CHARACTERIZING THE BODY MODEL: HOW AGE, SEX, AND TRAINING MODERATE BODY REPRESENTATION

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CHARACTERIZING THE BODY MODEL: HOW AGE, SEX AND TRAINING MODERATE BODY REPRESENTATION

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Dedication

This thesis is dedicated to my family. Thank you for your support and encouragement.

Abstract

We rely on body representation to guide our actions in the environment. We gain knowledge on the size and shape of our bodies both through offline (memory) and online (somatosensory signals) information. Based on evidence from double dissociation studies, body representation has been divided into the body image (offline visual representation of the body) and body schema (online somatosensory representation that guides action). However, there is no agreement on their definitions as different models explain these taxonomies in unique ways. Moreover, a third taxonomy has been recently proposed, the body model. In this thesis, I characterize and contrast the three taxonomies of body representation with respect to somatosensory feedback, the effects of age, sex, and training. I propose that the body model is haptic based and long-term representation, that is sexually dimorphic. I end by discussing whether the body model is a unique representation of the body.

Preface

This thesis investigated body representation, specifically the body model. The body model was first defined in the hand and thus my research focused on this body part (see appendices 1-7). My contributions to the field include that the body model is a stable representation that does not update with physical growth (Appendix 1), that it is sexually dimorphic (Appendix 2), that long- term training alters this representation (Appendix 3), and that the distortions in the body model are different than those found in the body schema or image (Appendix 4). The first 3 Appendices have been published in academic journals, and Appendix 4 is currently under review. In addition, I found that body model size is similar between older and younger adults (Appendix 5), that professional piano players have more accurate representations of their hands (Appendix 6), and that kinesthetic feedback may refine this representation (Appendix 7). These finding are currently being prepared for publication. In the introductory chapter, the studies of the thesis (Appendix 1-7) are placed within the theoretical frameworks of body representation, specifically the dyadic and triadic taxonomies and the perception and action model.

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Many thanks to my crazy family who have helped me in countless ways over the past 12 years of university. Thank you to C.C. for occasionally admitting when I am right! More importantly thank you for supporting me in all my crazy life decisions. Hopefully Nori will one day stop bugging you about your “amazingly intelligent” sister haha. I look forward to our trip to the Bahamas ;) To my parents, thank you for housing your 30-year-old daughter over the course of the Covid-19 pandemic. During that time, numerous individuals told me there is no way they could return to living with their parents as an adult. The fact that we were able to survive each other makes me think that we have a pretty special bond. Thank you for supporting me both emotionally and financially over my university career. I promise this is my last year as a student.

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ANOVA	Analysis of Variance
APC	Anterior parietal cortex
BSD	Body structural description
MP joint	Metacarpal phalangeal joint
PAM	Perception and action model
PMT	Proprioceptive matching task
PPC	Posterior parietal cortex
SII	Secondary somatosensory area
VPL	Ventral posterior nucleus

1. Introduction

Body representations are defined as the cognitive structures that are concerned with encoding and tracking the state of the body (De Vignemont, 2018). Body representations can refer to the representation of the body as a whole, or of individual body parts. These representations not only inform us about the size and shape of our bodies, but also provide us with the necessary tools to interact with our environment. Specifically, when we engage with our surroundings, we use our bodies as a metric guide for our actions. Even a simple task such as reaching out and picking up a cup of coffee requires an accurate understanding of the length of one's arm and the size/shape of one's hand. Thus, accurate body representations appear to be a necesity for every day actions.

The brain houses at least two independent representations of the body (Anema et al., 2009; Dijkerman & de Haan, 2007; Paillard, 1999), namely a representation used for perception (body image) and a representation used for action (body schema). These taxonomies have been heavily debated in recent years (for review see; De Vignemont, 2010). One problem is the inconsistent terminology that has plagued body representation research and thus caused much confusion. Specifically, many studies on body representation use the terms body schema, image, and representation interchangeably, or have different definitions for each specific representation. This makes interpreting body representation data between studies quite difficult. In fact, several models of these taxonomies (the dyadic, triadic and perception and action model), all define these representations in different ways.

The goals of this current review are threefold; 1) to provide a brief overview of the relevant taxonomies of body representation; 2) to discuss the recently identified body model; and 3) discuss how the body model relates to each of the other two taxonomies. The following section will provide a brief overview of the three most relevant taxonomies, the body image, the body schema, and the body model.

1.1 The dyadic taxonomy of body representation

The dyadic taxonomy of body representation postulates that the body image is the stable representation of the body that serves perceptual functions (e.g., body concept, memory of one and other bodies, etc.) whereas the body schema is the constantly updating sensorimotor representation that serves action (Anema et al., 2009; Gallagher, 1986, 2006; Gallagher & Cole, 1995; Head & Holmes, 1911; Paillard, 1999). The definitions of these taxonomies are based off double dissociation studies (Anema et al., 2009; Head & Holmes, 1911; Paillard, 1999). For example, one such study asked two patients to complete a tactile localization task (Anema et al., 2009). In this task, a tactile stimulus was presented on the back of the participant's hand. They were asked to indicate the location of the tactile stimulus either by pointing to the location on a drawing of a hand (body image), or by reaching out with their other hand and touching the location (body schema). One patient (JO) exhibited body image related impairments; JO was unable to identify the position of the stimulus on the drawing of the hand but was able to use their hand to indicate where they had been touched. The other patient (patient KE) displayed the opposite pattern in terms of body representation. KE failed to localize the position where they had been touched using their own hand. However, KE was able to accurately identify the stimulus location on the drawing of the hand. This study highlights that the body image and body schema are two distinct representations, and that damage to different areas of the brain (one described only as the area supplied by the middle cerebral artery, and the other as a stroke that affected the VPL of the thalamus) causes disturbances in different body representations.

In addition, research has proposed that there are temporal differences between the body image and schema (De Vignemont, 2010; O'shaughnessy, 1980). Body image has been considered a long-term, stable representation of the body, whereas the body schema is interpreted as short-term and highly plastic. The plasticity of the body schema is necessitated due to constantly changing body position and orientation (Dijkerman & de Haan, 2007; Longo, 2015c). If the body schema was long-term, completing actions in our environments would be impossible, because we would have no knowledge of the current state of our body.

