.60, SD = 0.86; $t_{(43)} = 4.45$, $p < .001$, $d = .68$). The crossed-hands deficit was reduced by the use of an anatomical response demand. One-sample *t*-tests revealed a crossed-hands deficit in both the anatomical ($t_{(43)} = 7.34$, $p < .001$, $d = 1.12$) and spatiotopic ($t_{(43)} = 12.23$, $p < .001$ $d = 1.87$) response demand.

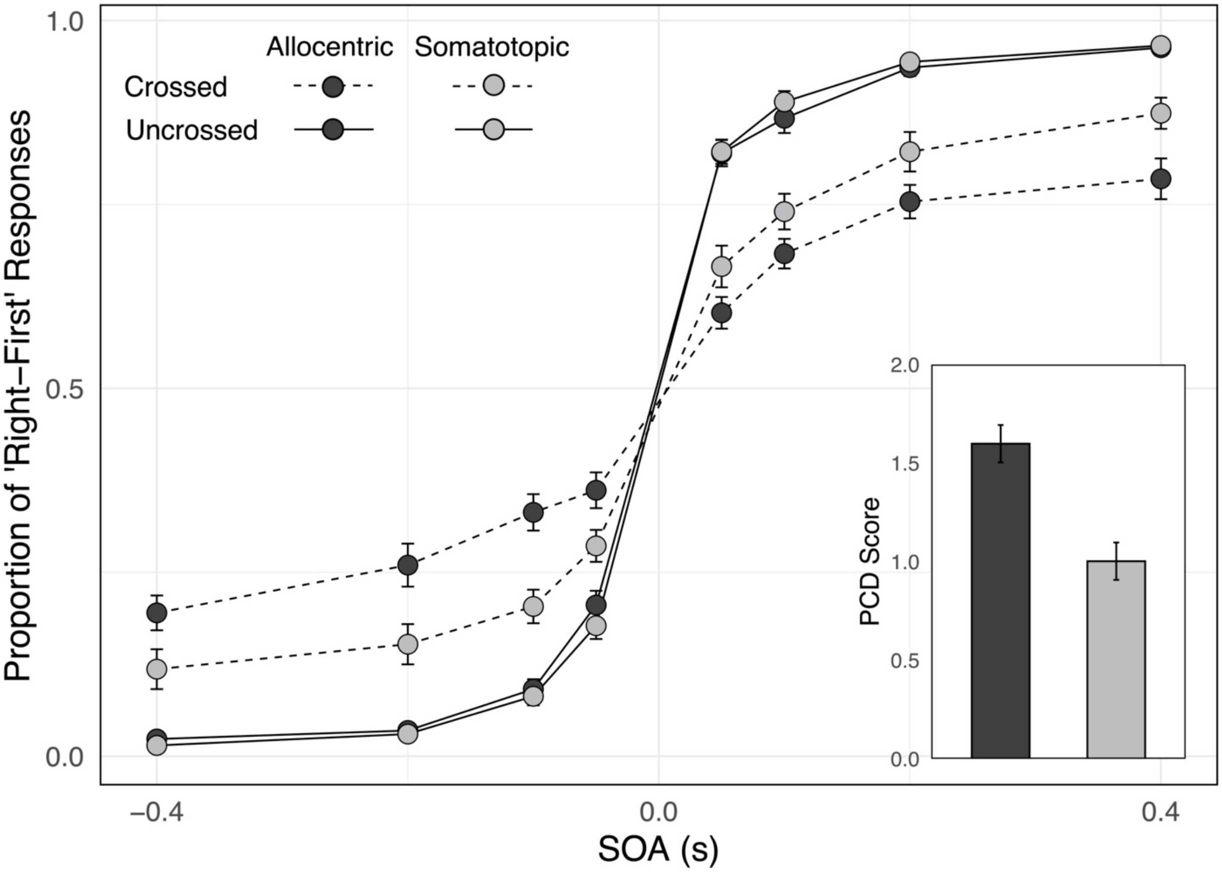

Figure 9: Proportion of right-first (hand for the anatomical condition, hemispace for the spatiotopic condition) responses across stimulus onset asynchrony (SOA) from forty-three female participants for both the crossed and uncrossed hand postures under both response demand conditions. Inset bar graph represents the average PCD score for each response demand. Error bars represent standard error corrected for a within-subject design (Cousineau, 2005; Morey, 2008).

Participant-Specific Model

The maximum likelihood estimate for each participant was the weight pair with the highest likelihood (see Fig. 10 for the joint posterior probability of all tested weight pair, see Fig. 11A for maximum likelihood weight pair). Using these weights we calculated each participant's expected responses (Fig. 12). The expected responses fit well with the participant's data ($R^2 = 0.93$, $p < .001$), suggesting the internal and external weight combination successfully captures participant performance. Based on the most likely weights, we computed an expected PCD score

(Fig. 11B). The expected PCD scores were highly correlated with the participants' actual PCD scores ($r = .96$, $p < .001$). We calculated an average internal and external weight for each response demand (Fig. 11C). Overall, a higher weight was placed on the internal reference frame ($F_{(1,42)} = 129.82$, $p < .001$, $\eta_g^2 = .29$). There was no significant difference in the weights between the different response demands ($F_{(1,42)} = 3.82$, $p = .06$, $\eta_g^2 = .01$). An interaction between reference frame and response demand was observed ($F_{(1,42)} = 26.54$, $p < .001$, $\eta_g^2 = .04$), such that when switching from an anatomical to a spatiotopic response, less weight was placed on the internal reference frame ($t_{(19)} = -4.62$, $p < .001$, $d = -.51$) while the weights placed on the external reference frame between two response demands were not significantly different ($t_{(19)} = 1.37$, $p = .18$, $d = .23$).

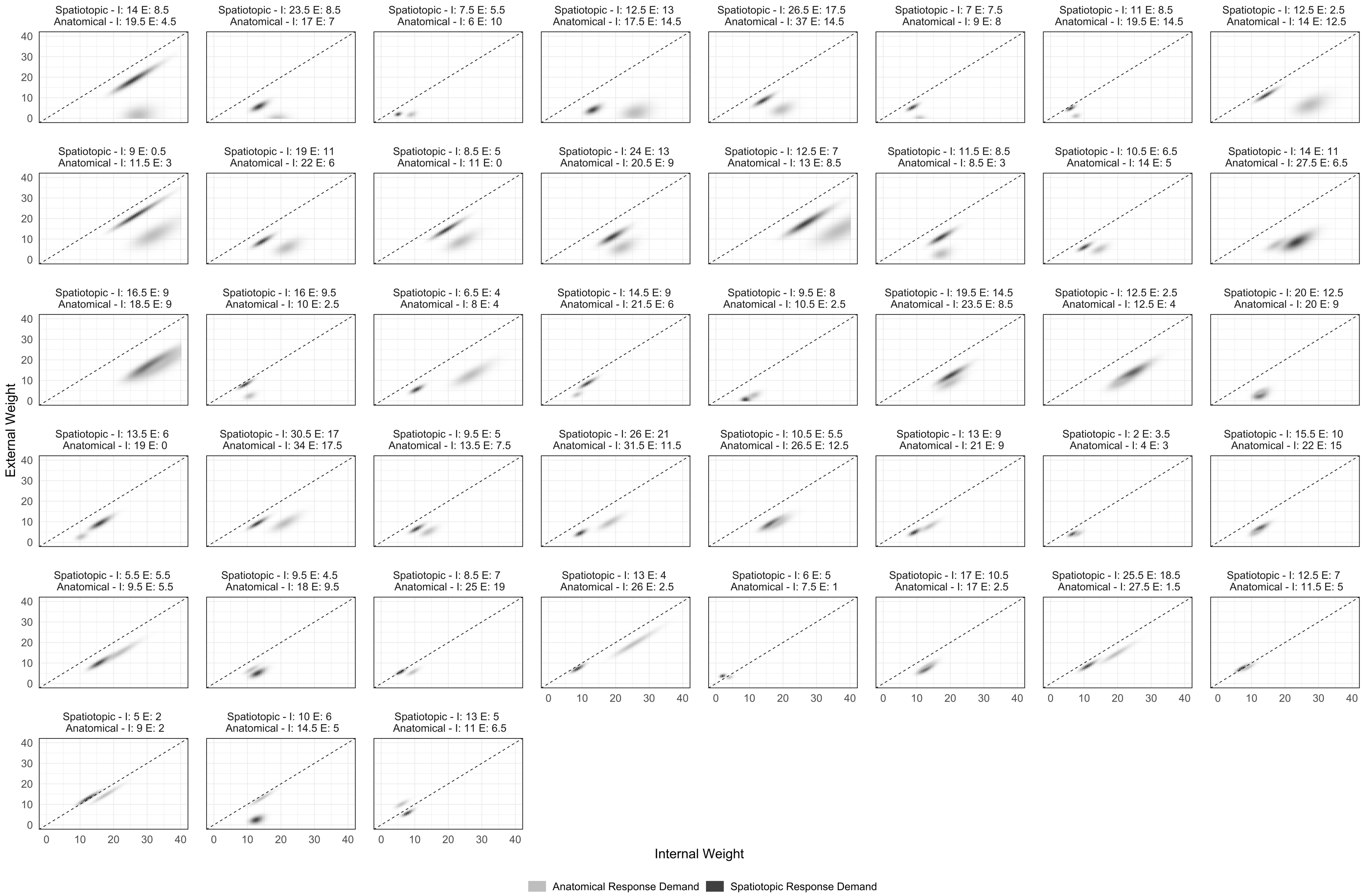

Figure 10: Joint likelihood distributions for the internal and external weights for each participant. The darker the point the greater the likelihood of the weight pair.

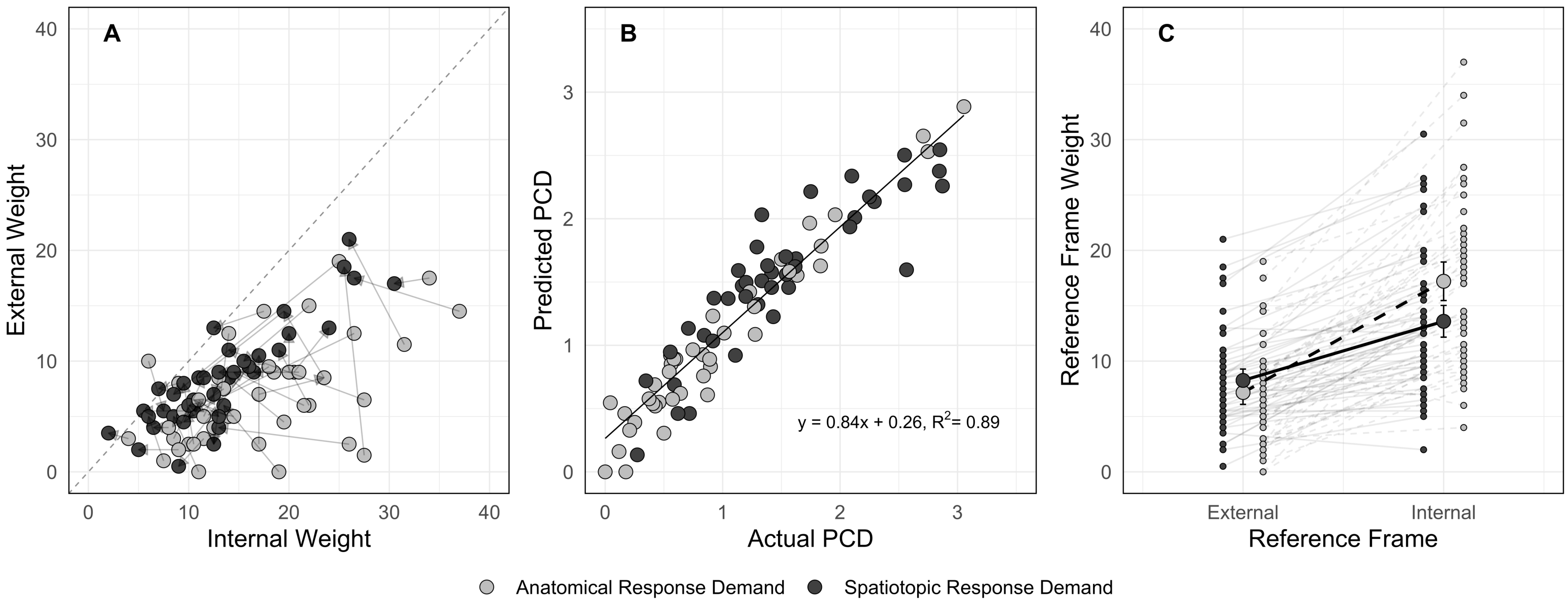

Figure 11: (A) The combination of internal and external weights that best fit the data, for each of the response demands, for each participant (connected by a line). (B) Comparison of the PCD score obtained from the participants' raw data to the PCD score calculated from their most likely weights. (C) Overall internal and external weight in each response demand. This was found by taking the average of each participants' weights. Error bars represent standard error of the mean corrected for within-subject comparisons. The smaller circles represent the weights from individual participants.

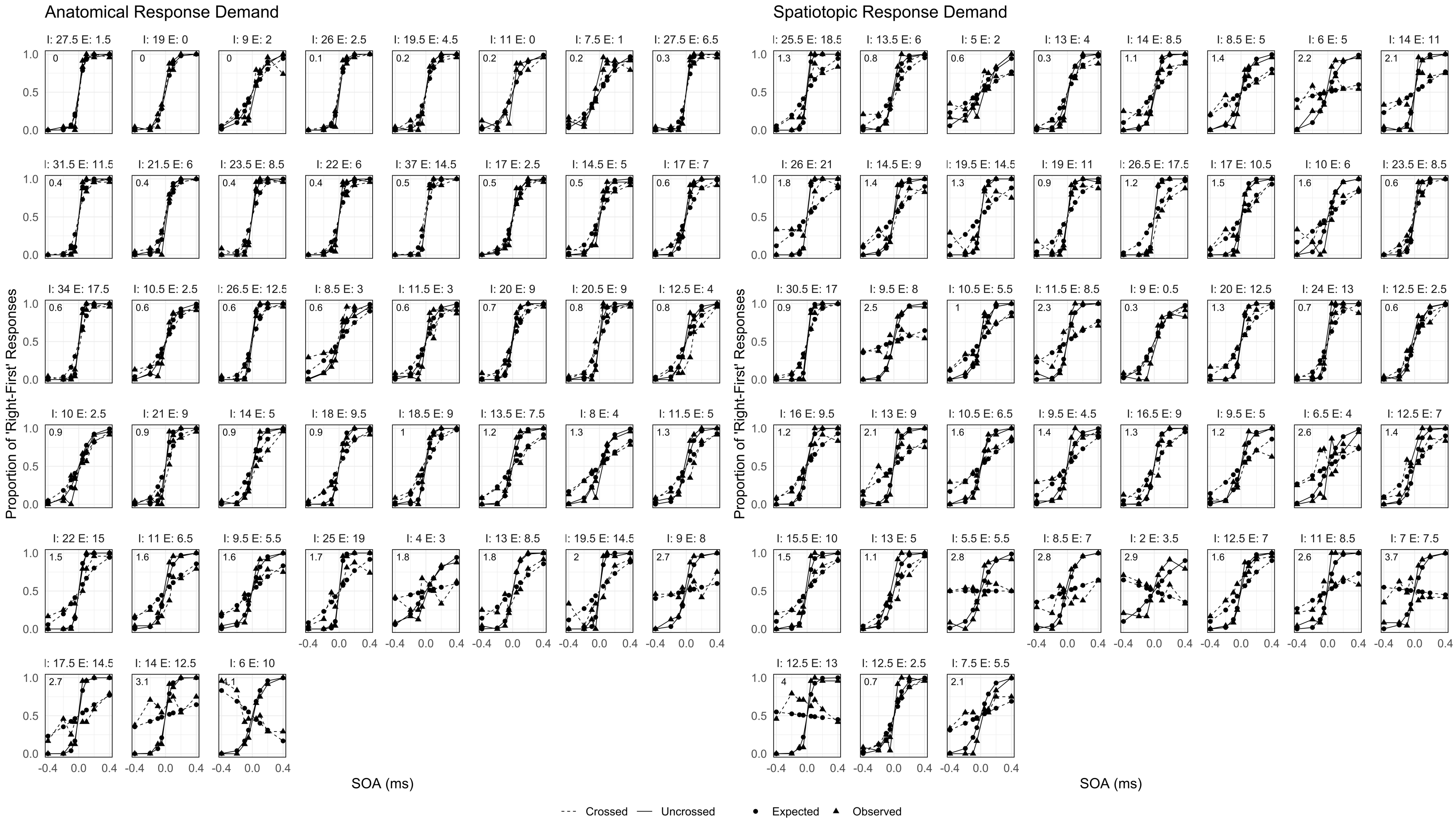

Figure 12: Individual participant performance from Experiment 2. The triangles represent the participants' observed data, and the circles represent the expected performance calculated from their most likely weights. The numbers on top of each figure represent the participant's maximum likelihood estimated internal and external weights. The number in the top left of each figure is the participant's actual PCD score. The graphs are sorted by PCD score in the anatomical condition.

Hierarchical Model

Each hypothesis was initialized with random values for each of its 92 parameters. The additional parameters are due to the increased number of participants. The same parameters from Experiment 1 were used for each participant and the population. The population internal weight was 16.00 [95 CI: 13.58, 18.17] with a population standard deviation of 6.80. The external population weight was 7.01 [95 CI: 5.47, 8.30] with a population standard deviation of 3.55 for the anatomical condition (Fig. 13C). The population internal task parameter was 0.77 [95 CI: 0.73, .81], and the external task parameter was 1.00 [95 CI: 0.91, 1.10], leading to an internal weight of 12.27 and external weight of 7.00 for the spatiotopic condition. The confidence interval on the internal task parameter was below 1, indicating a decreased internal weight for the spatiotopic response demand, while the confidence interval of the external task parameter included 1 implying no change in this weight.

The highest probability internal and external weights for each participant were estimated by the posterior means (Fig. 13A). The expected data computed from these weights were a good fit for the participants data ($R^2 = 0.92$, $p < .001$; Fig. 14). The participant's observed PCD score was correlated with the expected PCD score ($r = .86$, p < .001; Fig. 13B). The internal weight ($r = .93$, $p < .001$) and external weight ($r = .77$, $p < .001$) were strongly correlated with the participant-specific weights (Fig. 15).

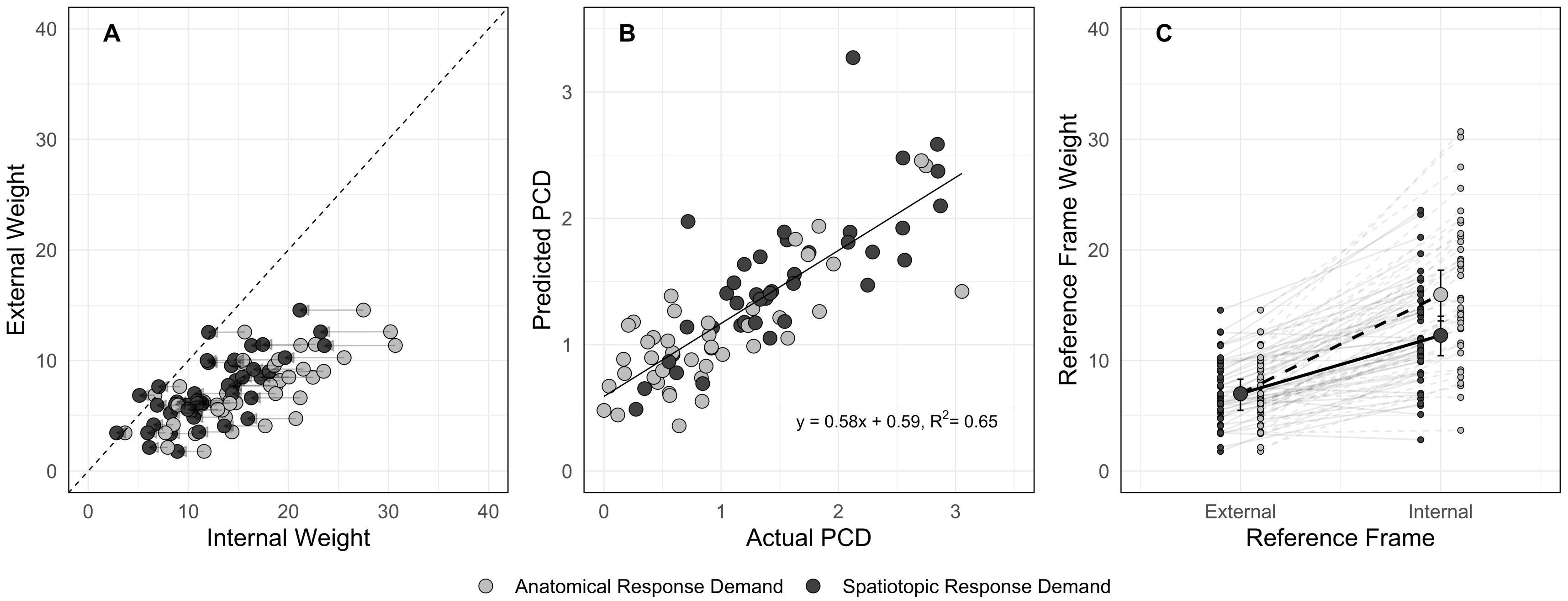

Figure 13: (A) Most likely weights for each participant in each response demand. The arrow connects the weights for each participant. (B) Comparison of the PCD score obtained from the participants' raw data to the PCD score calculated from the most likely weights. (C) Overall population internal and external weight in each response demand. Error bars represent 95 percent credible intervals. The small circles represent individual participant weights.

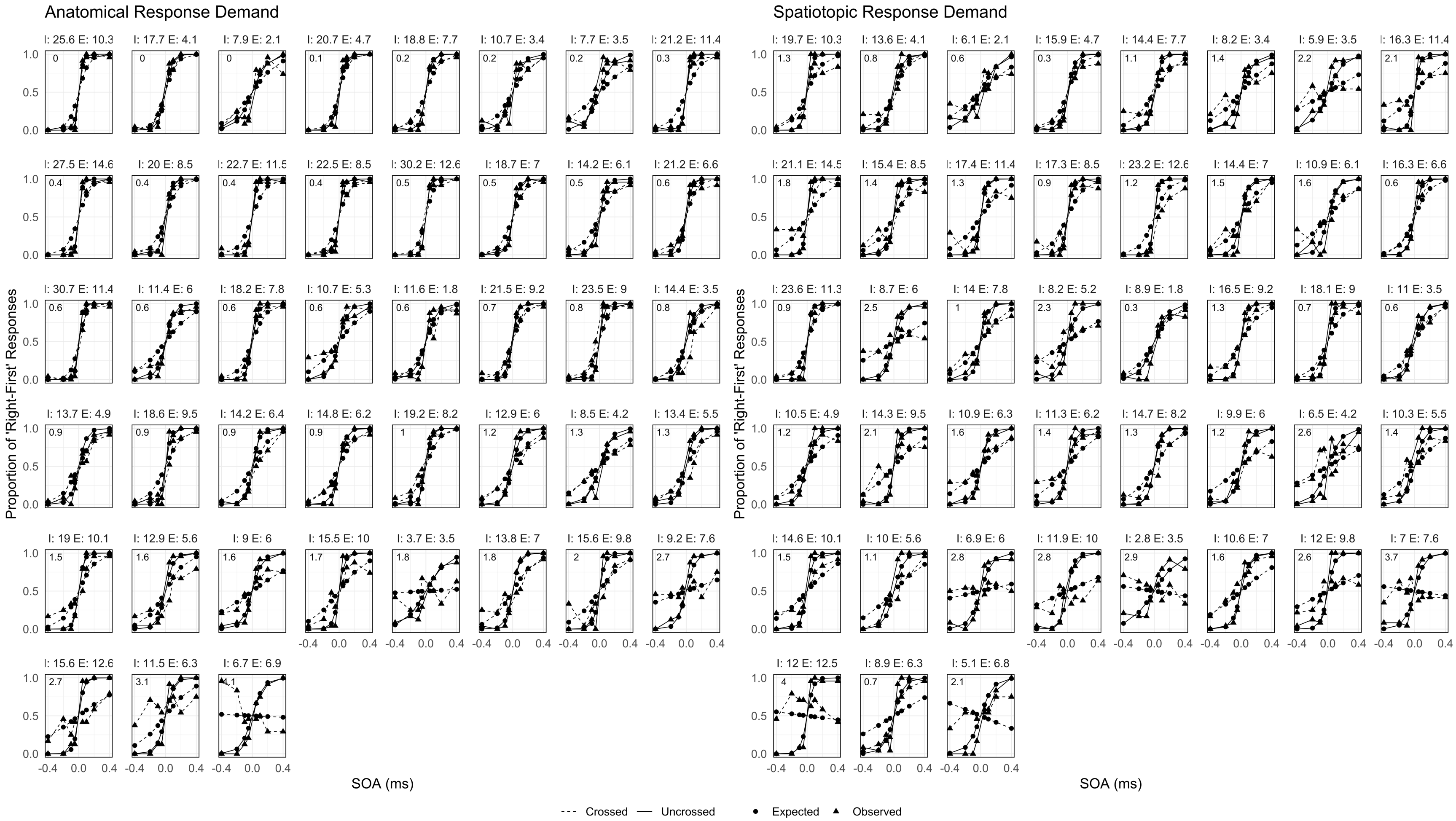

Figure 14: Individual participant performance from Experiment 2. The triangles represent the participants' observed data, and the circles represent the expected performance calculated from their most likely weights in the hierarchical model. The numbers on top of each figure represent the participant's maximum likelihood estimated internal and external weights. The number in the top left of each figure is the participants actual PCD score. The graphs are organized by PCD score in the anatomical condition.

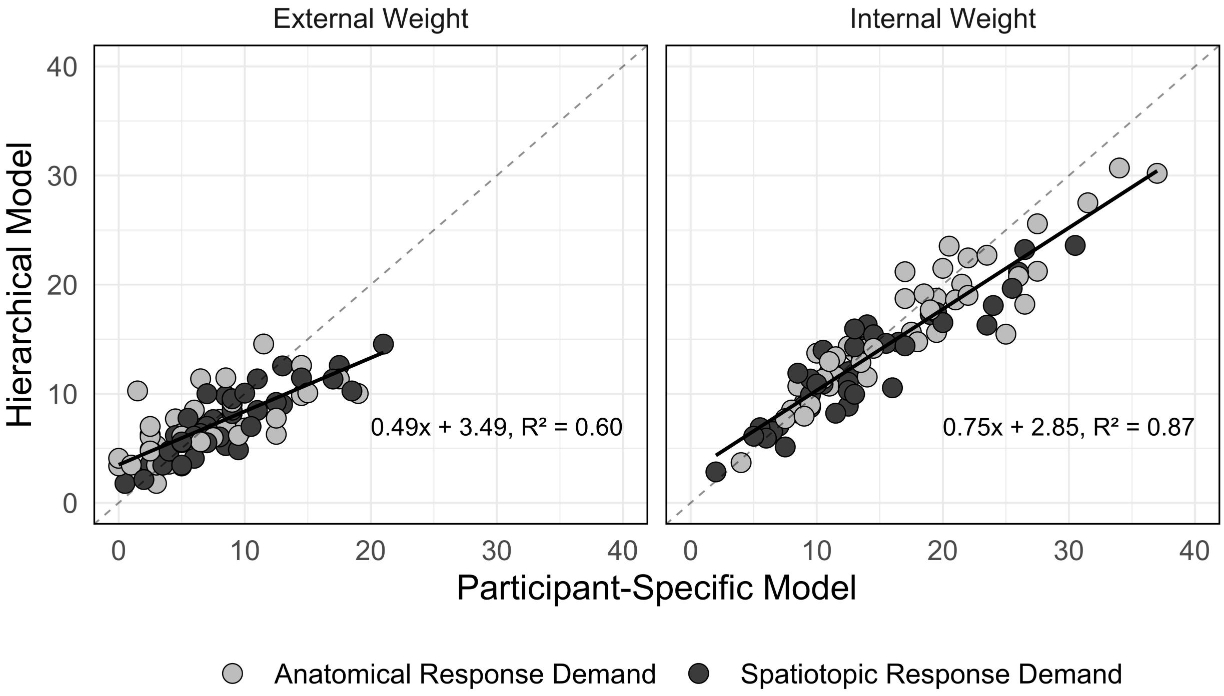

Figure 15: Comparison of the weights obtained from the participant-specific model and the hierarchical model for Experiment 2. There was a moderate correlation obtained for both the internal weight and external weight.

The PPMC successfully captured the average PCD score, but not the correlation between the two response demands (Fig. 16). The observed data shows a moderately positive correlation between the anatomical and spatiotopic response conditions (*r* = .50, *p* < .001), while the model predicts a stronger correlation between conditions (*r* = .79).

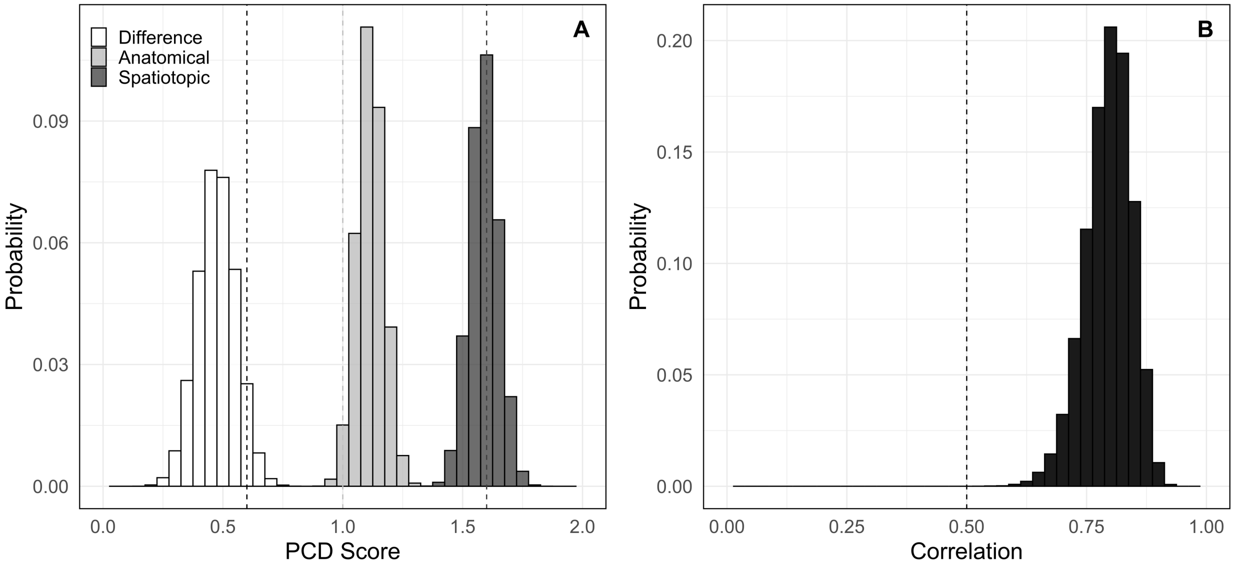

Figure 16: (A) Posterior predictive distributions of PCD scores for the anatomical and spatiotopic conditions, and the difference between the spatiotopic and anatomical conditions. (B) Posterior predictive distribution of the correlation between the anatomical and spatiotopic PCD scores. The vertical dotted lines represent the observed values from the raw data from Experiment 2.

Discussion

In Experiment 2, we replicated Experiment 1: a larger crossed-hands deficit was observed using a spatiotopic response demand compared to an anatomical response demand. This was measured through both the crossed-hands proportion of right-first responses being closer to chance and by a larger PCD score in the spatiotopic condition. These results support the theory that the spatiotopic response demand emphasised the external reference frame.

When using a participant-specific model to determine the internal and external weight for each response demand using a maximum likelihood estimation, both the spatiotopic and anatomical conditions had similar external weights; the internal weight was lower in the spatiotopic condition compared to the anatomical response demand. The hierarchical model replicated the results from the participant-specific model, whereby the external weight remained the same in both conditions and the internal weight was 1.3 times lower for the spatiotopic response demand.

Posterior predictive checks on the average PCD score revealed that the model provided a good estimate of the participant's average PCD score. However, the model again predicted a stronger correlation between the participants' anatomical and spatiotopic response demand PCD scores than was observed in the data. If the 8 participants who revealed a smaller crossed-hands deficit in the spatiotopic condition were removed, the observed correlation ($r = .79$, $p < .001$) more closely matched the predicted correlation from the PPMC.

General Discussion

Across two experiments we observed a larger crossed-hands deficit under a spatiotopic response demand compared to an anatomical response demand. This effect was measured using the PCD score (a measure of performance difference between the uncrossed and crossed postures), which was larger for the spatiotopic response demand compared to the anatomical response demand. These results replicated previous papers using this manipulation (Cadieux and Shore, 2013; Crollen *et al.,* 2019). The spatiotopic condition requires responses to be made in external spatial coordinates. This has led to the hypothesis that the spatiotopic response demand should place more emphasis on the external reference frame. The fact that these behavioural measures showed worse performance in the spatiotopic response demand supported this hypothesis.

To measure the weight placed on the internal and external reference frame, we employed a modified version of the model designed by Badde et al. (2015a). We first fitted each participant's data based on their equations for creating the psychometric functions, using a participant-specific model. Next, we employed a modified version of the hierarchical model. The participant-specific approach fits each participant independently. The only estimate of the population weights from this technique is through the mean of the participant weights. While this results in a slightly better fit for the individual participant data, it also increases the chance of the parameter fits being influenced by noise in the individual data. This technique is appropriate if the participants' weights are in fact statistically unrelated, such that the parameter estimates for each participant can be based on that participant's data alone. The hierarchical model, in contrast, assumes that participant's weights come from a Gaussian population distribution, with unknown mean and standard deviation parameters. Therefore, each participant's data contributes, by influencing the population parameter fits, to the parameter estimates of the other participants. This results in the individual parameter estimates being less swayed by noise in the individual participant data, and also allows for a more sophisticated estimation of the population weights.

Both the participant-specific model and the hierarchical model provided similar results for each experiment. For Experiment 1, both methods revealed a larger external weight for the spatiotopic response demand compared to the anatomical response demand, while the internal weight remained unchanged. In Experiment 2, the spatiotopic condition resulted in a smaller internal weight compared to the anatomical response demand, while the external weights remained the same. The slopes of the crossed-hands conditions are computed as the difference between the internal and external weight; as such, an increase in the external weight or an equivalent decrease in the internal weight will result in the same slope. Given that each experiment showed worse crossed-hands performance in the spatiotopic condition than the anatomical condition, both options are able to fit the crossed-hands data. The difference between these two options is only evident in the slopes of the uncrossed psychometric functions. Since the uncrossed posture is created from the sum of the internal and external weights, an increase in the external weight results in a slightly steeper uncrossed slope for the spatiotopic response demand, whereas a decreased internal weight would result in a shallower uncrossed slope. While the uncrossed performance in the two experiments was similar, in Experiment 1 the spatiotopic condition had slightly better uncrossed performance compared to the anatomical condition, which the model attributes to an increased external weight. In contrast, the spatiotopic condition had slightly worse uncrossed performance compared to the anatomical condition in Experiment 2, which the model attributes to a decreased internal weight.

The participant parameters from the participant-specific model and the hierarchical model were slightly different (Figs. 6 and 13), as a result of the additional population parameters, specifically the population standard deviation. Seeing as the participant-specific approach fits all participants independently, this technique assumes there is no relation between participants, or that the standard deviation is extremely large. In the hierarchical model, as the estimated standard deviation approaches infinity, the weights would become equivalent to the participant-specific approach. Here, for both participant parameters, higher weights in the participant-specific approach were slightly smaller in the hierarchical model, and lower weights were slightly larger in the hierarchical model compared to the participant-specific approach. The smaller range of participant weights estimated by the hierarchical model suggests that the participants' weights are indeed related via a population distribution with finite standard deviation.

At the individual level, not all participants showed the same trend of worse performance in the spatiotopic response demand. A small subset of participants in each experiment showed the opposite, a smaller deficit in the spatiotopic response demand. There were no commonalities regarding these participants' performance or the order in which they completed the response demands. One possibility is that these participants more successfully ignored the external reference frame in the spatiotopic condition than the anatomical condition. Alternatively, these participants could be performing the task differently than the rest. The spatiotopic response demand requires participants to locate the tactile stimulus in external coordinates (hemispace instead of hand). In this condition, instead of a direct mapping from the location of the hand to the response, there is a direct mapping from hemispace to response. Given that the response matches the location of the stimulus in external space, the more a person can focus and utilize the external reference frame, the better their performance should be. The conceptualization for the anatomical response demand task remains the same. The critical difference between the anatomical and spatiotopic response demand, based on this conceptualization, is which reference frame the participant must ignore when the hands are crossed in order to respond correctly. In the anatomical condition the response is mapped internally, therefore ignoring the external reference frame results in better performance. In the spatiotopic condition where the response is mapped externally, ignoring the internal reference frame, and focusing on external information, would improve performance. It is possible that some participants are conceptualizing the spatiotopic response demand in this way. This hypothesis for how individuals are performing the task would require slight modifications to the equations for constructing the spatiotopic psychometric curves.