The dyadic taxonomy has gained much criticism as of recent years. Some of these criticisms are methodological; for example, the original double dissociation studies had small number of patients which could have influenced the descriptions of the body image and body schema (Kanayama & Hiromitsu, 2021). There are also more conceptual criticisms. One such criticism, is that depending on the situation, our actions appear to rely on both online and offline representations (De Vignemont, 2010; N. Kanayama & Hiromitsu, 2021). For example, while an expert guitar player moves their fingers in an automatic fashion (need for identification of body parts on a stored map), an inexperienced guitar player would need to see their fingers in order to complete the same action (reflective conscious action). Therefore, in some cases action necessitates an offline map of the body, which is not considered in the dyadic taxonomy. Moreover, it has been argued that there is both a perceptual and a conceptual part to the body image (De Vignemont, 2010; Kanayama & Hiromitsu, 2021), with the conceptual component of the body image provides a structural map of the body, featuring the boundaries between body parts as well as the semantic/linguistic representation. This again, is not considered in the original proposal of the dyadic body representation.

An updated view is that the body image and schema are co-constructed (Pitron, Alsmith, & de Vignemont, 2018; Pitron & de Vignemont, 2017). In this proposal the body image and schema are considered functionally independent, however the interaction between the two results in their construction. Specifically, the body schema drives the formation of the body image, while the body image can influence the body schema. In this view, the body schema plays a larger role in the formation of body representations. This proposal is discussed in greater detail at the end of this review.

1.2 The triadic taxonomy of body representation

The triadic taxonomy of body representation provides a narrower definition of body image compared to the dyadic taxonomy (see Table 1). The triadic taxonomy divides body image into two separate sub-categories: the body structural description, and the body semantics (Buxbaum & Branch Coslett, 2001; Raimo et al., 2019). The body structural description (or visuo-spatial body map) is a map of the body that includes the relationship between body parts (i.e., body part boundaries; Buxbaum & Branch Coslett, 2001). This sub-representation combines the offline features of the body schema, with the perceptual nature of the body image. Body semantics on the other hand refers to the lexical aspect of body representations (e.g., naming of body parts and functions; Coslett, Saffran, & Schwoebel, 2002; Laiacona, Allamano, Lorenzi, & Capitani, 2006). The definition of the body schema remains as the online sensorimotor representation of the body responsible for the estimation of current body positions relative to other body parts (as in the dyadic taxonomy).

While this taxonomy provides a more restrictive definition, particularly of the body image, several limitations still exist. While, the body image has been narrowed down, it still may feature too broad a definition (De Vignemont, 2010). One suggestion is that the body schema can be further divided into primary somatosensory representations, body form representations, and postural representations (Medina & Coslett, 2010). By this definition, primary somatosensory representations are the representations of the skin surface; the body form representations depict body size and shape, and the postural representations are responsible for encoding limb position. The triadic taxonomy suggests that while the distinction between body image and schema may exist, the definitions need to be more refined to specific functions.

1.3 The perception-action model (PAM) of body representation

The PAM focuses on differentiating the body image and the body schema based purely on functional differences. The PAM of body representation is based on the well-known perception-action model for vision (Millner & Goodale, 1995) and touch/proprioception (Dijkerman & de Haan, 2007). The visual model dissociates a what-system (ventral stream) concerned with object identification and a how-system (dorsal-stream) which is responsible for visually guided actions (Goodale & Milner, 1992). The PAM of body representations postulates that the body image is a by-product of the ventral somatosensory stream, and the body schema a by-product of the dorsal somatosensory stream (Dijkerman & de Haan, 2007). Furthermore, the body image is responsible for perceptual identification and recognition of the body (e.g., body part judgements; Dijkerman & de Haan, 2007; Paillard, 1999) and the body schema is the representation responsible for action (posture, limb size, strength). Dijkerman and de Haan (2007), identified the anatomical projections of the ventral and dorsal somatosensory PAM. The ventral perceptual body image processes information that travels from SII (secondary somatosensory) to the APC (anterior parietal cortex) and end in the insula, whereas the body schema involves projections from the APC to the PPC (posterior parietal cortex, either through direct projections, or via SII; Dijkerman & de Haan, 2007).

This model has also been criticized. One such criticism, states that vision for perception and for action are non-dissociable (Hurley, 1998; Noe, 2004, O'Rega & Noe, 2001). These authors argue that perceptual experiences and action are interrelated and dependent on one another. If this is the case, then body representations cannot be defined by the PAM. Moreover, in recent years, the PAM of body representation has been updated to describe body representation pathways/networks as multimodal in nature and less independent from one another (de Haan & Dijkerman, 2020). In this review, de Haan and Dijkerman highlight that significant crosstalk occurs between the perception and action streams of somatosensation. In fact, they proposed more than just two streams to include streams for social signalling, and for working and long-term memories. Their most important argument revolves around somatosensory processing being a multimodal process, involving various brain regions including areas in the occipital and inferior parietal cortices, and in the insula; all of which are multimodal regions.

All taxonomies of body representation have been debated and criticized, and in some cases, this has led to new proposals. The common takeaway from these taxonomies, however, is that they include a body schema which is separate from all other representations (De Vignemont, 2010).

Table 1: This table contains descriptions of the relevant taxonomies of body representation.

Taxonomy	Representation	Definition
Dyadic	Body image	Offline, visual representation
	Body schema	Online, sensorimotor representation of the body
Triadic	Body structural description	Visio-spatial map of the body
	Body semantics	Lexical descriptions of the body
	Body schema	Online, sensorimotor representation of the body
Perception-action	Body image	Perceptual identification and recognition
	Body schema	Representation for action

2. The body model

In the last 10 years a new representation of the body has been proposed and defined; the body model (Longo & Haggard, 2010). In this review, we will define this new taxonomy and compare it with the body image and body schema.

The body model is the representation of the body's spatial content, which serves position sense (Longo & Haggard, 2010). To clarify, we gain knowledge of the position of our bodies in space (position sense) through various afferent signals from the somatosensory periphery (joint receptors, muscle spindle, Golgi tendon's). These signals provide information about joint angles only, and therefore, we must rely on a stored representation of the distances between these joints (body model). Without this additional information, localizing a body part in space would be impossible (Longo, 2015c). In their original report, Longo and Haggard (2010) measured the body model by asking participants to perform a localization task. In this task, participants were asked to localize where they believed 10 landmarks (the tips and metacarpal phalangeal joints) were located on their unseen hand. The results showed that the body model of the hand was systematically distorted. Participants overestimated hand width and underestimated finger length. This finding has been replicated in numerous studies from various different labs (Cocchini, Galligan, Mora, & Kuhn, 2018; Coelho & Gonzalez, 2018, 2019; Coelho, Schacher, Scammel, Doan, & Gonzalez, 2019; Coelho, Zaninelli, & Gonzalez, 2017; Longo, 2014; Longo & Haggard, 2012; Peviani & Bottini, 2018; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Tagini, Scarpina, & Zampini, 2021; Van der Looven, Deschrijver, Hermans, De Muynck, & Vingerhoets, 2021), suggesting that the distortions observed in the body model are an intrinsic characteristic of this representation. While studies on the body image and the body schema have found over/underestimations of body parts, these studies have typically focused on emotionally charged areas such as the waist or thigh, or the full body (Fuentes, Longo, & Haggard, 2013; Sadibolova, Ferre, Linkenauger, & Longo, 2019; Sand, Lask, Høie, & Stormark, 2011; Sisson, Franco, Carlin, & Mitchell, 1997). One could argue that the hand is a body part that is not emotionally charged yet exhibits distortions that resemble those found for the thigh or waist.