This may also be causing the low correlation between the anatomical and spatiotopic response demand PCD score in the observed data. When the hierarchical model fits all participants using the same strategy, a large correlation is observed as performance in the spatiotopic condition always has a larger PCD score than the anatomical condition. When the participants showing the opposite effect are removed, the observed correlation is much closer to the correlation estimated by the PPMC.

Given that participants might use different strategies, the use of a single performance model for all participants might be a limitation. The ability to assign different participants to different performance models might help differentiate which participants are using similar strategies. This could be implemented as another level in the hierarchy. Future studies with more explicit instructions are needed to better understand the different strategies that may be used on this task. One such instruction could be to ask participants to locate the stimulus based on the hemispace, rather than the hand of the vibration in the spatiotopic response demand. This instruction explicitly ties the response to external coordinates; therefore, if participants show a smaller deficit under these new instructions it would suggest some participants in the original study were adopting the strategy of responding based on the hemispace.

The results from this study support previous research showing that task instructions influence the weights placed on the internal and external reference frames. In one study, participants received one low and one high frequency vibration, one on each hand (Badde et al., 2015b). The participant had to make two responses to the vibrations. First, the participants indicated the hand that received the first stimulus. After making the temporal response, participants were asked to determine the location of the stimulus of a certain frequency (either high or low depending on the participants). This secondary response used either internal instructions (location tied to the hand) or external instructions (location tied to a side of space). A smaller deficit was observed under internal compared to external instructions. Even though the task instructions only affected the second response, performance on the primary temporal response was altered by the task instructions, showing that task instructions result in a reweighting of internal and external information.

Task instructions have also been shown to affect performance during a tactile congruency task (Gallace et al., 2008; Schubert et al., 2017). In this task, participants had to locate a tactile target on the hand while ignoring a tactile distractor presented on the opposite hand. Under internal instructions participants located the target based on where on the hand it occurred; external instructions had participants indicate the target location relative to gravity. Accuracy was higher when the distractor occurred at a congruent compared to incongruent location, however what was considered congruent changed based on the instructions. Under internal instructions congruency was judged anatomically (e.g., target and distractor on palm), while under external instructions congruency was based on gravity (e.g., target and distractor at upper location). The weights applied to each reference frame are affected by the task instructions.

Both the behavioural data, as well as the model results, support integration accounts for the deficit (Badde *et al.,* 2015a; Shore *et al.,* 2002), as opposed to non-integration models (Yamamoto and Kitazawa, 2001). Integration models posit that both reference frames are used when localizing the tactile stimulus, and the different weights placed on each reference frame determine the final perceived location. In the crossed posture when the external reference frame is more heavily relied on, this can sometimes lead to erroneous localization. According to integration accounts, a larger crossed-hands deficit will occur when an individual places greater weight on the external reference frame, and will decrease as weight is transferred to the internal reference frame. This was supported by the results of the present study, where the anatomical and spatiotopic response demand manipulations biased participants towards the internal and external reference frames respectively. As a result, a larger crossing effect was observed under a spatiotopic response demand. Modelling revealed that the spatiotopic condition caused either a greater external weight, or a smaller internal weight. Both options placed a relatively larger emphasis on external information. Other manipulations to the crossed-hands tactile TOJ task have shown support for an integration of the reference frames. Altering visual information through blindfolding (Cadieux and Shore, 2013), placing the hands behind the back (Kóbor *et al.,* 2006), or viewing uncrossed hands (Azañón and Soto-Faraco, 2007), results in a smaller crossing effect, presumably by removing conflicting external information. Furthermore, congenitally blind individuals do not show a crossed-hands deficit (Crollen *et al.,* 2019; Röder *et al.,* 2004) unless the response modality emphasizes the external reference frame (Crollen *et al.,* 2019) suggesting they do not automatically integrate internal and external reference frames.

The use of this probabilistic model allowed direct exploration about how various manipulations affect the use of each reference frame. This provides a deeper understanding of how information is weighted when locating a touch. Without this model, the theoretically construed weights could only be inferred based on the size of the deficit. Future studies could apply this model to other manipulations assumed to influence reference frame weights (i.e., visual information) in order to test these assumptions quantitatively.

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Appendix A: Supplementary Materials

Experiment 1

Convergence metric

Table S1: Convergence metric (R interval) for the population parameters.

Population Parameter	R Interval
External Standard Deviation	0.98
External Task Context Parameter	1.01
External Weight	1.00
Internal Standard Deviation	1.00
Internal Task Context Parameter	1.01
Internal Weight	1.00

Table S2: Convergence metric (R Interval) for the participant parameters.

Participant	R Interval (External)	R Interval (Internal)
1	1.00	1.00
2	1.00	1.00
3	1.00	1.00
4	1.00	1.00
5	1.00	1.00
6	1.00	1.00
7	1.02	1.02
8	1.00	1.00
9	1.01	1.00
10	1.00	1.00
11	1.00	1.01
12	1.00	1.00
13	1.00	1.00
14	1.00	1.00
15	1.01	1.02
16	1.01	1.01
17	1.01	1.01
18	1.01	1.01
19	1.01	1.00
20	1.00	1.00

Acceptance Rate

Table S3: Acceptance rate for each MCMC run. Acceptance rate was calculated after the burn-in period (50,000 trials).

Iteration	Acceptance Rate
1	0.25
2	0.25
3	0.25
4	0.25
5	0.25

Parameter value by trial

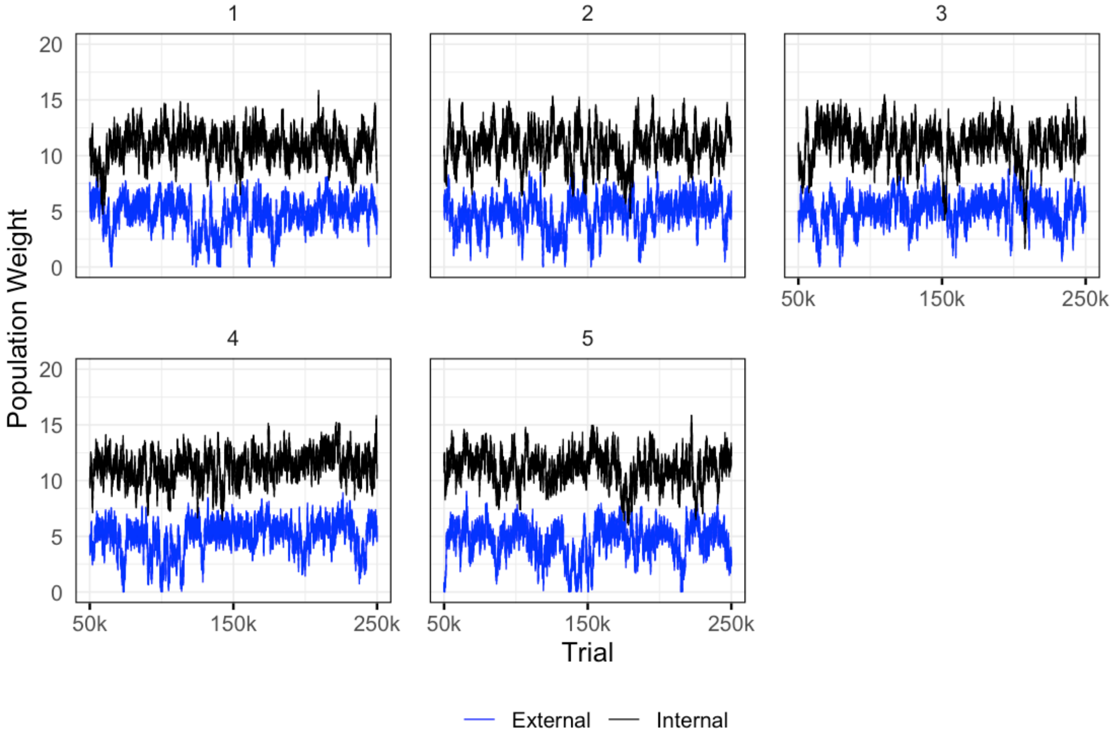

Figure S1: Chosen population weight parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

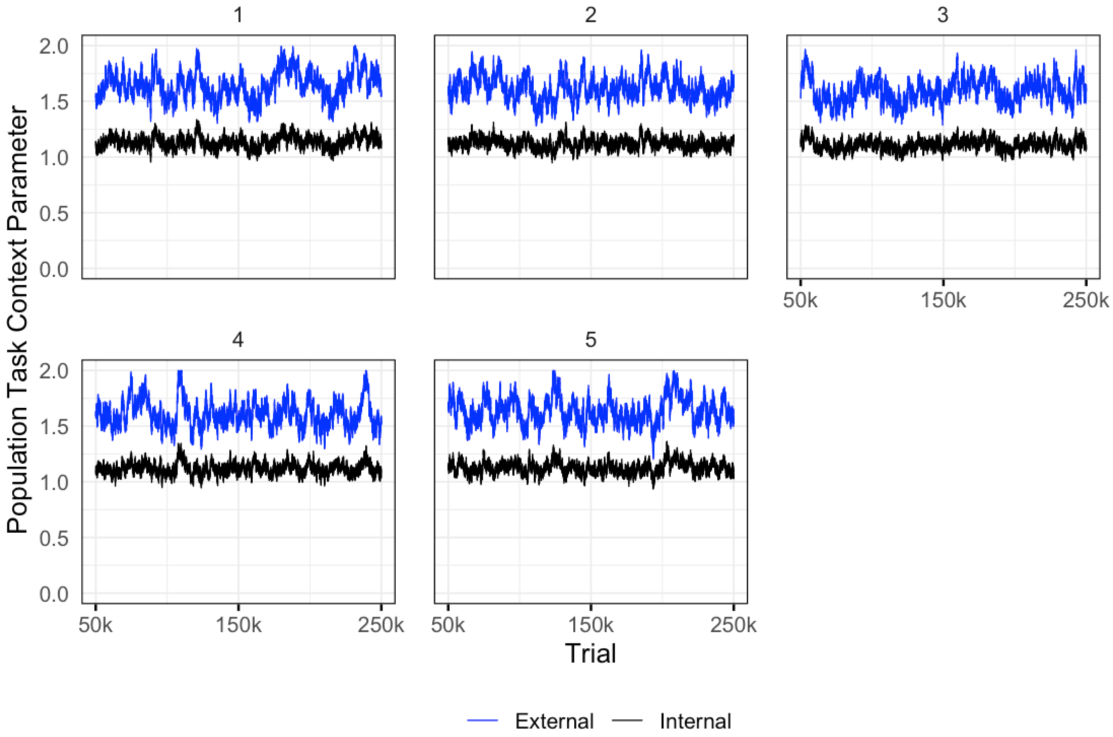

Figure S2: Chosen population task context parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

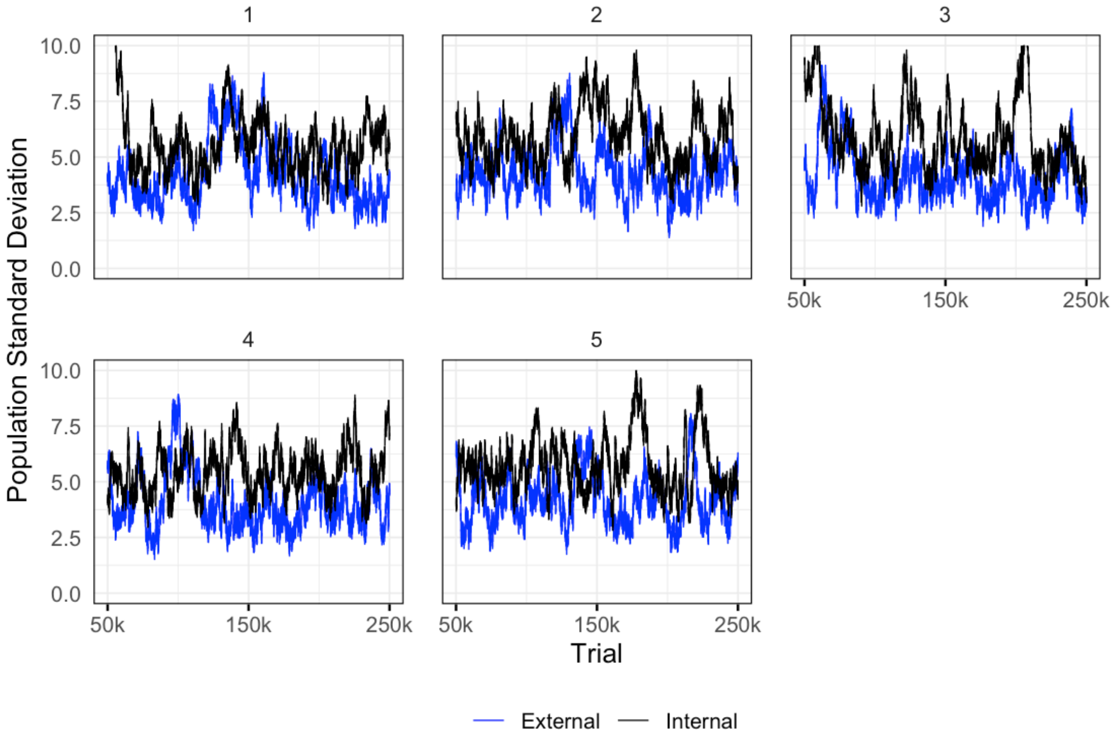

Figure S3: Chosen population standard deviation parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

Posterior distributions for each parameter separated by iteration

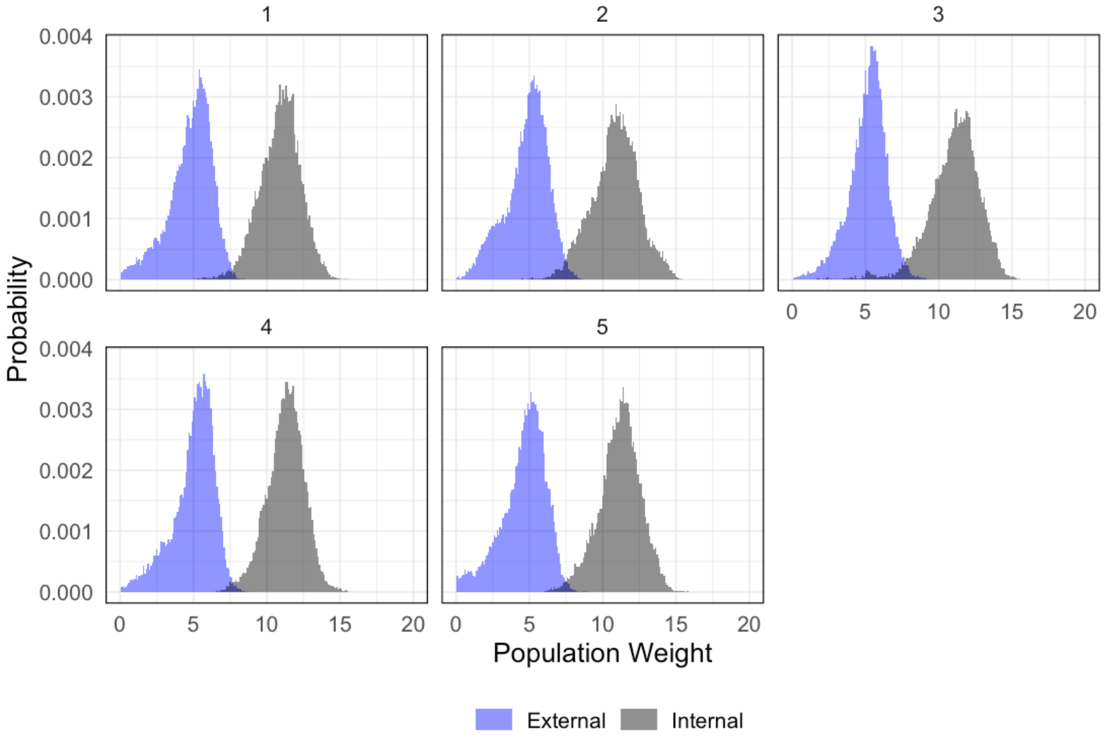

Figure S4: Posterior distributions of the population weight parameters for each MCMC run. The outputted histogram for each weight parameter was normalized to obtain the probability for each weight (number of observations of each weight divided by the total number of observations).

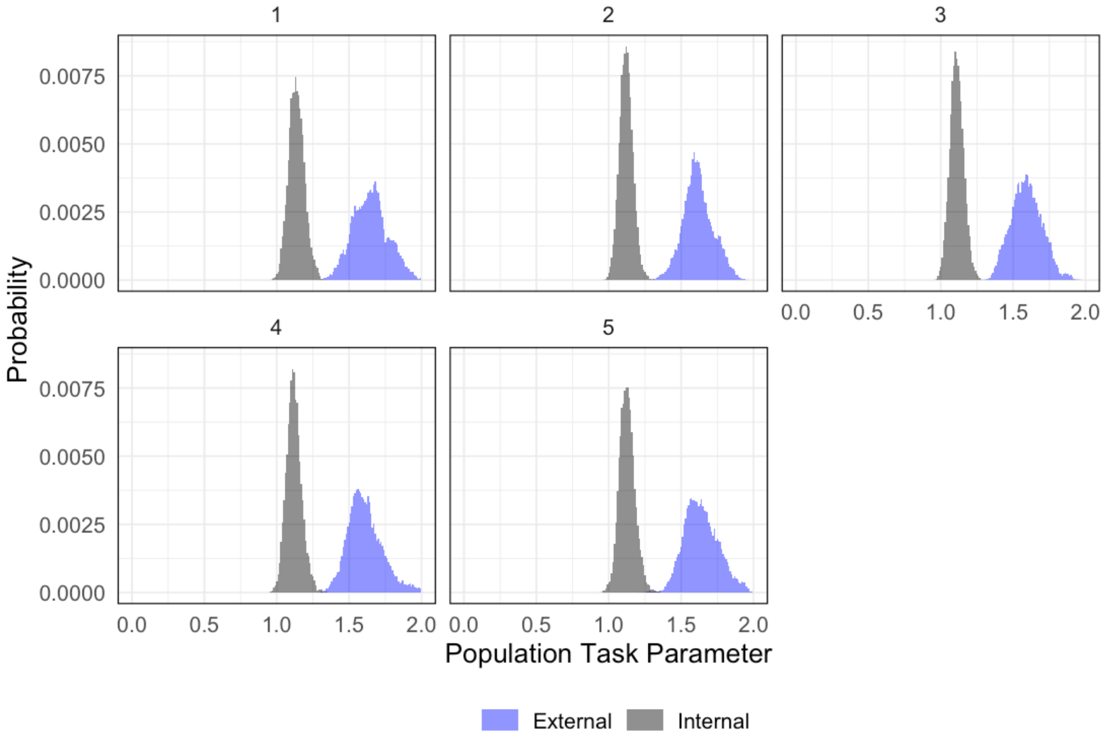

Figure S5: Posterior distributions of the population task context parameters for each MCMC run. The outputted histogram for each task context parameter was normalized to obtain the probability for each task context parameter (number of observations of each parameter divided by the total number of observations).