In the past few years significant research has been done to better understand and characterize the body model, particularly of the hand. Thus, the literature in this review focuses on the hand, however, some studies have found that systematic distortions in the body model are not isolated to the hands. Specifically, the leg and the face have also been found to be distorted (Mora, Cowie, Banissy, & Cocchini, 2018; Mora, Sedda, Esteban, & Cocchini, 2021; Stone, Keizer, & Dijkerman, 2018; Stone et al., 2020). In the localization task that Stone and colleagues (2018) developed, participants sat with their leg horizontally stretched underneath a tabletop and were instructed to point to the perceived location of each landmark on their leg. They pointed using a cursor on a computer screen that was presented vertically in front of them. They found that participants perceived their upper legs (from hip to knee) as long and thin, and their lower legs (from knee to ankle) as short and wide (Stone et al., 2018).

A separate set of studies has investigated the body model of the face (Mora et al., 2018; Mora et al., 2021). The face is a unique body part, as our visual memory of the face is reversed (we only see ourselves in the mirror or in photos/video). Moreover, these authors argue that the face constructs our sense of self and our identity. Results from their study show that overestimation of face width was present in all facial features (e.g., the mouth, the nose, the eyes). The authors argue that this pattern of overestimation resembles the somatotopic representation of the face and that regional perceptual differences may be due to functional influences and different experiences of those facial regions. They specifically found that the upper region of the face was underestimated whereas the bottom region was overestimated. This reflects the somatotopic representation which features lips as overrepresented compared to the forehead (Huang & Sereno, 2007). Furthermore, the representation of the right side of the face was found to be larger than the left. This asymmetry replicates what we have found in the body model of the hands; the right hand is overrepresented compared to the left (Coelho & Gonzalez, 2018, 2019; Coelho et al., 2017). Taken, together the reports on the leg and face demonstrate that body model distortions are not isolated to the hand.

At this point it is unclear whether the body model fits into the dyadic, triadic or PAM taxonomies of body representation. One suggestion is that the body model is a stored representation of the body that is combined with a postural schema (the dynamic representation of current body postures (similar to the body schema)) to help localize the body in space (Longo, Azañón, & Haggard, 2010; Tamè, Azañón, & Longo, 2019). In this definition the postural schema is informed by both proprioceptive signals and efferent copies of motor commands. However, this suggestion does not address whether or not the body model itself is a subpart of the body schema or image, or if it is a unique representation. Further identifying the characteristics of the body model, may lead to a better understanding of the taxonomies of body representations themselves (and how they relate to the body model). In the following section of this review, I will further define the body model in terms of its characteristics and how it differentiates from the body image and the body schema. I will also discuss the various conditions in which the systematic distortions of the body model exist and change. First, I will review the possible causes of the systematic distortions in the body model representation.

2.1 What causes the distortions in the body model?

2.1.1 Pixel theory: Longo postulates that these perceptual distortions are due to the body model being informed by the somatosensory homunculus (Longo, 2015a; Longo & Haggard, 2011). It has been known since Penfield's early work that the homunculus is the cortical representation of the tactile receptors of the body (Penfield & Rasmussen, 1950). Body parts with more tactile receptive fields (e.g., hands, lips) are represented as larger in the homunculus compared to those with fewer tactile receptive fields (e.g., back). Longo argues that the body model distortions reflect the geometry of the receptive fields on the body. He theorizes that when we judge the distance between two tactile stimuli on our skin, the brain "counts" receptive fields (pixels) between the two stimulated locations.

Therefore, the higher the number of pixels, the larger the distance between the two stimuli. For example, the receptive fields on the dorsum of the hands are oval shaped, with their axes running along the length of the hand (rather than circular; Longo, 2015a; Longo & Haggard, 2011). This oval shape results in more receptive fields positioned across the hand compared to those situated along the hand. Therefore, if we are presented with two stimuli running across our hand, we will "count more pixels". This would cause the width of the hand to be over-estimated, while fingers length (along the hand) would be underestimated. Support for this theory was found in a study in which participants perceived two tactile stimuli as 40% further apart when the stimuli was presented across compared to along the hand (Longo and Haggard, 2011). Longo argued that touch is being informed by a "fat squat" representation of the hand (the body model).

A caveat of this theory is that tactile perception and perception of position sense (i.e., the body model) might not be the same representation. In a follow-up study, Longo and colleagues found no correlation between tactile perception and the body model, which refutes the idea that both touch and position sense are informed by the same representation (Longo & Morcom, 2016).

2.1.2 Testing method: It is possible that the body model is accurate, however, the testing methods produce the systematic distortions (Ingram, Butler, Gandevia, & Walsh, 2019; Medina & Duckett, 2017). There are five possible methodological issues that may influence the distortions in the body model: 1) localization biases, 2) overestimation of spatially close landmarks, 3) distortions beyond body parts, 4) sensory adaptation, 5) interactions with the body schema.

2.1.2.1 Localization biases: Ingram and colleagues challenged whether the localization task is in fact measuring body representation (Ingram et al., 2019). They argue that it is possible that the overestimation of hand width and underestimation of finger length is really a reflection of a proximal (closer to the body) and ulnar (closer to the pinky) bias for location.

However, there is evidence that the systematic distortions are not a result of localization biases (Longo & Haggard, 2010; Coelho et al., 2017; Coelho et al., Under review). Longo has reported that the distortions in the body model are not due to a foreshortening effect (Longo & Haggard, 2010). In their original study, they asked a group of participants to rotate their hands 90°. If underestimation of finger length was due to a general foreshortening in the near-far axis, then the group with the rotated posture should have exhibited the opposite pattern of distortions (underestimate hand width, overestimate finger length). However, Longo and Haggard found nearly identical results in this group, participants underestimated finger length in both groups. Moreover, my previous research found that even when participants performed the task with a point of reference (without a home-spot; a location above the forearm in which the participant must return between points) some systematic distortions were still present (Coelho et al., 2017). In a further study, I also discovered that different frames of reference (proximal-distal vs distal-proximal) both produced underestimations of finger length (Coelho et al., under review) indicating that distortions are not the result of foreshortening. These studies strongly support that the distortions of the body model truly exist.