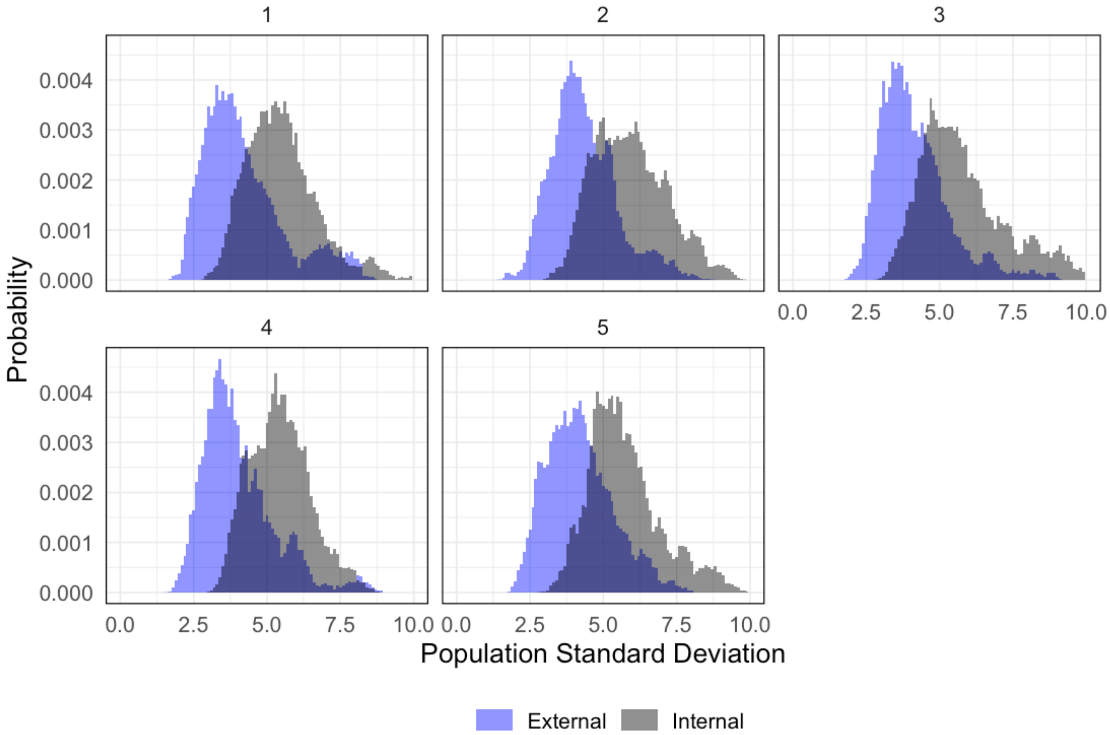

Figure S6: Posterior distributions of the population standard deviation parameters for each MCMC run. The outputted histogram for each standard deviation parameter was normalized to obtain the probability for each standard deviation (number of observations of each standard deviation divided by the total number of observations).

Overall posterior distributions for each parameter

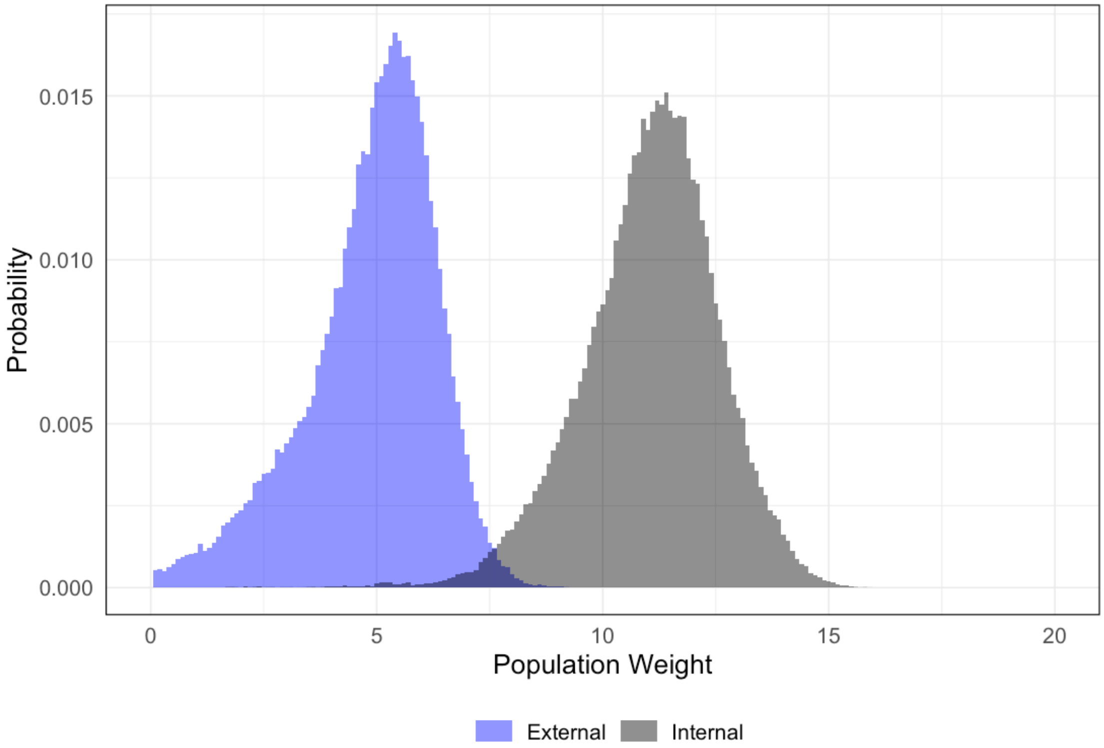

Figure S7: Overall posterior distribution for the population weight parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

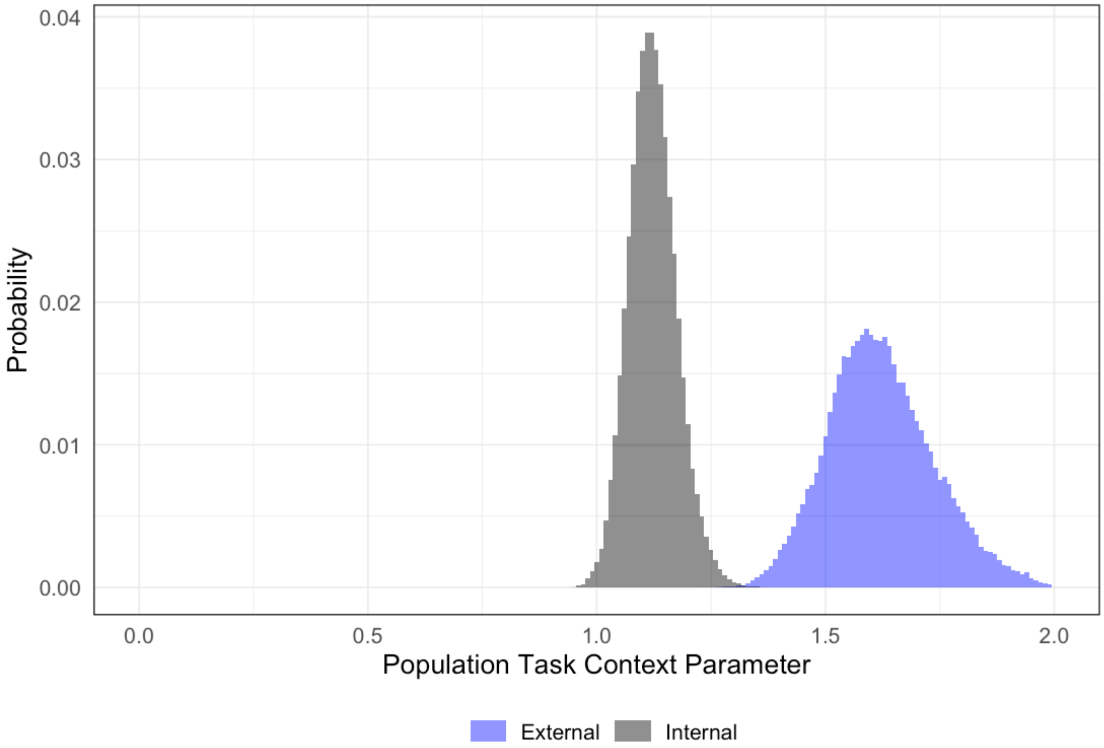

Figure S8: Overall posterior distribution for the population task context parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

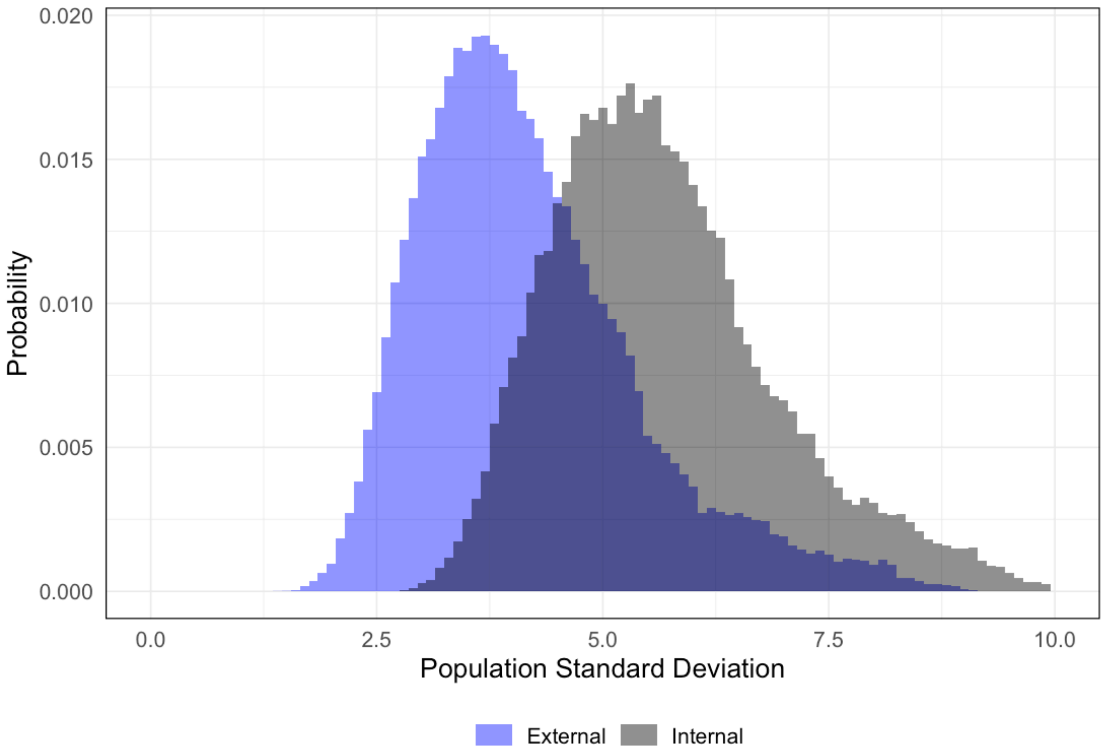

Figure S9: Overall posterior distribution for the population standard deviation parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

Posterior distribution of weights

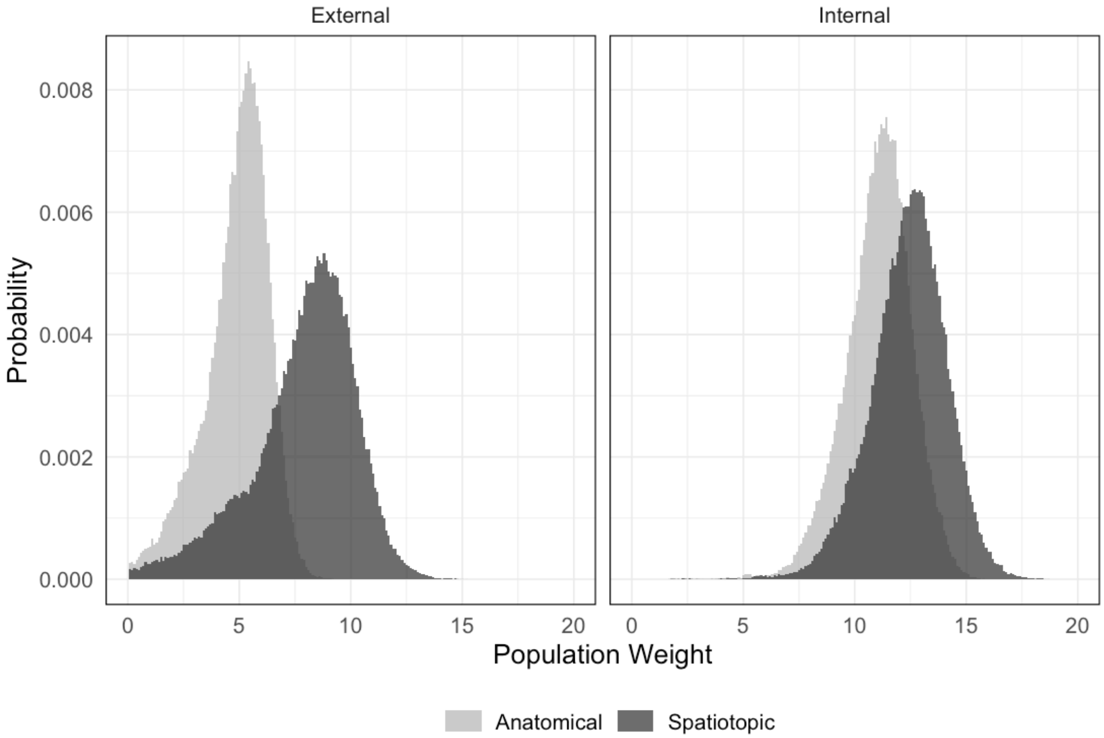

Figure S10: Overall posterior distribution for the population weight parameters for each condition. The values for the spatiotopic condition were calculated by multiplying the anatomical weight parameter by the task context parameter on each trial.

Experiment 2

Convergence Metric

Table S4: Convergence metric (R Interval) for the population parameters.

Population Parameter	R Interval
External Standard Deviation	1.02
External Task Context Parameter	1.00
External Weight	1.00
Internal Standard Deviation	1.01
Internal Task Context Parameter	1.00
Internal Weight	1.00

Table S5: Convergence metric (R Interval) for the participant parameters.

Participant	R Interval (External)	R Interval (Internal)
1	1.01	1.00
2	1.01	1.01
3	1.00	1.00
4	1.02	1.02
5	1.01	0.99
6	1.00	1.00
7	1.00	1.00
8	1.00	1.01
9	1.00	1.00
10	1.01	1.00
11	1.00	1.00
12	1.00	0.99
13	1.01	1.00
14	1.00	1.00
15	1.00	1.00
16	1.00	1.00
17	1.00	1.01
18	1.00	1.00
19	1.00	1.00
20	1.00	1.00
21	1.00	1.00
22	1.01	1.01
23	1.00	1.00
24	1.00	1.00
25	1.00	1.00
26	1.05	1.04
27	1.00	1.00
28	1.03	1.03
29	1.01	1.01
30	1.01	1.00
31	1.00	1.00
32	1.00	1.01
33	1.00	1.00
34	1.00	1.00
35	1.01	1.01
36	1.00	1.00
37	1.00	1.00
38	1.00	1.00
39	1.01	1.01
40	1.00	1.00
41	1.00	1.00
42	1.00	1.00
43	1.00	1.00

Acceptance Rate

Table S6: Acceptance rate for each MCMC run. This was calculated after the burn-in period (50,000 trials).

Iteration	Acceptance Rate
1	0.26
2	0.25
3	0.26
4	0.26
5	0.25

Parameter value by trial

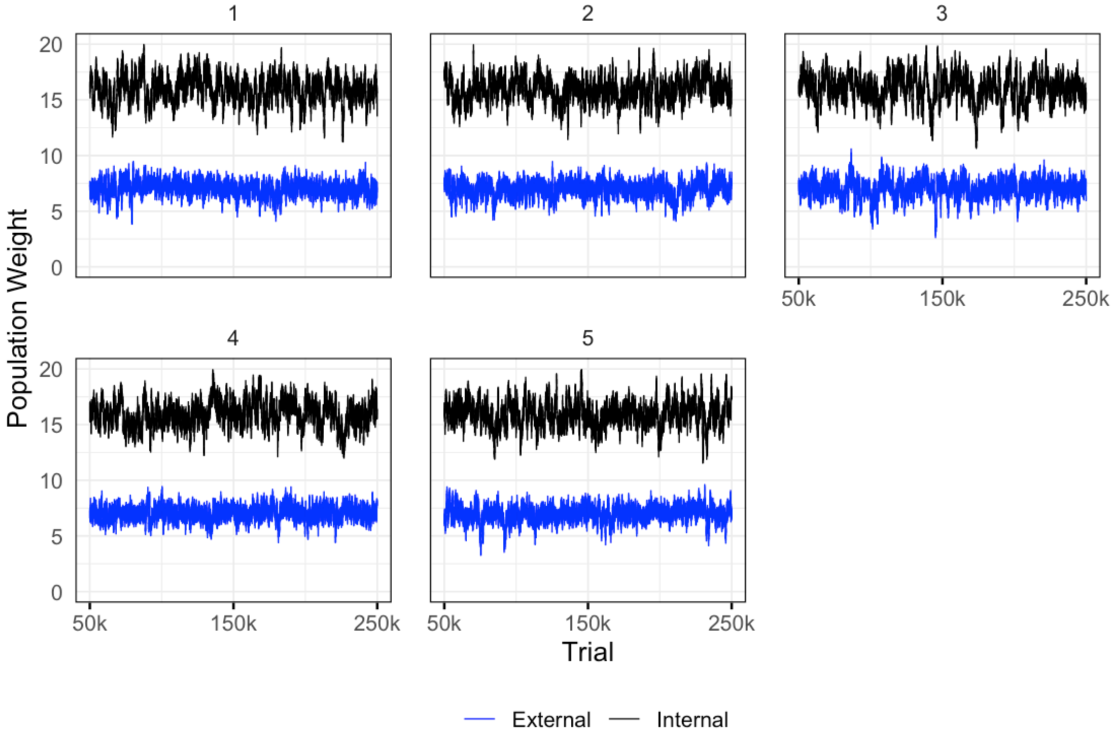

Figure S11: Chosen population weight parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

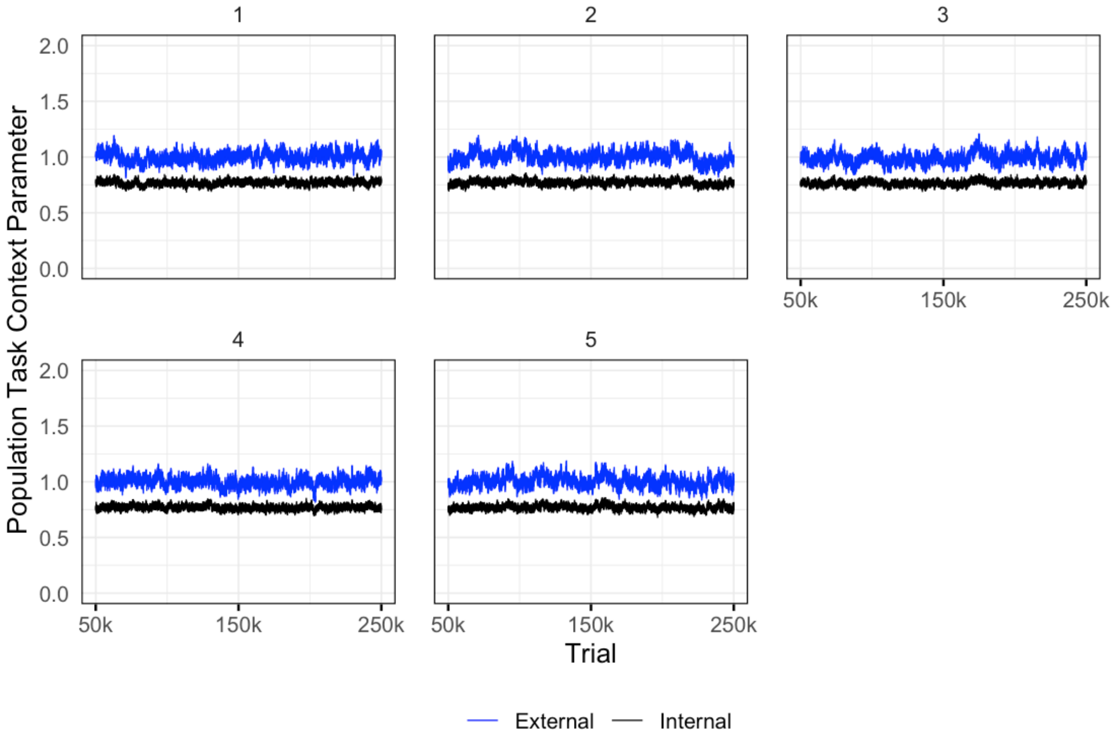

Figure S12: Chosen population task context parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

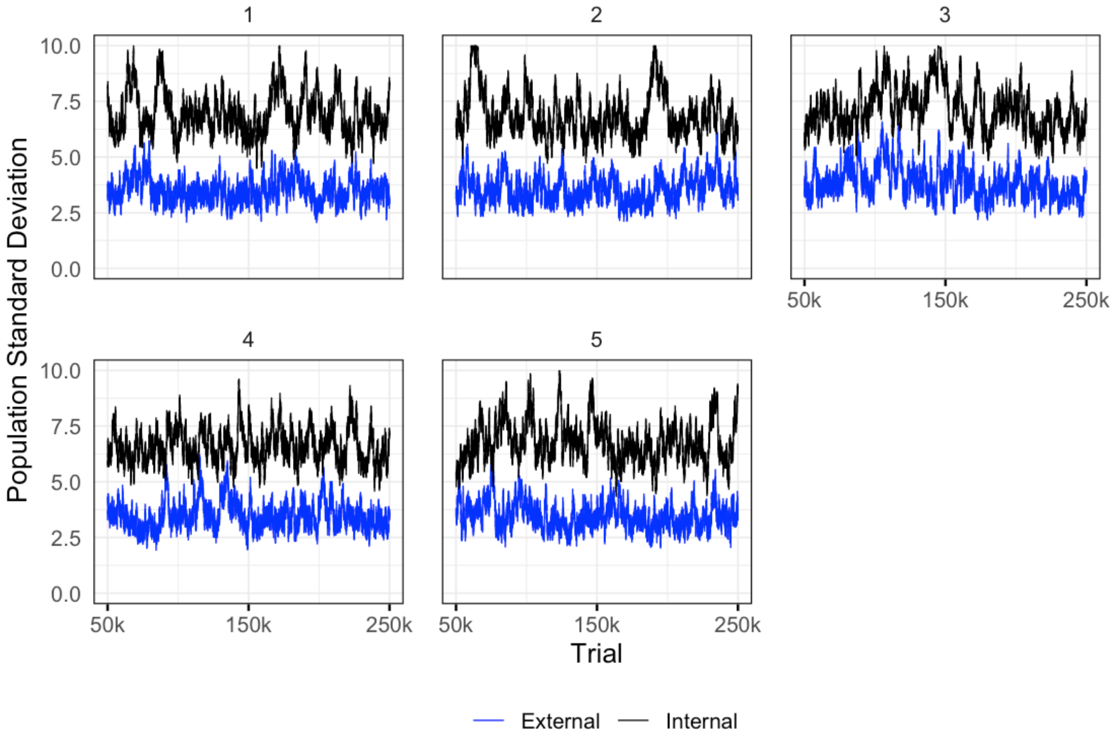

Figure S13: Chosen population standard deviation parameter values on every trial. The first 50,000 trials were removed as the burn-in period.

Posterior distributions for each parameter separate by iteration

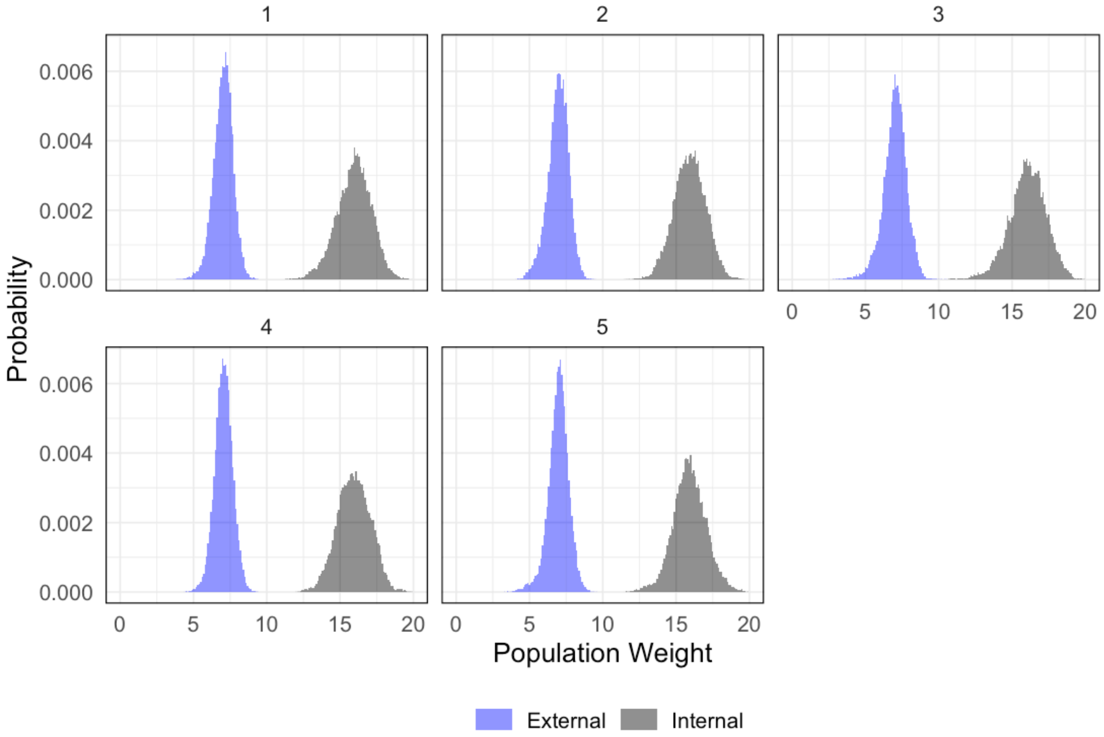

Figure S14: Posterior distributions of the population weight parameters for each MCMC run. The outputted histogram for each weight parameter was normalized to obtain the probability for each weight (number of observations of each weight divided by the total number of observations).

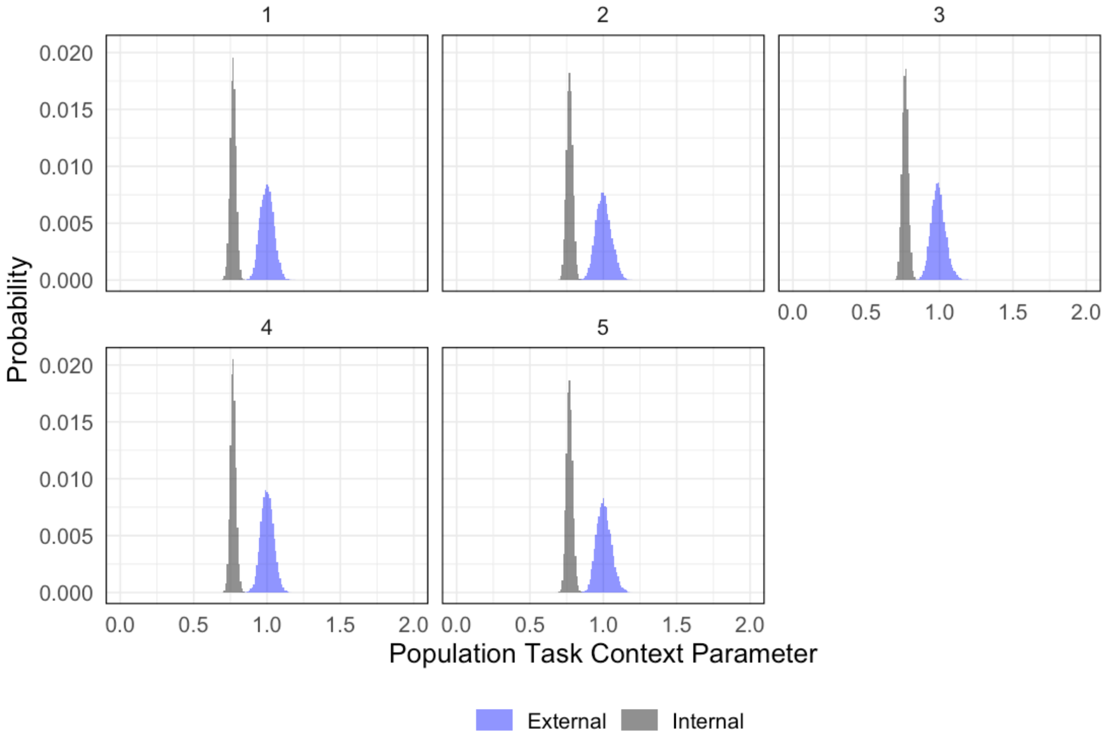

Figure S15: Posterior distributions of the population task context parameters for each MCMC run. The outputted histogram for each task context parameter was normalized to obtain the probability for each task context parameter (number of observations of each parameter divided by the total number of observations).

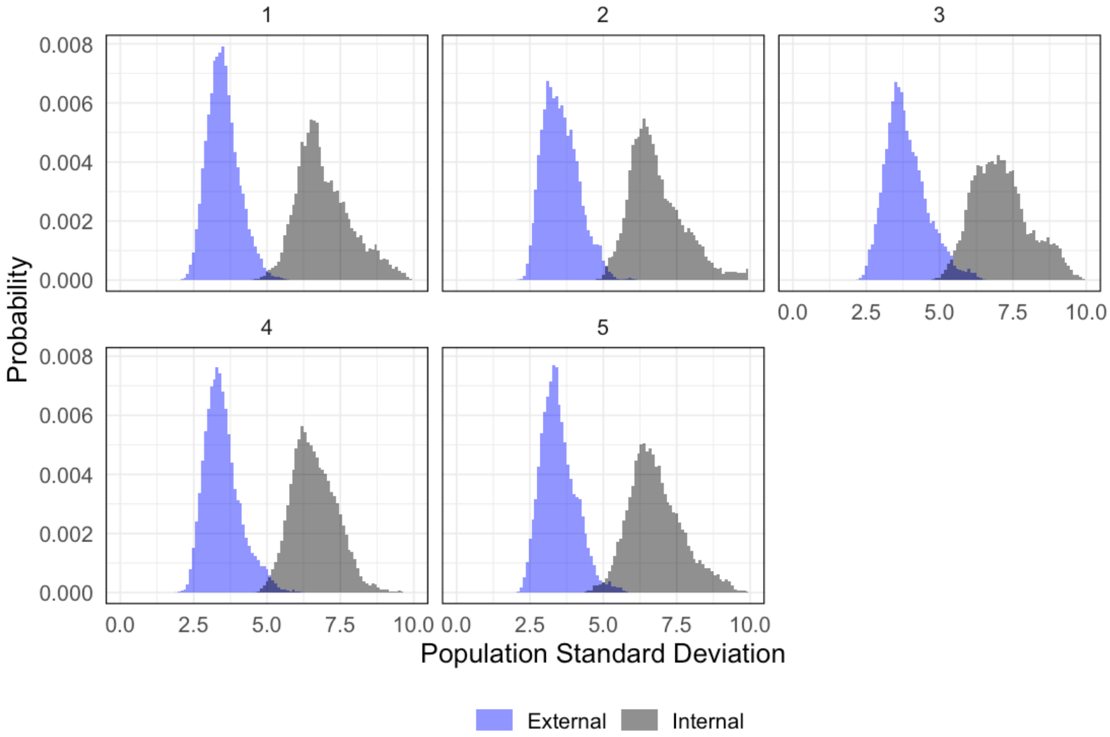

Figure S16: Posterior distributions of the population standard deviation parameters, for each MCMC run. The outputted histogram for each standard deviation parameter was normalized to obtain the probability for each standard deviation (number of observations of each standard deviation divided by the total number of observations).

Overall posterior distributions for each parameter

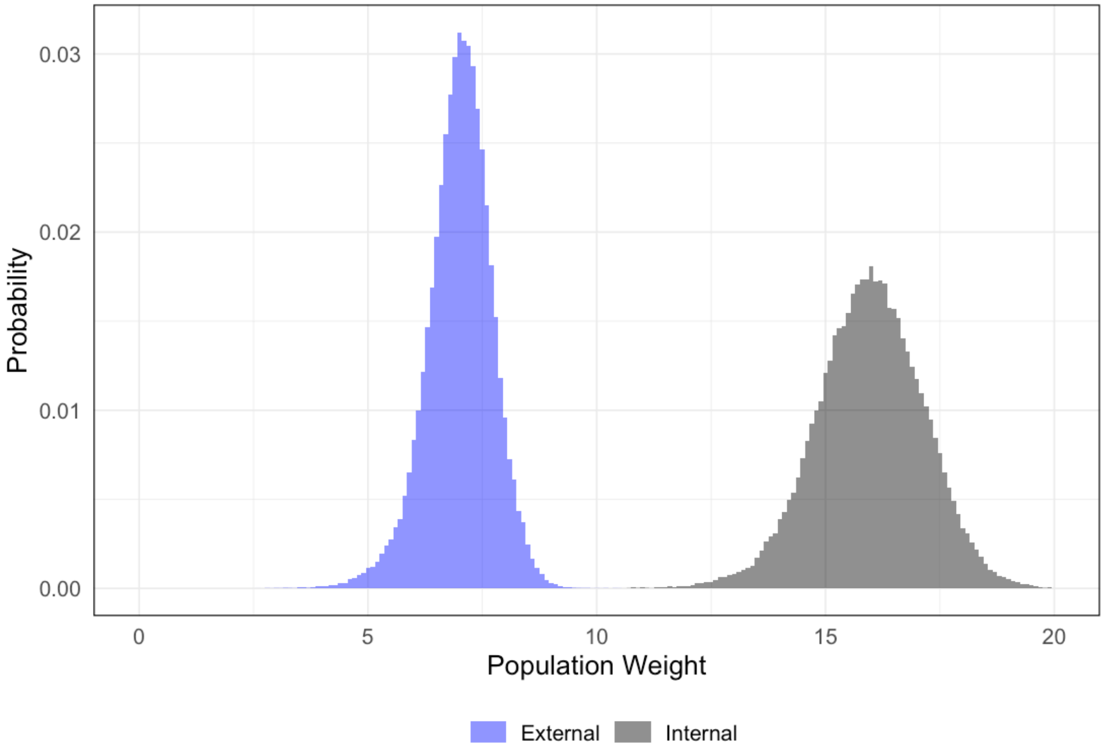

Figure S17: Overall posterior distribution for the population weight parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

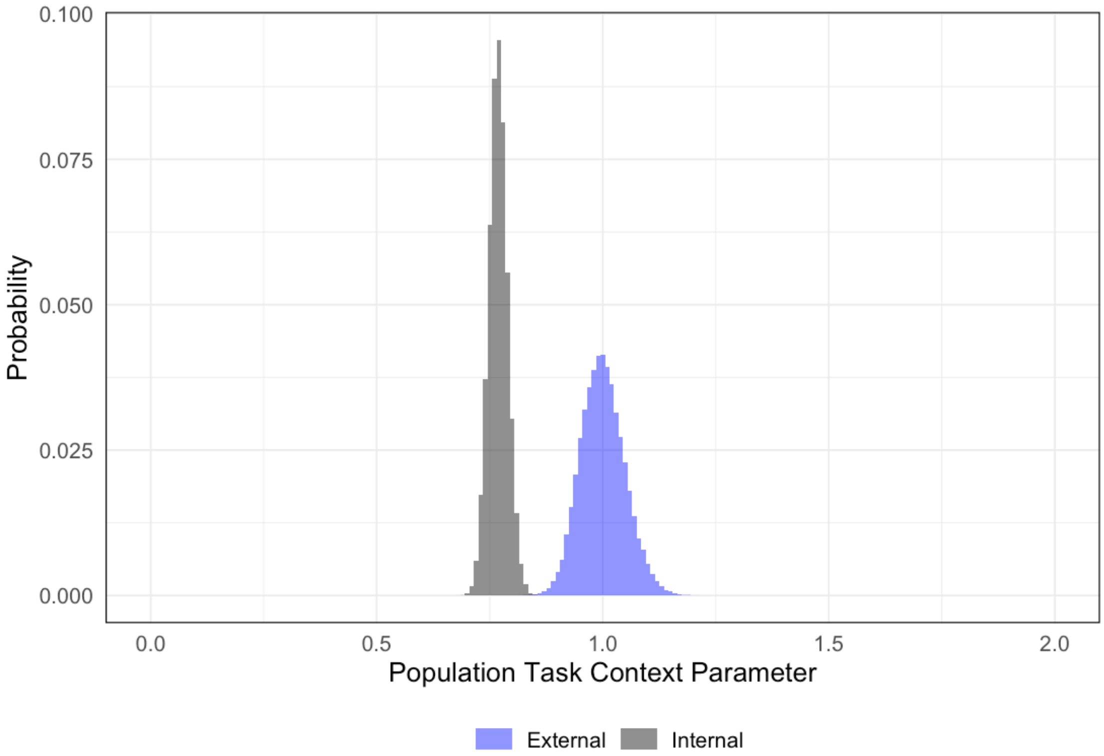

Figure S18: Overall posterior distribution for the population task context parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