2.1.2.2 Overestimation of spatially close landmarks: Medina and Duckett (2017) found that participants overestimated the distance between spatially close consecutive localization judgements (e.g., the tip of the thumb and the tip of the index finger). Their analysis revealed that when they controlled for this bias, there was no evidence of a distorted body model (across the medial-lateral axis; hand width).

Research from our lab (Coelho et al., 2017) has found the opposite of Medina and Duckett (2017). Specifically, I found that when participants point in a systematic order (from landmarks spatially close to each other), the resulting body model is more accurate compared to when participants estimate in a random order. This directly opposes the suggestion that the body model distortions are due to overestimation of spatially close landmarks to one another. In fact, our results suggest that the overestimation of hand width occurs at a higher magnitude when the landmarks are not directly beside one another.

2.1.2.3 Distortions beyond body parts: Medina and Duckett (2017) also argue that the systematic distortions are not body specific. When they asked participants to localize dots on an array that resembled a human hand, the participants overestimated the distance between subsequent dots.

Several studies have found that while non-body objects exhibit systematic distortions, these distortions are of a much smaller magnitude compared to those found in the body (Peviani, Magnani, Bottini, & Melloni, 2021; Saulton et al., 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016) . For example, one study asked participants to complete the localization task with their hand, a CD-case, a post-it pad, and a rake (Saulton et al., 2015). They found that while all items featured an underestimation of length and an overestimation of width (reminiscent of the systematic distortions in the hand), the magnitude of distortion was significantly less compared to when they measured the participants hands. In a follow-up study, the same authors found that the larger magnitude of distortions in the hand persists despite objects having visual similarities with the hand, or participants having to memorize the features of objects (Saulton et al., 2016). Importantly, these authors argued that the localization task measures an implicit representation that is specific to the body.

2.1.2.4 Sensory adaptation: A separate factor that may be a contributing to the distortions found in the body model is the length of the testing process. It is likely that during the ~15 minutes that the participant places their hand against the tabletop sensory adaptation occurs. Sensory adaptation is the phenomenon that after a stimulus is presented for a given amount of time (usually < 14 sec; Weill-Duflos, Sakr, Haliyo, & Régnier, 2020) , neurons stop firing in response to said stimulus (Wark, Lundstrom, & Fairhall, 2007; Weill-Duflos et al., 2020). Sensory adaptation is the reason why we cannot feel the socks we put on in the morning when we go about our daily life. So, during the localization task, it is possible that after the first few estimations, sensory adaptation occurs, and the participant can no longer rely on haptic feedback to form their estimates (thus leading to the more distorted body model). Developing research in our lab indicates that this might be the case (Coelho & Gonzalez, 2021; see appendix 1). In this study, I had participants only complete one estimate per landmark, which dramatically reduced the amount of time the participant was required to have their hand fixed against the tabletop. In this study, adult participants underestimated finger length, but had accurate estimates of hand width. Thus, perhaps the distortions in the body model are in-part due to sensory adaptation. Further research is needed to test this hypothesis.

2.1.2.5 Influence of the body schema: A final consideration is the possibility that during the localization task other body representations are also being measured. For example, pointing to a landmark necessitates the body schema for the pointing hand (De Vignemont, 2010). A recent study from our lab found that there was a relationship between body model and the body schema (Coelho et al., under review). It is possible that one reason why the body model and the body schema correlated is that they are inseparable during the localization task. There is one previous study that modified the localization task so that the participants could verbally estimate the perceived location of each landmark (Ingram et al., 2019). In this task, the participant sat with their hand hidden underneath a grid. The participant would verbally indicate the perceived position of each landmark on that grid (no pointing). The authors found that the systematic distortions were still present, in fact underestimation was more pronounced in this group. However, a severe limitation to this study was that the grid featured squares that were all 1cm x 1cm large, meaning that the participant could not be as specific with their location judgments. It was therefore possible that two perceived locations (e.g., knuckle of the index and the middle finger) could be situated in the same grid, causing the participant to change their estimate of one of these locations (despite them perceiving the two landmarks as spatially different). In other words, it is possible that a participant perceived the location of two landmarks within the same 1cm x 1cm square, but changed their estimates because they did not want to place two estimates withing the same square. More research is needed to address these limitations.

2.1.2.6 Evidence against a "testing method bias": Perhaps the best evidence to refute a "testing method bias" is that similar results have been found in different labs across the world using different testing methods (Coelho et al., 2017; Longo & Haggard, 2010; Saulton et al., 2015). For example, Longo and colleagues measure hand width from the pinky knuckle to the knuckle on the index finger (Longo, 2014, 2015c; Longo & Haggard, 2010, 2012). I however, measure width from the tip of the thumb to the tip of the pinky (entire hand). I chose to include the thumb into the measure of hand width due to its relevance in reaching and grasping. For example, a power grasp requires the entire width of the hand (including the thumb). Longo has reported that the distance between the thumb and index finger is perceived the most accurately (Longo & Haggard, 2010), which therefore may cause my measure of overall hand width to be less distorted. I have consistently reported smaller magnitudes of distortion in terms of width compared to the studies conducted by Longo and colleagues (Coelho & Gonzalez, 2018, 2019, 2021; Coelho et al., 2019; Coelho et al., 2017). There is some evidence that measuring the fingertips (instead of the knuckles) also causes differences in the magnitude of distortions (Longo & Haggard, 2012; Peviani & Bottini, 2020). Peviani and Bottini (2020) argued that the difference in magnitude between errors on fingertip and knuckle location is due to anatomical and physiological differences between the two landmarks. They hypothesized that the fingertips when compared to the knuckles may have poorer/noisier afferent somatic input informing fingertip proprioception (when the task does not involve movement; the localization task) and thus errors of fingertip localization are of a greater magnitude than the knuckles.

Another key difference in testing procedures is the orientation of the hand during the localization task. Longo and colleagues ask participants to place their hand palm down underneath a tabletop (Longo, 2014, 2015c; Longo & Haggard, 2010, 2012). My research has required the participant to place their hand palm up, pressed against the surface of a tabletop. I ask participants to orient their hand in this way because otherwise the depth of distance between the tabletop and hand may influence their perception. Longo and Haggard have reported that testing the palmar side of the hand results in a less distorted body model (Longo, 2020; Longo & Haggard, 2012). A possible explanation for the difference in magnitude between the hairy (dorsal) and palmar side of the hand lies in the pixel theory (Longo, 2017; 2020; Longo & Haggard, 2011). Receptive fields on the hairy skin (dorsal side of the hand) are oval shaped, which means there are more receptive fields situated across that hand than along the hand. This may in turn result in the larger overestimations of hand width on the hairy side of the hand.