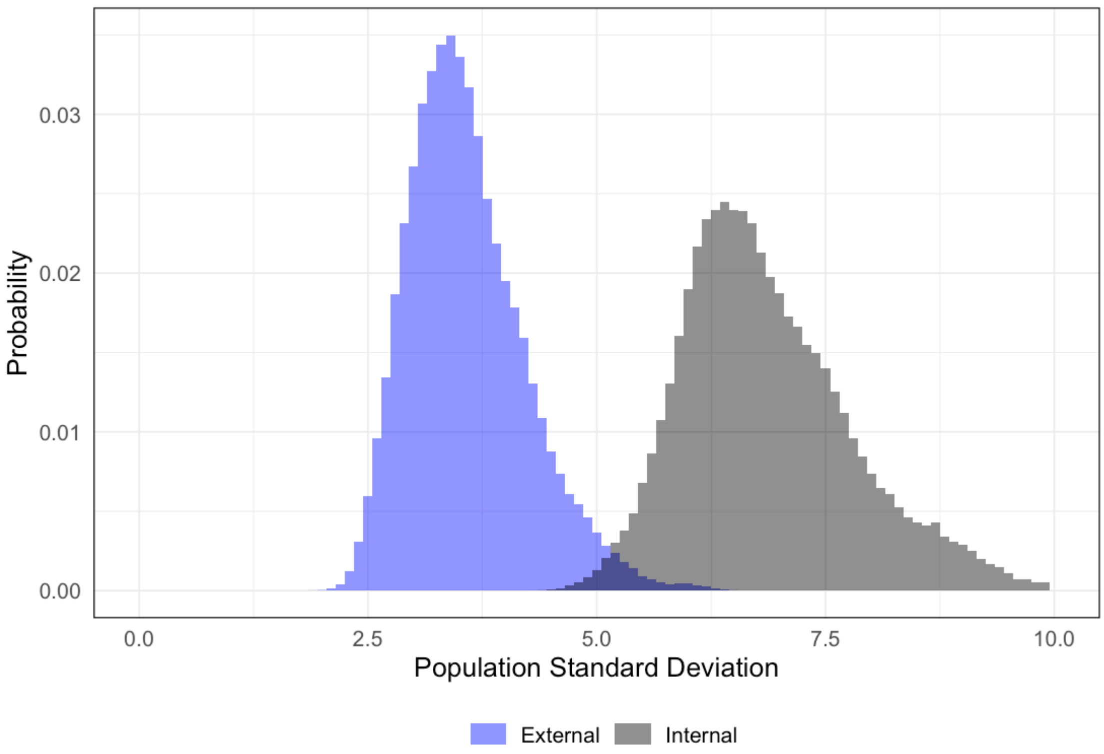

Figure S19: Overall posterior distribution for the population standard deviation parameters. The output from the 5 MCMC runs have been combined together to obtain the overall probability of each parameter.

Posterior distribution of weights

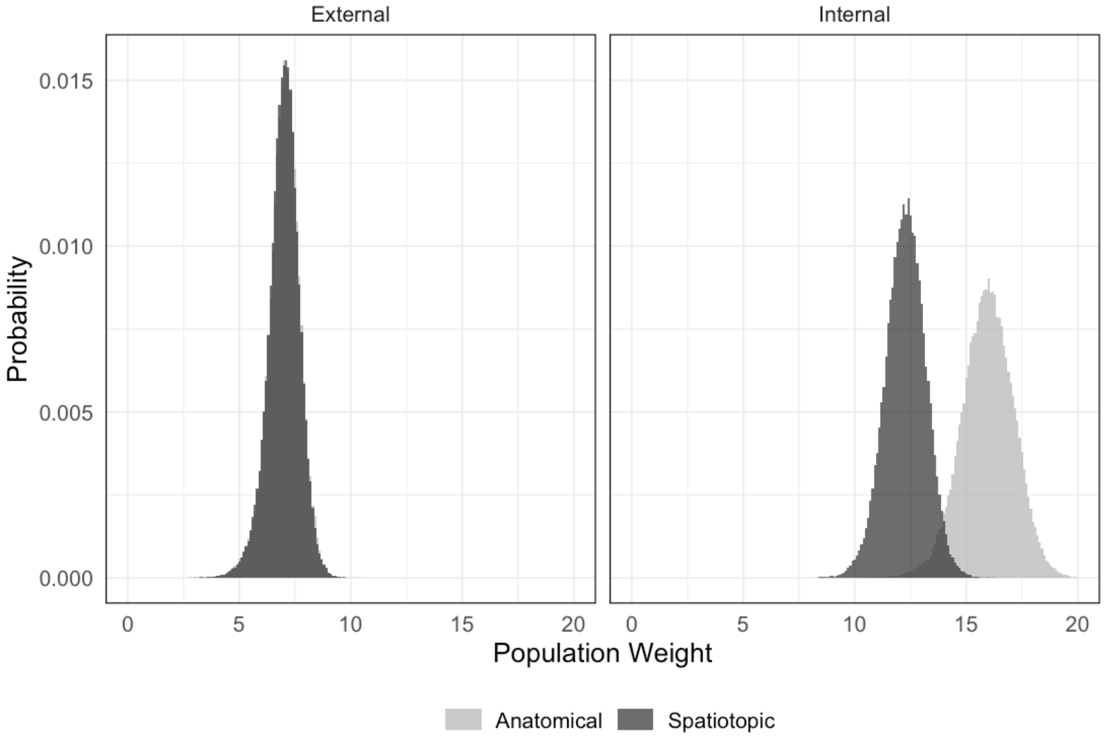

Figure S20: Overall posterior distribution for the population weight parameters for each condition. The values for the spatiotopic condition were calculated by multiplying the anatomical weight parameter by the task context parameter on each trial.

CHAPTER 4: HAPTIC AWARNESS CHANGES WHEN LYING DOWN

Unwalla, K., Cadieux, M.L., & Shore, D.I. (submitted). *Scientific Reports*

Abstract

Accurate localization of touch requires the integration of two reference frames—an internal (e.g., anatomical) and an external (e.g., spatial). Using a tactile temporal order judgement task with the hands crossed over the midline, we investigated the integration of these two reference frames. We independently manipulated the reliability of the visual and vestibular information, both of which contribute to the external reference frame. Visual information was manipulated between experiments (Experiment 1 was done with full vision and Experiment 2 was done while wearing a blindfold). Vestibular information was manipulated in both experiments by having the two groups of participants complete the task in both an upright posture and one where they were lying down on their side. Using a Bayesian hierarchical model, we estimated the perceptual weight applied to these reference frames. Lying participants on their side reduced the weight applied to the external reference frame and produced a smaller deficit; blindfolding resulted in a further reduction. These findings reinforce the importance of the visual system when weighting tactile reference frames, and highlight the importance of the vestibular system in this integration.

Introduction

The location of sensations on the skin surface are coded in an internal reference frame—adjacent locations on the skin activate adjacent neural tissue in the somatosensory cortex. To interact with the objects causing these sensations, this internal, body-centric reference frame, is remapped to an external reference frame, most likely coded in the posterior parietal cortex [1]. To accurately localize a touch in space, both the posture of the body and its position in space must be considered since the limbs have multiple degrees of freedom. One posture—crossing the hands over the body midline—has provided great insight into the two reference frames used to localize a tactile stimulus in space. The present experiments examined the impact of altering visual and vestibular frames of reference during tactile localization.

The tactile temporal order judgment (TOJ) task provides an excellent index of the deficit that occurs when crossing the hands over the midline. This task asks participants to indicate which hand received the first of two vibrations, one presented to each hand [2,3,4,5,6]. This task is completed while the participants' hands are uncrossed and when the hands are crossed over the midline. Consistently, accuracy is reduced when the hands are crossed compared to uncrossed. The integration model of this crossed-hands deficit [2,4] assumes that tactile remapping occurs automatically, producing spatial coordinates for the touch. Responding to the tactile stimulus requires integrating the external, spatial, coordinate with the internal, skin-based, coordinate. The deficit observed when the hands are crossed arises because of differential weights placed on the two coordinates when determining the location of the touch. It is important to note that in a crossed-hands posture, these external coordinates point to the incorrect response. As a result, the integration model suggests that a larger weight placed on the external reference frame should lead to a larger crossed-hands deficit.

In line with the integration model, removing visual information leads to a smaller crossed-hands deficit [7]. The use of a blindfold likely decreases the reliability of the external reference frame by impeding the ability to visually locate the hands in external space. Similarly, late-blind individuals also show a smaller crossed-hands deficit with the magnitude of the deficit being similar to that observed among blindfolded participants [8]. No crossed-hands deficit is measured in congenitally blind participants, with high accuracy observed in both crossed and uncrossed postures [8,9]. Together, these results highlight the role of vision in establishing the reliability of the external reference frame.

Similarly, we predict that the reliability of the external reference frame may be reduced by manipulating the perceived direction of upright (i.e., the subjective vertical). Multiple cues contribute to the subjective vertical, such as the orientation of mono-oriented objects in the visual environment, the impact of gravity on the vestibular organs, and the pressure felt from surfaces underneath our body [10,11]. Lying down misaligns these sources of information with respect to the direction of upright and reduces the reliability of the subjective vertical.

Evidence for this reduced reliability can be derived by comparing the subjective visual vertical (SVV) to the perceptual upright (PU) [10]. During the SVV task, participants indicate when a line is oriented with the direction of gravity: “what direction will a ball fall when dropped”. For the PU task, participants are asked to indicate whether a visually presented letter is a ‘p’ or a ‘d’. The reported letter provides an indirect measure of the participants’ perception of upright, as both are identical characters, except rotated 180 degrees. These tasks were differentially affected by lying down on one side. When sitting upright, both the SVV and the PU produce similar responses: all cues (body, visual, and gravity) indicate the same direction for upright. Lying down produces different responses in these two tasks: the SVV remains aligned with gravity while the PU aligns with the body, revealing two different perceptual directions of upright.

These conflicting signals, when lying down, should degrade the overall reliability of determining which way is up. Altering the reliability should impact the relative weights placed on the internal and external reference frame. Since body-based cues for upright will be misaligned with visual and gravitational cues (obtained through the vestibular system), the overall reliability of the external reference frame should be reduced, leading to a lower external weight, and a smaller crossed-hands deficit. However, it is also possible that the reliability of the subjective vertical does not influence the external reference frame, in which case, we would expect to see a similar magnitude of deficit in the crossed-hands posture when lying down compared to when sitting upright.

In the present studies, participants completed a tactile TOJ task by indicating which hand received the first vibration with their hands crossed and uncrossed. They completed this task while sitting upright or lying on their left side. Experiment 1 allowed participants to see their hands and the room around them. Experiment 2 removed the misaligned visual information by having new participants perform the same task wearing a blindfold. The key finding relates to the relative size of the crossed-hands deficit when sitting upright and lying down; the impact of blindfolding should replicate previous findings demonstrating a reduced deficit [7].

Methods

Participants

Participants reported normal or corrected-to-normal vision and were naïve to the purpose of the experiment. All participants provided written informed consent prior to participation, and were remunerated with one course credit. All procedures were approved by and conformed to the relevant guidelines and regulations of the McMaster Research Ethics Board, and complied with the tri-council statement on ethics (Canada). For Experiment 1, twenty participants (10 males; 14 right-handed) with an average age of 18.4 years were recruited from the McMaster University, using an online recruitment tool. For Experiment 2, twenty (10 males; 16 right-handed) new participants, with an average age of 22.5 years were recruited using the same recruitment and screening procedures. Sample sizes were determined based on the conventional number of participants used in past tactile TOJ studies. No participants were removed in either experiment for analysis.

Apparatus & Stimuli

Participants were seated at, or lying down on a table (73.7 cm in height). When lying down a soft foam mattress was placed on the table for comfort. They held two wooden boxes, separated by 18 cm with their thumbs in contact with the tactile stimulators. In the lying down position the participants' hands were supported by foam triangles to mimic the hand position while upright (**Fig. 1**). The tactile stimulator (100 Ohm Oticon-A bone-conduction vibrator, measuring 1.6 cm in width and 2.4 cm in length) was placed on top of the response buttons, and the entire apparatus was enclosed in a small wooden box with a Plexiglas top. A 2 cm diameter hole was cut into the Plexiglas for participants to place their thumbs and push down on the vibrator to make a response. The vibrators were driven by an amplified 250 Hz sine wave that was suprathreshold and identical for all participants. All stimulation was controlled by a set of reed-relays connected to the parallel port of a DELL Dimension 8250, running Windows XP software. Matlab was used to deliver the stimulation and collect the participants' responses.

Participants wore earbud headphones playing white noise to mask the sounds produced by the tactile vibrators.

Experiment 2 used the same apparatus, but additionally had a pair of swimming goggles with the lenses painted black as a blindfold for participants.

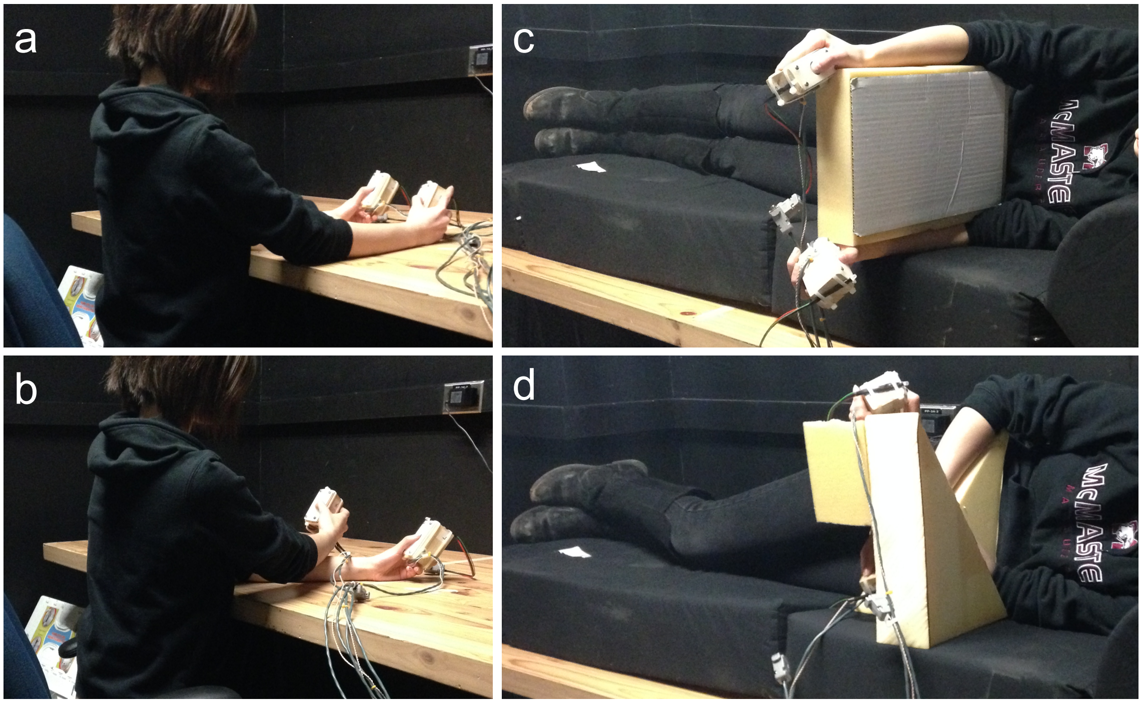

Figure 1: Hand and body postures used for Experiments 1 and 2. (a) participant sitting upright with hands uncrossed, (b) participant sitting upright with hands crossed, (c) participant lying on left side with hands uncrossed, and (d) participant lying on left side with hands crossed.

Procedure

Participants first completed two practice blocks, each with 16 trials. The first block of practice trials was completed with their hands uncrossed, and the next with their hands crossed over the midline. Hands were crossed with their right hand on top. The practice trials were completed either upright or lying down, depending on which posture the participant was to complete first. The experimenter was in the room during the practice trials to provide feedback and answer questions. Participants then completed 12 experimental blocks, each with 64 trials.

The number of trials was chosen in order for the experiment to be completed within 1-hour and to ensure the participant did not get uncomfortable or tired. The experimenter would start the block and leave the room, check on the participant after each block and start the next block. The experimental blocks were broken down into four sets of three blocks each. The first six blocks were completed either sitting upright or lying on their side, and the subsequent six were completed in the alternate body posture. Within each body posture, three consecutive blocks were completed with their hands uncrossed, and the other three with their hands crossed. The starting hand posture and body posture were counterbalanced across participants.

Each trial began 800 ms after the participant's previous response. Each trial consisted of two 20 ms vibrations, one to each thumb, separated by one of four fixed stimulus onset asynchronies (SOAs): ±400, ±200, ±100, ±50 ms, where negative SOAs indicate the vibration was to the left hand first. This resulted in 24 trials for each body posture, hand posture, and SOA. After the second vibration occurred, participants responded by pressing down on the vibrator held in the hand that received the first vibration. If no response occurred within three and a half seconds of the second vibration, the trial timed out. To alert the participant that they missed a trial, both buttons vibrated three times. To move on, participants pressed and released both buttons. Time out trials and trials with premature responses (i.e., responses made less than 100 ms after the second vibration) were removed from all analyses. This resulted in the removal of 16 trials across 9 participants in Experiment 1, and 32 trials across 10 participants in Experiment 2.

Experiment 2 followed the identical procedure, except all participants were blindfolded for the entire experiment.

Analysis

The magnitude of the crossed-hands deficit was evaluated using the proportion correct difference (PCD) score [3, 12]. The difference in accuracy between the crossed and uncrossed postures were summed across SOAs. To determine whether the size of the deficit differed based on body posture and visual information, a 2x2 analysis of variance (ANOVA) was conducted on the PCD scores with body posture (upright vs. lying down) as a within-subject factor and visual information (blindfold vs. no blindfold) as a between-subject factor. One sample *t*-tests, comparing the PCD score to 0 were conducted to evaluate the presence of a crossed-hands deficit. Given that these were hypothesis driven tests, we did not correct for multiple comparisons. For the ANOVA, effect-size was computed as eta-squared, and as Cohen's d for the *t*-tests. All significance tests were two-sided and used an alpha level of 0.05.