It is important to note that despite these methodological differences I have replicated Longo's results on numerous occasions (Coelho & Gonzalez, 2018, 2019; Coelho et al., 2019; Coelho et al., 2017), and he has replicated my results (Longo, 2017, 2018, 2019; Longo & Morcom, 2016). This replication suggests that the distortions in the body model are not a result of testing procedures, but rather a characteristic of this representation.

Taken together, methodology appears to contribute to the *magnitude* of distortions found in the body model tasks, however, the existence of these distortions does not depend on the methodology being used.

3. Sensory influences on body image, body schema, and body model

We create the representation of our bodies based on the various sensory signals (vision, haptics, etc.) as well as from visual memory (offline). One possibility that could explain the various taxonomies of body representation is that they arise from different sensory modalities. The following section will summarize the studies investigating how vision or haptic feedback influence each taxonomy.

Body image: The body image has long been described as a visual representation. In an early definition of the body image, it was described as the picture of our body in our mind (Schilder, 1936). Double dissociation studies (informing the dyadic taxonomy of body representation) described patients who have an intact body image as those who were able to *visually* identify the location of a tactile stimulus on a picture of their body (Anema et al., 2009; Gallagher & Cole, 1995; Paillard, 1999). Furthermore, body image disturbances have been described as a disturbance of a visual body representation (Bruch, 1962; Smeets, Klugkist, van Rooden, Anema, & Postma, 2009).

The term body image is regularly used to refer to the visually based representation of body shape and size. The visual component of the body image is also what is frequently measured in current body image tasks. For example, in Longo's attempt to dissociate between the body image and the body model, he used the template matching task, which relies purely on vision (Longo & Haggard, 2010). In this task, participants were required to select the image of their hand that was anatomically accurate, from an array of images of different sized hands (over and underestimated). The results showed that participants accurately selected the image that reflected their physical hand size. However, in the localization task, (to measure body model) which is informed by both somatosensory and visual feedback, distortions appeared.

While the visual contributions of the body image have long been acknowledged, more recent studies have shown that somatosensory information can also alter the body image (Gandevia & Phegan, 1999; Türker, Yeo, & Gandevia, 2005). Specifically, these studies show that when somatosensory feedback is eliminated (e.g., cutaneous anesthesia) this produces the illusion that the effected body part is larger. For example, dental anesthesia, causes the perception of the mouth to be bigger. This indicates a bidirectional relationship between body image and somatosensory processing. Longo has argued that somatosensory and visual body representations are not entirely independent from one another (Longo, 2015a). This would refute the hypothesis that the body image arises solely from visual information.

While understudied in comparison to vision and somatosensation, audition has also been shown to affect the body image (Tajadura-Jiménez et al., 2015; 2019; Nava & Tajadura-Jiménez, 2020). For example, Tajadura-Jiménez et al., 2015, found that altering footstep sounds changed the perception of participants body size. In this study, participants were required to walk wearing sandals that produced clear auditory feedback under three conditions: 1) control condition, where participants heard their natural footstep sounds, 2) high frequency condition, in which the high frequency (1-4 kHz) footstep sounds were amplified, and those with low frequency footstep sounds (83-250 Hz) were attenuated, 3) low frequency condition in which the amplification/attenuation was reversed (83-250 Hz were amplified). After completing the walking portion of the experiment, the participant was required to adjust a 3D avatar on a computer screen until it best represented their perceived body size. Participants made smaller estimates of body width after the high frequency feedback condition compared to both the control and the low frequency conditions. Suggesting that the high frequency condition caused participants to perceive their bodies as thinner. Taken together, the results from this section suggest that while body image is a visual representation of the body, there is a multimodal (haptic, audition) component to this representation.

Body schema: Head and Holmes first described the body schema as the representation of position and movement of the body that is primarily derived from proprioceptive and kinesthetic afferent impulses (Head & Holmes, 1911). As with the body image, it is now accepted that this is a multimodal body representation, where notably visual information has been found to contribute to the body schema (Berlucchi & Aglioti, 1997; Maravita, Spence, & Driver, 2003). For example, in visual illusions where the body appears larger than its physical size, the perception of touch is also altered (Bruno & Bertamini, 2010; Taylor-Clarke, Kennett, & Haggard, 2004). This finding supports the view that the body schema is influenced by both somatosensory and visual representations.

Unlike the body image, most measurements of body schema have included both visual and haptic feedback. For example, many studies on the body schema ask participants to navigate through a door-like aperture that varies in size from trial to trial (Beckmann, Baumann, Herpertz, Trojan, & Diers, 2021). At a certain point during the trials the participant must rotate their shoulders to fit through the aperture. The size at which the participant perceives themselves as being too big to fit through the door, the first rotation occurs. These studies have reported over/underestimations of body size in the body schema. It is possible that this task is measuring both the body schema and the body image. Keizer and colleagues found that the point at which the participants judge their bodies as being too big to fit through the aperture was related to the misinterpretation of their visual body image (Keizer et al., 2013).

Body model: If the systematic distortions in the body model are a result of the receptive fields on the hand (Longo's pixel theory), this would suggest that the body model relies on haptic information (Longo, 2015c; Longo & Haggard, 2011). However, previous research finds that while haptic information is the most relevant to the body model, visual information also contributes to these distortions (Coelho & Gonzalez, 2018; Gallagher, 1986; Longo, 2014; Peviani, Melloni, & Bottini, 2019; Stone et al., 2018). More specifically, it appears that non-informative vision is partially responsible for the distortions in the body model. For example, in my previous study (Coelho & Gonzalez, 2018) I asked participants to complete the localization task in one of three different conditions: 1) vision+haptics, 2) haptics-only, and 3) vision-only. The participants in the vision+haptics group completed the task in the traditional fashion. Briefly, they placed their hand palm up against a tabletop (haptic feedback from the table) which was covered with a black tablecloth, so they could not see their hand. However, they had non-informative visual feedback about the experimental set-up. The haptics-only group completed the localization task with their hand against the tabletop (haptic-feedback) but wore a blindfold (no visual feedback of any kind). The vision-only group were asked to *imagine* that their hand was placed up against the tabletop but held it behind their back (no haptic feedback from the table). This last group had non-informative visual feedback, as they could see the experimental set-up. My results showed that all three groups exhibited distortions in the body models. However, the haptic-only group had the most accurate estimations. This replicated previous work which found that the most accurate body model was informed only by haptic feedback (Longo & Haggard, 2014). Moreover, in my study the pattern of distortion found in the visual+haptics group was closer to the pattern of distortion in the haptics-only group. In my paper, I argued that haptics dominates during body model tasks (in support of the pixel theory), because when haptic information is taken away, the hand maps produced featured very different distortions (e.g., the distance between the thumb and index finger was underestimated in this group only). Visual information is still used to form the body model, however, as some estimates in the vision-only group were consistent with the pattern of distortion in the vision+haptics group. This is in-line with previous neurophysiological research on the representation of limb position in monkeys (Graziano, 1999). This study found that the position of the arm was represented by a convergence of proprioceptive and visual cues. Neurons in the premotor cortex responded to the position of the arm when it was hidden from view. The same neurons also responded in a similar fashion to the seen position of a fake arm; indicating that both proprioceptive and visual information were used to calculate the position of their arm. It is possible, that during the body model task, haptic information is the most relevant (mechanoreceptors are activated when the fingers are against the tabletop, giving an accurate sense of the location) whereas visual information in the task may be distracting (no visual information of where the hand is under the table), leading to a reliance on haptically-guided estimates. Afterall, if the body model is reflecting the sensory receptive fields on the hand, this would be considered a haptic representation of the body (Longo, 2015a). The visual influence on the body model is likely due to vision being our dominant and most reliable sense during spatial perception (Azañón et al., 2016; Power & Graham, 1976; Rock & Victor, 1964). The results from my study and others (Coelho & Gonzalez, 2018; Gallagher, 1986; Longo, 2014; Peviani et al., 2019; Stone et al., 2018) suggest that vision and haptics interact during the body model task to form this representation.

To date, only the visual and haptic contributions to the body model have been explored. However, it has been stated that position sense is informed by tactile, visual, proprioceptive, auditory, and vestibular sources (Medina & Coslett, 2009). Further research is needed to identify how other sensory modalities influence the body model (e.g., audition). Afterall, as I move my hands across the keyboard, I receive auditory feedback for every key press. This feedback will help to identify where each finger is in space (position sense). Therefore, it is possible that auditory feedback combined with haptic information would produce a more accurate body model. This has yet to be explored.

4. The effects of age, sex, and training on body representations

4.1 Age

Body image: It is unclear at what age we develop a body image. There have been conflicting reports on the accuracy of the body image in children. Some evidence suggests that this representation is underestimated (Cardinali, Serino, & Gori, 2019; Steinsbekk et al., 2017). Cardinali and colleagues (2019) presented children with an array of different sized model hands. They asked the participants to indicate which model best matched their physical hand size. They found that 6-10-year-old children selected hands that were smaller than their real hand, indicating, that they perceived their hands as smaller than their anatomical size. Moreover, there was a negative relationship between perceived hand size and age, with the older children generating greater underestimation. Other studies, however, have found that the body image of the hand is accurate during childhood (Van der Looven et al., 2021). These researchers asked children to perform the template matching task. In this task, the child was presented with an array of photos of their hand. These photos were either accurate, smaller, or larger than their physical hand size. The children consistently selected the image of their hand that matched the anatomical hand size. Therefore, the extent to which the body image in children is underestimated or accurate is still being debated.

There are few studies on body image in older adults. One study asked older and younger adult participants to manipulate the perceived dimensions of the upper limbs on an avatar presented on a computer screen (Sorrentino et al., 2021). They found that older adult participants underestimated arm length more so than the younger participants. This result suggests that older adults may underestimate their body image. More research is needed in this area.

Body schema: Previous research has stated that the body schema is not 'hardwired', but rather develops progressively until eight years of age (Assaiante, Barlaam, Cignetti, & Vaugoyeau, 2014; Wittling, 1968). Assaiante and colleagues (2014) found that the body schema develops through childhood based on the sensory information obtained during movement as well as through the socially driven ideals of body size (TV, media, peer/parent interactions; Gallagher, 1986). They further argued that the internal representation of the body must continually update during childhood because during this period it is consistently changing. This suggestion is in line with an additional study that found that the body schema updates with the physical growth that occurs during childhood (in children aged 6+; de Haan et al., 2018). In this study, children were asked to move their hand through different sized apertures and to estimate the distance between two tactile stimuli on their forearm. Children performed similarly to adults on both tasks.

The authors argue that this is evidence of the continuous updating for the body schema during development.

Few studies have explored the body schema in older adults (Costello & Bloesch, 2017). It has been hypothesized that due to a reduction of sensory processing capabilities older adults may have different somatosensory body representations (Carmeli, Patish, & Coleman, 2003; Sorrentino et al., 2021). In line with this suggestion, it has been shown that older adults underestimate arm length in a bisection task (Garbarini et al., 2015). In this task, blindfolded participants were instructed to estimate the midpoint of the distance between their elbow and tip of their hand, using their index finger. They found that older adults underestimated the midpoint of their forearm. It appears that with aging body schema, just like the body image, becomes underestimated.

Body model: One possibility as to why we can effectively interact with our environments while relying on a distorted body model, is that as adults we have years of practice using a body that has stayed relatively the same size. In particular, I argued in a previous study that hand size is not a sensitive area for weight loss/gain (Coelho & Gonzalez, 2018), and therefore physical size would have stayed consistent since late adolescence. So perhaps, practice with the same sized body allows us to effectively complete manual actions with a distorted representation. Children, however, experience rapid growth spurts during pre- and adolescence. Importantly, it has been noted that children during this period also experience clumsy bursts. One proposed reason for this clumsy behaviour is that during rapid growth perception of the body may not align with physical body size (Longo, Azañón & Haggard, 2010). My previous research supports this suggestion (Coelho & Gonzalez, 2021, see appendix 1). Specifically, I found that children have larger body models than adults; they overestimate hand width and have accurate estimates of finger length. This is the first report of accurate finger length in the body model. The reason for this enlarged representation is unknown, but I argued that these results suggest that the body model is not a product of experience, but rather a stable feature arising from an early age (before physical growth spurts during adolescence occur). My previous work (Coelho et al., 2019; see appendix 3) suggests that a smaller body model allows for more precise movements. If one were to perceive their hand as smaller than its physical size, this will allow to perform more precise movements with the hands. Therefore, I postulated that an enlarged representation of the hand may actually contribute to uncoordinated movements. Another possibility as to why children have an enlarged representation of their hands during the localization task, is that they prioritize different sensory modalities, specifically vision. Previous research has found that children have an increased reliance on vision during spatial perception tasks (Petrini, Caradonna, Foster, Burgess, & Nardini, 2016). As previously stated, others and myself have found an increase in distortions when vision is relied upon to complete the localization task (Coelho & Gonzalez, 2018; Longo, 2014). This possibility warrants further research.