Reference frame weights were calculated using the equations outlined by Badde et al. (2016). These equations were implemented using a modified version of their hierarchical model. An internal and external weight (ω) pair were used to generate the slope (θ) of the logistic function; the probability of a right-first response as a function of SOA (t) for both crossed and uncrossed postures (Equation 1). For the uncrossed posture the internal and external reference frames provide congruent information, so θ is the sum of the internal and external weights. In the crossed posture the reference frames conflict, so θ is the difference between the weights.

$$(1)\ p(t) = \frac{1}{1+e^{-\theta t}}$$

Where:

$$\theta_{uncrossed} = \omega_{internal} + \omega_{external}$$

$$\theta_{crossed} = \omega_{internal} - \omega_{external}$$

Each experiment (blindfold vs. no blindfold) was modelled separately. For each experiment, a Markov Chain Monte Carlo (MCMC) simulation using a Metropolis-Hastings sampling algorithm, simulated using R studio, was used to provide an estimate of the population internal weight, external weight, and the standard deviation associated with the weights (see Badde et al., 2016). These parameters were approximated by truncated Gaussian distributions (limits = 0, ∞), with unknown means and standard deviations. Strictly positive, uniform hyperpriors were applied to all population parameters. The priors on the individual participants' weights were constrained by the population distribution.

On each trial of the MCMC simulation, a new hypothesis was generated. Each hypothesis consisted of 46 parameters, 6 population-level parameters and 40 participant-level parameters. The 6 population parameters were: the mean internal and external weights ($\mu_{internal}$ and $\mu_{external}$) and standard deviations ($\sigma_{internal}$, $\sigma_{external}$) in the upright posture, and an internal and external weight task context parameter ($\delta_{internal}$ and $\delta_{external}$). The task context parameter determines the magnitude of the effect the body posture manipulation has on the internal and external weight. A context parameter less than 1 indicates the weight was reduced when lying down; a context parameter greater than 1 indicates that the weight increased when lying down; while a context parameter equal to 1 would indicate no change in the weights when lying down. As is customary in MCMC modelling, the manipulation (lying down) was assumed to affect all participants equally; as such, the weights while lying down were calculated by multiplying each participants' upright weights by the population task context parameters. For example, if the task context parameter was 2, then the weights while lying down would be twice as large as the weights while upright. To be clear, the posterior distributions of two parameters were approximated for each individual participant: an internal and external weight ($\omega_{internal}$ and

$\omega_{external}$) for the upright condition; the lying down condition used these same weights and multiplied them by the population context parameters ($\delta_{internal}$ and $\delta_{external}$). One hypothesis generated four psychometric curves for each participant—two for each body posture and two for each hand posture.

(2)

$$p(H|D)$$

$$\propto \prod_{i}^{N} p(d_i |\, \omega_{int\ i}, \omega_{ext\ i})_i \prod_{i}^{N} p(\,\omega_{int\ i}, \omega_{ext\ i} \big| \mu_{int,}\mu_{ext}, \delta_{int,}\delta_{ext}, \sigma_{int}, \sigma_{ext}) p\big(\mu_{int,}\mu_{ext}, \delta_{int,}\delta_{ext}, \sigma_{int}, \sigma_{ext}\big)$$

Where:
$H = \{\omega_{int\ i}, \omega_{ext\ i}, \mu_{int,}\mu_{ext}, \delta_{int,}\delta_{ext}, \sigma_{int}, \sigma_{ext}\}$
$i = 1$
N = number of participants in the experiment

(3)

$$\log(\,p(d_i|\omega_{int\ i}, \omega_{ext\ i})) = \sum_{\mathrm{t}} r_{t\ i} \cdot \log\big(p_i(t)\big) + l_{t\ i} \cdot \log\big(1 - p_i(t)\big)$$

Where:
p(t) is defined in Equation 1
d_i = the data from participant i
$\omega_{int\ i}, \omega_{ext\ i}$ = the hypothesized internal and external weight values for each participant
$r_{t\ i}$ = number of right-first responses
$l_{t\ i}$ = number of left-first responses (i.e., the number of trials – number of right first responses)
t in {±400, ±200, ±100, ±50}

Bayes' formula was used to calculate the posterior probability of a hypothesis, H, given the data set (D) (Equation 2). The probability of each participant's data (d_i) given the participant's hypothesized weights were calculated using the binomial distribution at each SOA (Equation 3), with proportion right-first responses p(t). This probability was then multiplied by the prior probability of the upright weights. The joint posterior, P(H|D), was then approximated using MCMC.

For each Experiment, five Markov chains with 250,000 samples were run, with the first 50,000 samples removed as the burn-in period. These values were chosen to ensure an appropriate convergence of the model. Experiment 1 had a convergence metric, $\hat{R}$, between 0.91 and 1.02, indicating that the chains had converged [13]. Experiment 2 showed similar convergence with $\hat{R}$ between 1.00 and 1.02. Random values for each of the 46 parameters were chosen as initial values for the chains. Future parameter values were chosen from a Gaussian distribution with a mean centered on the previous parameter value and proposal standard deviations of 0.26 for the weights, and 0.23 for the population standard deviations, and 0.02 for the task context parameter. We selected these values to obtain acceptance rates between 20–35 percent [14]. In Experiment 1 all runs had an acceptance rate of 21 percent, and in Experiment 2 the acceptance rate was between 32 and 33 percent.

Results

A separate PCD score was calculated for each participant in both the upright and lying down postures. Data from Experiment 1 and Experiment 2 were submitted to the same ANOVA with body posture (upright vs. side) as a within-subject factor, and vision (no blindfold vs. blindfold) as a between-subject factor. Based on the PCD scores, lying down produced a smaller deficit (M = 0.26, SD = 0.59) compared to sitting upright (**Fig 2;** M = 1.28, SD = 1.03; $F_{(1,38)}$ = 37.37, $p < .001$, $\eta_g^2 = .30$). Blindfolding further reduced the deficit (M = 0.50, SD = 0.63) compared to intact vision (M = 1.04, SD = 1.18; $F_{(1,38)}$ = 8.21, $p = .007$, $\eta_g^2 = .11$), replicating results using similar methods [7]. There was no significant interaction between body posture and vision ($F_{(1,38)} = 1.70$, $p = .201$, $\eta_g^2 = .02$). One-sample *t*-tests comparing the PCD score to 0 confirmed that the crossed-hands deficit remained with intact vision (Upright: $t_{(19)} = 6.16$, $p < .001$, $d = 1.38$; Side: $t_{(19)} = 2.37$, $p = .03$, $d = 0.53$) and while blindfolded (Upright: $t_{(19)} = 6.12$, $p < .001$, $d = 1.37$; Side: $t_{(19)} = 2.23$, $p = .03$, $d = 0.51$), but the size of the deficit when lying down and blindfolded was less than 5% the size of the deficit seen when upright with vision.

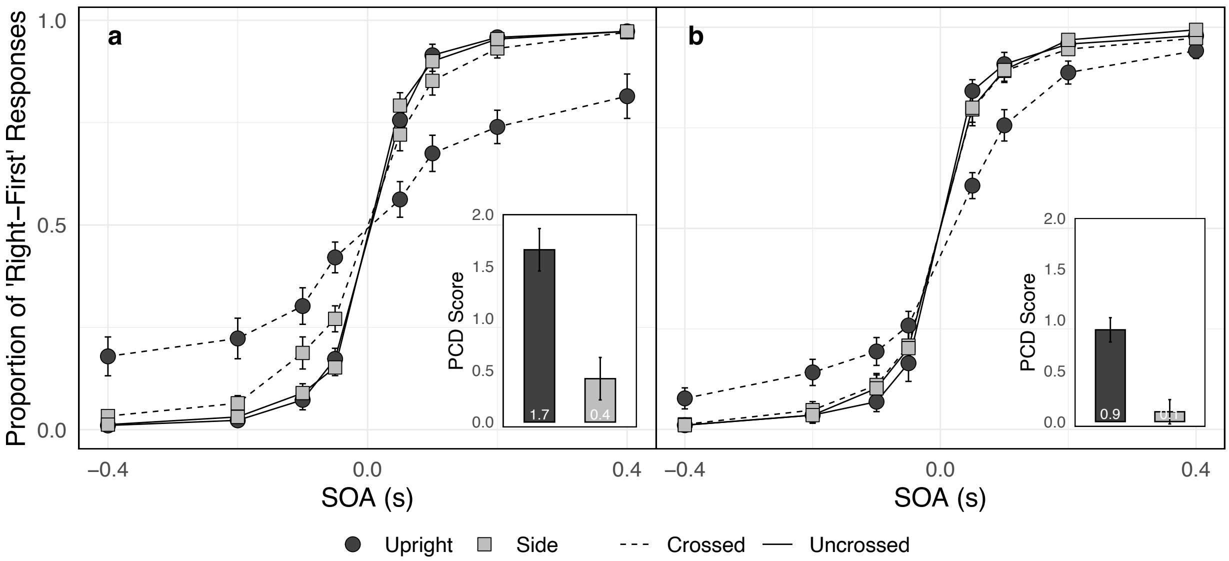

Figure 2: Overall proportion of right-first responses while wearing (**a**) no blindfold and (**b**) a blindfold. Participants indicated which hand was vibrated first, and the average proportion of 'right-first' responses was calculated at each SOA. Negative SOAs indicate the left hand received the vibration first. The average PCD score for each condition is represented in the bar graphs. Error bars represent standard error of the mean corrected for a within-subject design [15,16].

Population estimates for the internal and external weights were derived using a Markov Chain Monte Carlo simulation, with the posterior probability of each hypothesis being calculated using Bayes' formula. To determine whether the internal and external weights (**Fig 3**) were affected by the manipulation of lying down, we calculated equal-tail 95 percent credible intervals on the task parameters. For both experiments, the external task parameter was less than 1 (Experiment 1: 0.31 [0.22, 0.41], Experiment 2: 0.16 [0.04, 0.30]), indicating a drastic reduction in the weight assigned to the external reference frame. The internal task parameter was larger than 1 (Experiment 1: 1.25 [1.16, 1.35], Experiment 2: 1.16 [1.08, 1.25]), indicating an increase in the weight placed on the internal reference frame. Based on the weight parameters observed across experiments, blindfolded participants presented with greater reductions to the external weight and a larger increase in the internal weight.

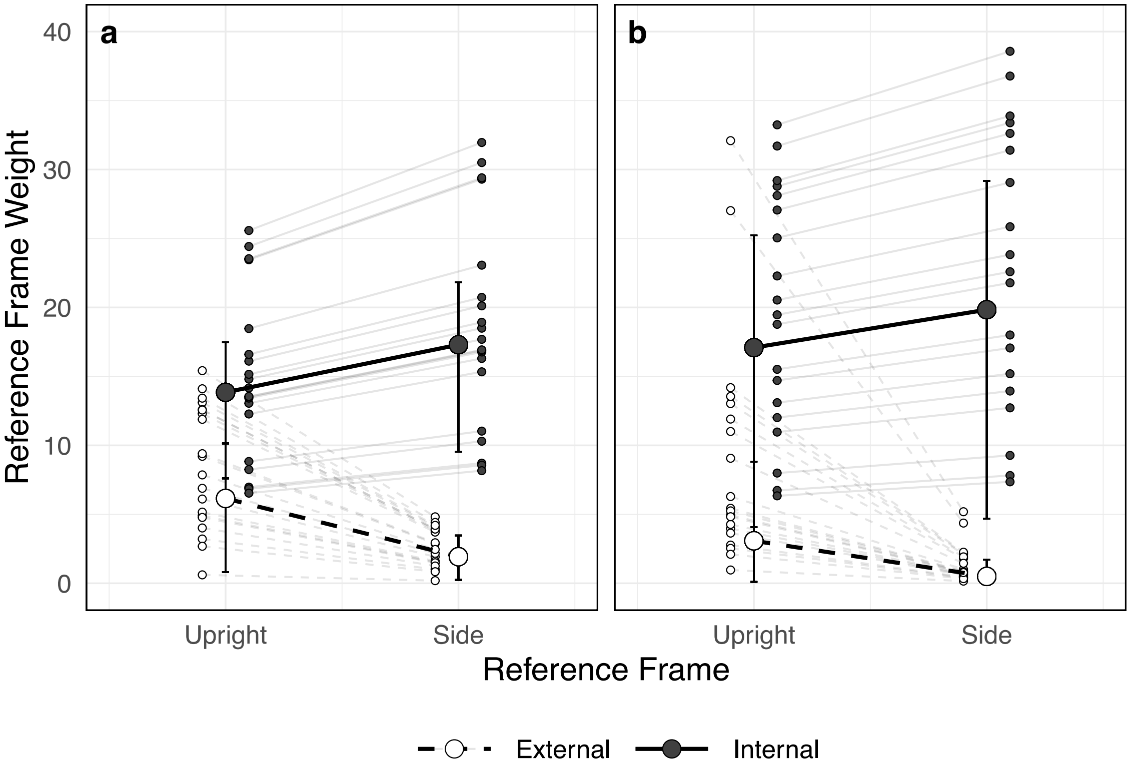

Figure 3: Overall population internal and external weights for each body condition based on whether participants were wearing (**a**) no blindfold or (**b**) a blindfold. Error bars represent 95 percent credible intervals calculated directly from the MCMC posterior distributions. The small circles represent individual participant weights.

Discussion

The novel findings here concern the effect of lying down on the size of the crossed-hands deficit. Based on the modelling of these data, we conclude that this reduced deficit comes primarily from reducing the weight to the external reference frame. This finding was replicated across the two experiments, with and without vision. When blindfolded (Experiment 2), we observed a further numerical decrease in the magnitude of the crossed-hands deficit. Modelling showed a concomitant decrease in the external reference frame weight. The smallest deficit was measured when blindfolding was combined with lying down suggesting that both manipulations contribute to the simulation of the external world in independent ways. It is important to note that the role of visual information was compared using a separate group of participants. As such additional studies are needed to confirm the combined influence of lying down and blindfolding.

The impact of blindfolding replicates previous findings [7]. In the absence of visual information, either through blindfolding [7] or being congenitally blind [8, 9], a smaller crossed-hands deficit is observed. Our results extend these previous findings by showing that the decreased deficit is the result of less weight being placed on external information. This further supports the external coordinates for touch being strongly linked to visual information.

Further evidence for the involvement of vestibular information during tactile localization comes from the application of galvanic vestibular stimulation (GVS), which stimulates the vestibular nerve. When applied, participants are less accurate at localizing where a touch occurred on the hand [17], and poorer at locating where their arm is in space [18]. Vestibular information also helps provide a sense of body ownership. Currently we accept that our sense of body ownership and posture are malleable and heavily influenced by vision. Consider the rubber hand illusion [19] where seeing a rubber hand brushed while simultaneously feeling your own hand brushed induces a sense of ownership over the rubber hand. When GVS is applied during the rubber hand illusion a larger proprioceptive drift is observed in the direction of the rubber hand, indicating greater ownership over the rubber hand [20].

It is generally accepted that the crossed-hands deficit is the result of a weighted integration of information from the internal and external reference frames. However, some recent studies have called into question the assumption that the conflict occurring during the integration process is the result of the external spatial location of the touch [21, 22]. These studies have shown that the external location may not be required to locate the touch to the hand, and instead the conflict may stem from information related to the body side of the touch or the canonical body posture of the hand. While these studies do present an exciting avenue for future research, their ability to explain the results of many previous crossed-hands tactile TOJ studies remains to be seen (i.e., the role of task demands [7, 9, 23], or the role of vision [7, 8]).

Based on the present experiments it is impossible to fully disentangle the contributions of visual, vestibular, and body-based information to the weight placed on the external reference frame. Future studies could attempt to separate these influences, for example, by disrupting the vestibular system using galvanic vestibular stimulation, or using a microgravity environment [24]. Future work could expand these underlying assumptions about this reference frame, as this has implications on how we understand our body representation [25].

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CHAPTER 5: GENERAL DISCUSSION

This thesis had three main objectives. First, to determine whether the crossed-hands tactile TOJ task is a useful measure of reference frame integration I investigated the task's reliability (Chapter 2). I then employed a probabilistic model to measure the underlying reference frame weights. Chapter 3 applied the model to investigate how a bias toward the internal or external reference frame would influence the weighted integration of each reference frame. Finally, in Chapter 4 I applied the model to better understand a novel manipulation to the crossed-hands deficit, whether body position would influence the magnitude of the crossed-hands deficit.

Here I briefly summarize the main findings of the current thesis. Chapter 2 assessed the reliability of the tactile TOJ task across two sessions and within a single session. Reliability was first assessed across two sessions, separated by one week. The magnitude of the crossed-hands deficit, as measured through the PCD score, remained consistent across both test sessions. Next, reliability was evaluated within a single test session. Split-half reliability estimates from 23 previous experiments in the Multisensory Perception Laboratory revealed stable performance within a session for both males and females. Taken together, the findings of Chapter 2 highlighted that a participant's performance on a tactile TOJ task, and therefore the size of their crossed-hands deficit, was consistent within and between sessions. The tactile TOJ task is frequently used to infer the weights placed on the internal and external reference frames, as well as to investigate individual differences in reference frame integration. Given the high reliability of the task, we have confirmed that this is a useful measure to assess reference frame weights and individual differences.

Chapters 3 and 4 investigated how two different manipulations influence the weights an individual places on each reference frame. Chapter 3 varied the task instructions to bias individuals towards either the internal or the external reference frame. By emphasizing the hand that receives the vibration, the anatomical response demand biased judgements towards the internal reference frame. In contrast, the spatiotopic response demand highlighted the hemispace of the vibration, biasing judgements towards the external reference frame. Results showed that the deficit increased under a spatiotopic response demand. A hierarchical model explained this increased deficit as the result of either a larger weight on the external reference frame or a smaller weight on the internal reference frame. Both options placed relatively more weight on external information, thereby showing that task instructions can alter how the internal and external reference frames were integrated.

The results from the probabilistic model seem to corroborate the predictions based on the integration model for the crossed-hands deficit, specifically that emphasis on external information resulted in a relatively greater weight placed on the external reference frame. Having established that the probabilistic model provides estimates of the internal and external reference frame weights, we applied the model to explore how body position and visual input influence reference frame weights. Chapter 4 had participants perform the crossed-hands tactile TOJ task while sitting upright and while lying on their side. When lying down, participants showed a smaller crossed-hands deficit. Modelling these data revealed that lying down resulted in a large decrease to the external reference frame weight, and a slight increase in the weight on the internal reference frame. We interpret the reduction of external weight to be caused by conflicting directions of upright. A follow-up experiment was completed with all participants blindfolded to assess whether the decreased deficit was the result of misaligned visual information. The addition of this manipulation resulted in a further reduced deficit. Moreover, blindfolding resulted in additional decreases to the external weight, and small increases to the internal weight. Other factors, in addition to incongruent visual information are responsible for the weight changes observed when lying down. Specifically, body-based cues or gravitational information obtained through the vestibular system play a role in the creation of the external reference frame.