The finding that children overestimate their hands is unique to the body model, as research on the body schema or the body image have found either accurate (Smit et al., 2018) or underestimated (Cardinali et al., 2019) representations. This strongly suggests that the body model develops independently from the body schema and the body image.

A recent report showed overestimation of hand width and underestimation of finger length in children (van Der Looven, 2021). However, this study measured the hairy side of the hand, whereas I measured the palmar side. Tests on the palmar side of the hand have showed reduced distortions when compared to the hairy (Coelho et al., 2017; Longo & Haggard, 2012). A full examination on the development of the body model on the palmar and hairy side of the hand is needed to understand if both sides develop at similar rates. Another methodological difference is that I used a shortened version of the localization task, and quicker testing time may reduce distortions because it would prevent sensory adaptation (Coelho & Gonzalez, 2021, see appendix 1). Therefore, the different results could be attributed to different testing methods between the studies.

Just like in the body image study where age was correlated with distortion of hand size (Cardinali et al., 2019), both my study (Coelho & Gonzalez, 2021) and Van der Looven's (2021) found that the perceived body model size decreases as a function of age. In other words, young children have the largest estimates of hand size. Further analyses revealed that this relationship is due to the increase in physical size that occurs from childhood to young adulthood (Coelho & Gonzalez, 2021). In other words, the estimated body model size remained consistent across the age groups (only physical hand size increased as a function of age, leading to smaller estimates in the older participants). If the body model size is 'fixed', then once we reach adulthood the relationship between age and body model distortion should disappear. To test this, I recruited a group of older adults (age 50+; see appendix 5) and asked them to complete the shortened version of the body model task (as was used in Coelho & Gonzalez, 2021). I found that older adults performed differently than children (older adults had smaller estimates of hand width and finger length), but they were no different than the younger adults. Intriguingly, even in adulthood a correlation still exists between age and magnitude of the distortion, specifically the older the participant, the greater the underestimation. A recent study investigating the body model and the body image in older adults (Sorrentino et al., 2021) found similar results. Compared to young adults, older adults underestimated arm length and had greater distortions in the arms and hands. Moreover, the distortions in the body model task were of a higher magnitude than those in the body image task, suggesting that these two representations are different in older adults. The authors argue that the observed differences between the taxonomies likely reflect the different sensory modalities informing them (body image task is a visual task, while the body model also involves somatosensation).

A possible explanation as to why older adults underestimate the body model, is that sensorimotor feedback may be reduced in older adulthood due to a decline in sensorimotor capabilities and the underuse of their limbs (Sorrentino et al., 2021). In other words, the older adults receive less sensorimotor feedback during their daily lives, which could lead to smaller estimations of hand size. In addition, proprioception (a key contributor to the body schema and body model) is altered in normal aging (Boisgontier, Olivier, Chenu, & Nougier, 2012; Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009). These previous studies have found a reduction in proprioceptive abilities in older adults. This could help explain why older adults show similar underestimations in all taxonomies of body representation (de Haan & Dijkerman, 2020; De Vignemont, Ehrsson, & Haggard, 2005; Maravita et al., 2003; Serino & Haggard, 2010). If proprioceptive and somatosensory information is less available, then all representations need to rely more on visual information which we find is more distorted. A separate possibility is that the loss of bone mass and shortening of the spine that occurs in late adulthood (Chumlea et al., 1989) may also influence the decrease in body representation size. Afterall, a slow reduction in spine length may not be updated into the body image, schema or model. Future research is needed to address this possibility.

More research is needed to identify how the body model changes with respect to other representations (e.g., the body schema and image) across adulthood.

4.2. Sex

Body image: Sociological studies on the body image have documented sex differences (Fisher, 1964). Specifically, women are more likely to perceive themselves as being overweight, or as needing to lose weight (Mintz & Betz, 1986). Body image concerns are also present in males; men are more often preoccupied with being muscular (Cafri & Thompson, 2004; Stice & Whitenton, 2002). Importantly, while fat and muscle dissatisfaction are related in terms of psychopathology (muscle dysmorphia has been considered the male anorexia; Mitchison & Mond, 2015), these concerns are independent of one another. For example, females with anorexia nervosa overestimate the body's fat content, but are accurate at estimating muscle mass (Maida, 2003; Olivardia, Pope Jr, & Hudson, 2000). Neuroimaging studies have noted different activation in the medial prefrontal cortex during body image tasks for females and males (Owens, Allen, & Spangler, 2010). Females have higher activation when viewing overweight images, whereas males react similarly to images of overweight and thin bodies. However, despite these studies exhibiting sex differences in body image, some studies have not shown such differences (Dolan, Birtchnell, & Lacey, 1987; Keeton, Cash, & Brown, 1990; Pasman & Thompson, 1988). It is possible that gender, a factor that has largely been ignored may actually be driving the inconsistent results across body image studies (Majid et al., 2020). More research in this area is needed. In fact, it has been argued that despite the prevalence of sex differences in body image disorders (anorexia, muscle dysmorphia etc.), little is known about the how women and men perceive their bodies (Burke et al., 2019).

Body schema: One study provides evidence of sex differences in the body schema (Wignall, Thomas, & Nicholls, 2017). In this study, participants were asked to estimate whether they would be able to fit through different sized apertures. They found that women made errors of width, whereas males made errors of height. This was the first time a sex-specific relationship between body size and body schema was found. The authors argue that body schema enlargement may be driven by normal perceptual biases and sociocultural beliefs about body ideals (women should be slimmer, males taller). The role of gender in body schema representation is completely missing.

Body model: My previous research was the first to identify sex differences in the body model of the hand (Coelho & Gonzalez, 2018a; see appendix 2). In this study I asked male and female undergraduate students to complete the localization task. Surprisingly, only females exhibited both characteristic distortions. Males had accurate estimates of hand width, but severely underestimated finger length (significantly more than females). These results mirror the literature on body dysmorphias, where women are more likely to suffer from disorders that feature an overestimation of body width (anorexia), while males are more likely to suffer from disorders characterized by an underestimation of body size (muscle dysmorphia; Burke et al., 2019; G. Kanayama & Pope Jr, 2011; Keski-Rahkonen & Mustelin, 2016). I proposed that a sexually dimorphic body model is an underlying reason for the sex differences in these disorders. In other words, the body model in healthy individuals is already ‘predisposed’ to be overestimated in females, and underestimated in males, thus body representation disorders are just exaggerations of these biases. Longo has replicated the sex differences observed in the body model of the hand (Longo, 2019). Research is needed to investigate if these differences are amplified in emotionally charged areas (e.g., the thigh or the abdomen) and whether they are modulated by gender and/or sexual orientation.