Individual Differences in Reference Frame Integration

The crossed-hands tactile TOJ task is one of the most commonly used paradigms to investigate reference frame integration during tactile localization. Chapter 2 highlighted that how an individual relies on their reference frames remains stable over time. As such, this task is a useful indicator of the processes underlying tactile localization, strengthening its use in understanding individual differences in reference frame integration.

While, based on the results of Chapter 2, there are small within-individual differences, there have been large between-individuals differences reported for crossed-hands tactile TOJ performance (Cadieux et al., 2010), yet few factors can accurately predict these performance differences. Sex at birth was one factor that seemed to predict a smaller deficit among males than females (Cadieux et al., 2010). However, Chapter 2 showed this sex effect may not be as prevalent as previously believed. Among all 23 experiments used in Chapter 2, only three experiments revealed a significant effect of sex and another three trended towards significance. It is possible that the effect of sex may not be a large source of individual differences observed on the tactile TOJ task. Alternatively, it is also possible that differences in the experimental design, methods, or measures across studies may have contributed to the inconsistencies in observed sex-related effects. For example, in the majority of studies that do show an effect of sex, participants were responding using hand buttons while sitting upright. The lack of additional conditions (i.e., body posture, task instructions, vision) in these studies increased the number of trials at each SOA, which may have reduced the noise in the measure, providing sufficient power to measure a sex effect. Another possibility is that these manipulations provide participants with a strategy that both males and females employ, causing similar performance on the task.

It is possible that other individual differences apart from sex may contribute to differences in susceptibility to the crossed-hands deficit, yet few have been reported. Certain clinical disorders have been shown to alter the magnitude of the crossed-hands deficit. For example, children diagnosed with autism show a smaller crossed-hands deficit than healthy controls (Wada et al., 2014). It is presumed that these children place a greater weight on internal information, resulting in a smaller deficit. In contrast, those who measure high on schizotypy show a larger crossed-hands deficit (Ferri et al., 2016). These individuals are predicted to place less emphasis on somatosensory information, and therefore weight external information to a greater degree.

One potential source of variation could be age, as older adults (65+ years) generally show heightened multisensory integration (de Dieuleveult et al., 2017; Mahoney et al., 2011), which could affect the crossed-hands deficit. That said, older adults perform equivalently to younger adults on the rubber hand illusion (RHI; Campos et al., 2018; Marotto et al., 2018; Palomo et al., 2017). Given that tactile, proprioceptive, and visual information are integrated during both the RHI and the tactile TOJ task, it is possible that age would not alter the magnitude of the crossed-hands deficit. Furthermore, the experiments in this thesis tested participants between the ages of

18 and 35 years-old, so this would not likely be a source of variation among the studies in this thesis.

Individual sensory abilities such as visual acuity might also affect the size of the crossed-hands deficit. Visual information alters the weight placed on the external reference frame. For instance, blindfolded participants, or late-blind individuals have a smaller crossed-hands deficit compared to sighted participants (Cadieux et al., 2013; Crollen et al., 2019; Röder et al., 2004). It is possible that lower visual acuity might reduce the reliability of external information, thereby reducing the weight placed on the external reference frame. If so, individuals with lower visual acuity might have a smaller crossed-hands deficit. The studies in this thesis controlled for this factor such that participants were screened to ensure that they had normal or corrected-to-normal visual acuity. However, it is possible that some differences may exist between individuals with normal compared to those with corrected-to-normal vision, or that differences will exist when corrective lenses are not used. Future studies could investigate this by measuring visual acuity and correlating these scores with the magnitude of the crossed-hands deficit.

Chapter 4 highlighted how vestibular information could alter the weight placed on the external reference frame. As a result, individuals with vestibular disorders might show systematic differences in the magnitude of their crossed-hands deficit. These individuals would likely present with a smaller deficit as a result of less reliable vestibular information compared to individuals without vestibular disorders. None of the studies included in this thesis controlled for the presence of a vestibular disorder. Future studies could test whether vestibular disorders do indeed alter the magnitude of the crossed-hands deficit. More research is required to fully understand the cause of these individual differences in the crossed-hands deficit.

Task Instructions Alter the Crossed-Hands Deficit

Chapter 3 showed that task instructions biased the weights placed on the internal and external reference frames. As a result of these different instructions, the magnitude of the crossed-hands deficit was altered. Our results replicated those of previous studies using the same manipulations (Cadieux & Shore, 2013; Crollen et al., 2019). These are not the only instructions that have been shown to impact the size of the deficit. There is some evidence that instructions that alter the attentional focus of the participant can influence the size of the crossed-hands deficit (Lorentz, 2020). For instance, a larger deficit is observed under instructions that ask participants to focus on the task as opposed to instructions that place the participants in a diffuse mental state.

Furthermore, changes to the tactile TOJ instructions were used to create the first touch localization (FTL) task (Badde et al., 2015a). The tactile TOJ task asks participants to indicate which of two vibrations occurred first, while the FTL task asks participants to indicate the location of the first vibration. Two instructional changes differentiate the tactile TOJ task from the FTL task. In the FTL task participants are told to ignore the second vibration, and they are also told to respond as fast as possible to the location of the first vibration. As a result of these instructional changes a smaller deficit was observed in the FTL task compared to the tactile TOJ task. In this study the effect of ignoring the second vibration, and making a speeded response are confounded. Therefore it is impossible to evaluate which instructional change influenced the weights. Regardless, this study provides additional evidence that the size of the crossed-hands deficit is influenced by the instructions provided when completing the task.

Even instructional changes for a response given after making judgements on the temporal order can affect the magnitude of the crossed-hands deficit (Badde et al., 2015b). For instance, in

Badde et al. (2015b) participants were presented with one high and one low frequency vibration stimulus, one to each hand. Participants first responded with regards to the temporal order of the two vibrations by indicating which hand received the first stimulus. After making the temporal order judgment, participants were asked to make a secondary spatial response by providing the location of the stimulus presented at a certain frequency (either high or low frequency depending on the participant). Two different instructions were provided for the secondary response. Internal instructions tied the location of the stimulus of a certain frequency to the hand, while external instructions tied the location of the stimulus of a certain frequency to a side of space. The size of the deficit observed for the TOJ task was smaller when the secondary spatial response used internal rather than external instructions. The change in the magnitude of the deficit shows that participants are able to flexibly adapt the weights placed on each reference frame, based on the demands of the task.

Other tasks have also shown an influence of instructions that bias attention towards either internal or external information. One such task is a tactile congruency task where participants had to indicate the location of a tactile target to the hand while ignoring a tactile distractor (Gallace et al., 2008; Schubert et al., 2017). External instructions required the participant to indicate whether the target appeared at an upper or lower location relative to gravity; internal instructions asked participants where on the hand the target was located. The tactile distractor was always presented on the opposite hand and could appear at a location that was congruent or incongruent with the target. Under internal instructions, accuracy was higher when the distractor occurred at an anatomically congruent location (e.g., target and distractor on palm) compared to an anatomically incongruent location (e.g., target on palm and distractor on back of hand). Similarly, when using external instructions, accuracy was best when the distractor was externally congruent (e.g., target and distractor at upper location) compared to externally incongruent. This once again shows that the weights applied to the internal and external reference frames can be altered by task instructions.

Most published studies investigating the crossed-hands deficit do not report the exact instructions used to administer the tactile TOJ task. As such, the results of many previous crossed-hands tactile TOJ tasks could have been partly influenced by the instructions provided to participants. Except for the studies intentionally manipulating instructions, all the studies conducted within the Multisensory Perception Lab used identical task instructions, therefore instructions would not account for the differences observed between these studies. Knowing that instructions can affect the size of the deficit, it might be important for future studies to publish the exact instructions used on the task. This would ensure that the results can be properly replicated, and allow for more accurate comparisons across different studies.

The Role of Sensory and Cognitive Inputs on the Integration of Reference Frames

The present findings add to a growing body of literature supporting the weighted integration of internal and external information during tactile localization. Many factors have been found to bias the weight placed on each reference frame. Studies attempting to strategically bias reference frame weights often take two different approaches. The first approach is to manipulate the presence or absence of the sensory information among individuals with normal sensory function (e.g., remove visual inputs through blindfolding). The second approach involves comparing individuals with normal sensory functioning to those with sensory impairments (e.g., blind individuals).

One of the most investigated sensory influences on reference frame integration is visual information. Blindfolded participants present with a smaller crossed-hands deficit compared to participants who are not wearing a blindfold (Cadieux & Shore, 2013). Viewing fake uncrossed hands compared to fake crossed hands, while the real hands are crossed, also reduces the crossed-hands deficit (Azanón & Soto-Faraco, 2007). The underlying process here may be similar to what occurs during the RHI, where vision of a fake hand being stroked overrides tactile and proprioceptive information (Botvinick & Cohen, 1998). False, but relevant, visual information can influence the weighted integration of reference frames. Early blind individuals do not present with a crossed-hands deficit, as the lack of visual information from birth leads to the integration favouring only internal information (Crollen et al., 2019; Röder et al., 2004).

Other sensory inputs apart from vision have also been shown to influence the weighted integration of internal and external information. Chapter 4 highlighted that vestibular information also affected tactile TOJ performance. This is the first study to manipulate vestibular inputs during a tactile TOJ task by having participants lie down during the task. It has previously been shown that vestibular input, from galvanic vestibular stimulation (GVS), interferes with accurate localization of touches to the hand (Ferrè et al., 2013). For instance, in Ferre et al. (2013), when GVS was applied, a touch on the hand was mislocalized as occurring closer to the wrist compared to when GVS was not applied. The vestibular system is also involved when locating the arm in space (Schmidt et al., 2013). For instance, in Schmidt et al. (2013) participants were asked to indicate when their hidden arm was aligned with a target light, while the arm was passively moved horizontally at a constant speed. Individuals showed larger arm position errors during GVS than in the absence of GVS. It has also been shown that GVS causes inaccurate arm movements towards a visual target (Bresciani et al., 2002). Given that accurate tactile localization uses both touch and proprioception, it makes sense that vestibular information would influence the magnitude of the crossed-hands deficit.

Information from the various senses are abstracted to inform the internal and external reference frames, but more than just sensory information influences the relative weighting of the reference frames. As mentioned previously, the magnitude of the crossed-hands deficit is sensitive to changes in task instructions. This suggests that cognitive processes may also modulate the weighted integration of the reference frames in a top-down manner. Other cognitive factors have been shown to affect the weights placed on each reference frame. For instance, having participants complete a working memory task concurrently with a tactile TOJ task resulted in a smaller crossed-hands deficit than when no memory task was performed (Badde et al., 2014). As a result of the secondary task, less cognitive resources are allocated towards the integration process. This causes both improved dual-task crossed performance (compared to single task) and worse dual-task uncrossed performance (compared to single task). In the crossed posture, the external reference frame points to the wrong hand, so by reducing the influence of external information under dual-task conditions, better crossed-hands performance is observed. The external reference frame provides redundant information when the hands are uncrossed, therefore worse uncrossed performance is observed when the influence of external information is reduced. The fact that an additional, unrelated task, was able to alter the deficit shows that the weight placed on the internal and external reference frames are subject to top-down influences.

Further evidence for cognitive influences on the weighted integration of reference frames comes from the fact that knowledge of future hand postures affects the size of the deficit (Hermosillo et al., 2011). Specifically, in a study by Hermosillo et al. (2011), participants were presented with two tactile stimuli on each trial and were told prior to each trial that they would either cross or uncross their hands once they responded to the temporal order of the stimuli. It is important to note that participants did not move their hands until after responding to the TOJ stimuli. Moving from an uncrossed to a crossed-hands posture after the TOJ response led to increased errors on the task, whereas going from a crossed to uncrossed posture led to reduced error rates. The anticipation of conflict (uncrossed to crossed posture), or removal of the conflict (crossed to uncrossed posture) seems to cause a re-weighting of internal and external information.

Limitations and Future Directions

Proportion Correct Difference Score

All of the studies included in this thesis were analyzed using the proportion correct difference (PCD) score. As mentioned in the introduction, this measure has many strengths. For instance, it is completely atheoretical, few SOAs are required to obtain an accurate score, and it summarizes both crossed and uncrossed performance into a single score. Since the PCD score defines the deficit with a single number, it is assumed that uncrossed performance remains stable across various manipulations and changes to the PCD score are caused by changes in the crossed posture. However, some manipulations may result in changes to the uncrossed posture as well. This was the case in a study by Badde et al. (2014), where the addition of a working memory task concurrently with a tactile TOJ task reduced uncrossed accuracy while improving crossed performance. If the Badde et al. (2014) study used the PCD score to analyze performance, then a very interesting change would have been overlooked. Furthermore, if the manipulation affects both the crossed and uncrossed curves equally, the PCD score would be unable to measure an effect, as in this case the relative difference between crossed and uncrossed performance would remain unchanged. One manipulation that often affects both crossed and uncrossed performance equally is the effect of practice on the tactile TOJ task (e.g., Unwalla et al., 2020). Under such circumstances, different measures for the crossed-hands deficit can be used such as the slope, JND, or analyzing crossed and uncrossed accuracy separately. Chapters 3 and 4 chose to implement a probabilistic model directly on the proportion of right-first responses in addition to using the PCD score.

Probabilistic Model

The probabilistic model employed throughout this thesis provided a theoretically-driven analysis of the crossed-hands deficit. The model was created to derive the weights placed on the internal and external reference frames during the crossed-hands tactile TOJ task, while participants were upright and responding using hand buttons. The implementation of this model in the current thesis required that an additional assumption be made, specifically, that the manipulations employed in this thesis affected the weights assigned to each reference frame. In other words, it was assumed that specific manipulations would result in participants reweighting the information provided by each reference frame. On the other hand, it is possible that the manipulation could cause some, or all, participants to adopt a different performance strategy. This strategy might go beyond simply reweighting the internal and external reference frames. However, the model in its current form cannot differentiate these two alternatives.

The typically assumed performance strategy for tactile TOJ tasks is that the stimulus must first be localized to the hand. Only once the stimulus has been localized can the response be made. Response demands influence tactile localization by altering the weights an individual places on each reference frame during the integration process. Chapter 3 provided some evidence against such a performance strategy. While the majority of participants showed a larger crossed-hands deficit under the allocentric response demand compared to the somatotopic response demand, a small group of participants showed the opposite effect. The fact that these participants showed a smaller deficit when biased towards external information points to the use of a different strategy, rather than a reweighting of the reference frames. The instructions used in Chapter 3 asked participants to locate the stimulus to the hand in both response conditions. This instruction might result in the majority of participants adopting the same strategy across both response demands. However, in the allocentric response demand there is a direct mapping between the vibration's hemispace (instead of hand) and the required response. As such, better performance could occur when an individual *uses* the information in the external reference frame, rather than tries to *ignore* it. This conceptualization changes the task in the allocentric condition from trying to ignore the misleading external information, to focusing and responding based on the external information. The probabilistic model, in its current state, assumes that all participants are using the strategy of locating the stimulus to the hand. If this is not the case for all participants, then the weights outputted by the model may not be an accurate representation for those participants.

There are two ways we could determine whether all participants are utilizing the same performance strategy. Experimentally, this could be tested by providing more explicit instructions, since we know performance is influenced by instructions provided during the TOJ task. One such instructional change might be to ask participants to locate the stimulus based on the *hemispace*, rather than the *hand* of the vibration in the allocentric condition. With these instructions participants may show a smaller deficit in the allocentric response demand, as the response explicitly relies on external coordinates. If so, this would suggest that some participants in the original experiments did adopt the strategy of responding based on the hemispace in the allocentric condition. Alternatively, it is possible to modify the model to allow for different performance strategies and see whether this accounts for the subset of participants.

One limitation of the probabilistic model is that to compare the weight changes across different conditions (i.e., body positions, response demands), these conditions must be completed within subjects. However, in Chapter 4 of this thesis, the manipulation of visual information was completed on unique groups of participants, therefore, the model cannot be applied to determine how visual information influences the reference frame weights. Therefore, there is limited power to make conclusions about how visual information impacts the weight placed on the internal and external reference frames. Future experiments could manipulate visual information within subjects to confirm the effect of visual information on the internal and external reference frame weights.

Role of Lying Down

The results from Chapter 4 showcased a previously unknown influence on the external reference frame, specifically the possible involvement of vestibular information. Follow-up experiments are required to properly disentangle the influence of vision, gravity, and body-based cues in order to fully comprehend how lying down influenced the external reference frame. This can be accomplished in a few different ways. One possibility is through the use of virtual reality (VR) to allow for the strategic manipulation of visual cues to upright, and specifically whether the visual cues to upright are congruent or incongruent with one's physical body orientation. VR head-mounted displays enable us to provide visuals that indicate a lying down position relative to gravity while they are sitting upright (incongruent) or lying down (congruent) and vice versa.

Using VR, if the deficit is reduced when the participant is lying down with visuals indicating a lying down position (congruent), this would further support a vestibular influence on the external reference frame. This would show that the effect of lying down observed in this thesis was not based on the incongruent visual information. In contrast, if the deficit is reduced when the participant is upright with visuals indicating a lying down posture (incongruent), this would suggest that incongruent visual information has a larger influence on the external reference frame than vestibular information. In this case, the effect of lying down observed in this thesis might only have occurred because of the incongruent visual information. However, the use of VR is only able to disentangle visual cues from vestibular and body cues. To better separate the contributions of vestibular cues from body and visual cues, the tactile TOJ task can be completed in a microgravity environment (Dyde et al., 2009; Jenkin et al., 2005; Jenkin et al., 2011). The microgravity environment would disrupt the vestibular system, without altering estimates of body position or visual orientation. Disruptions to the vestibular system can also be accomplished with a galvanic vestibular stimulator (GVS; Fitzpatrick & Day, 2004). If the crossed-hands deficit is reduced under either microgravity or GVS, this would strongly suggest a role for vestibular information during tactile localization.

Conclusion

Knowing where a touch occurred is crucial to determining the boundary of what is and what is not our body (Botvinick & Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007). Localizing touch requires using information from both the internal and external reference frames. Accurate localization occurs when these two pieces of information are integrated together. This integration process weights the information from each reference frame based on the reliability of each input. Our bodies are constantly moving and interacting with the world around us. Here we have shown that visual information, vestibular information, body position, and task instructions can bias the weighted integration of the internal and external reference frames. What we define as our body is constantly being constructed based on the information available in the present moment.

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