4.3 Training

Previous research has shown that somatosensory representations can change in response to experiences, an example of brain plasticity. Plasticity refers to the ability of the central nervous system to update with different events and experiences, both in response to environmental stimuli and pathological processes (Kolb & Whishaw, 1998). There is a growing body of literature that suggests that the body model is plastic, however, changes seem to only occur after long-term experience. The following section summarizes how body representation changes through experience in the different taxonomies, subdivided into discussions regarding short and long-term changes.

4.3.1 Short-term changes to body representation

We are limited in our actions by the size of our limbs; we are only able to reach the top cupboard if we are a certain height and/or if our arms are sufficiently long. However, we can use tools (stepping stool or a mechanical grabber) that physically change our capabilities for a brief amount of time. This physical change allows us to temporarily extend both our physical body and our action capabilities. Thus, an excellent way to examine if body representations rapidly update, is to examine if they change after tool-use. It is accepted that both manipulated objects and even items of clothing become incorporated into the body schema (Aglioti, Smania, Manfredi, & Berlucchi, 1996; Martel, Cardinali, Roy, & Farnè, 2016). Less is known about the short-term plasticity of the body image and the body model. The following section review this literature.

Body image: Short term changes to body image are still not well understood. One study's view is that body image does not change as a function of tool-use (Cardinali et al., 2011). In this study, participants sat with their right arm hidden underneath a black fabric. Situated beside their arm was a 'ruler' that the participant could read. On each trial the experimenter would verbally indicate a target landmark (fingertip, wrist, etc.). The participant was then tasked with guessing the number on the ruler that corresponded with the landmark on their unseen forearm. The participant performed 18 trials with a mechanical grabber (tool that extended the length of their arm) between body image measurements. The authors found that body image did not update following tool-use. In other words, they estimated forearm length to be the same in both the pre- and post-tool test. This was in line with the authors' prediction that tool-use, as an action task (rather than perceptual), should not change the body image. However, some have argued that the body image can be susceptible to change due to tool use, but only if the task relies heavily on visual information (Cardinali et al., 2011; Miller, Longo, & Saygin, 2015). For example, one study asked participants to judge if an image of a hand was wider than their own, both before and after using a large hand-shaped tool (much bigger than their hand; Miller et al., 2015). The authors found that when the task was performed with visual feedback, participants estimated their hand to be wider and shorter after training. However, if they performed the same task with only haptic information available, no body image change occurred. These authors argued that visual information is necessary for tool-induced plasticity in the body image. This finding informed Pitron and colleagues' (2018) position that body image may feature tool incorporation (Pitron et al., 2018). However, at this point it remains unclear if the body image is altered following tool-use (Martel et al., 2016).

Body schema: The body schema was originally described as the short-term, highly plastic representation of the body (Head & Holmes, 1911; Paillard, 1999). It has been argued that the plasticity of this representation is necessary due to the body constantly changing position and orientation (Dijkerman & de Haan, 2007; Longo, 2015c). If the body schema did not update with the movement of our bodies, we would be unable to interact with our environment. We need an updated representation of the current state of our body (the body schema) in order to guide our actions. Research has shown that following tool-use, the body schema is updated to include the metrics of such tool into its representation (Cardinali, 2011; Cardinali et al., 2011; Cardinali et al., 2009; Maravita & Iriki, 2004; Martel et al., 2016; Sposito, Bolognini, Vallar, & Maravita, 2012). One example is the work by Sposito and colleagues in 2012. These researchers asked participants to perform a forearm bisection task (indicate the midpoint of their forearm) before and after manipulating different sized tools for 15 minutes. The authors found that after using a 60 cm tool, participants estimated the midpoint of their forearm to be closer to the hand (i.e., they had a longer representation of their forearm). This effect was not present with the 20 cm tool, probably because this tool did not substantially change the participants reaching ability (Sposito et al., 2012).

Body model: The extent to which tool-use alters the body model in the short-term is debatable. One study that investigated the short-term effect of tool use on the body model of the forearm, showed that following active training with a rake, participants' forearm maps were longer (Galigani et al., 2020). In contrast to this result, I found that short-term training with a baseball glove did not result in changes to the body model of the hand (Coelho et al., 2019; see appendix 3). To test this, we recruited a group of participants with no prior baseball experience and asked them to complete the hand mapping task both before and after 15-minutes of training. The training consisted of wearing a baseball glove and playing catch with an elite baseball player. My results showed that the novice baseball players did not embody the tool into their body model during the 15 minutes of training. Perhaps tool-induced plasticity in the body model depends on the body part (forearm vs hand) or the familiarity with the tool. If the novice baseball players did not feel like the glove was aiding their performance, this may have caused them to not embody the tool into their body model. Conversely, most participants would be familiar with using a rake, and thus changes to the body model could occur. This thought is in line with previous research on the body schema which has suggested that gains in performance (e.g., reaching further or being able to catch a ball) must be present for plastic changes to occur (Sposito et al., 2012).

4.3.2 Long-term effects of training on body representations

Research has shown that long-term motor training can lead to changes in behaviour and the associated motor and somatosensory cortical representations (Cardinali et al., 2009, Tyc et al., 2005; Jäncke et al., 2000, Kami et al., 1995). For example, motor training in piano players has been shown to attenuate hand preference. Regardless of handedness, piano players tend to perform equally well with both hands in motor tasks (Amunts et al., 1997). This phenomenon is associated with changes in cortical representations of the body (Chieffo et al., 2016). Specifically, while non-trained participants show larger cortical representation of their dominant hand, piano players had similar cortical maps for the left and right hands. In fact, the cortical motor representation of the right hand of piano players is slightly smaller than the one found in non-trained participants (Chieffo et al., 2016). It is possible that these changes in cortical motor representation due to long-term experience influence the body image, the body schema, and the body model. The following section reviews this literature.

Body image: According to the dyadic taxonomy of body representation the body image is described as the stable, long-term view of the body (Gallagher, 1986, 2006). This description would suggest that the body image should not be plastic. The fact that individuals who are born lacking one or multiple limbs, report conscious experience of bodily sensations about their missing limbs, supports the idea that body image does not update with haptic input or proprioceptive feedback because in these individuals there is neither. Moreover, they experience a body image that includes the missing limbs. This observation has led to the idea that body representations are innate or hardwired (Melzack, 1990). However, more recent research has argued against this hypothesis, specifically stating that body image is acquired from experience during pre- and post-natal development (Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013; Price, 2006). For example, Fuentes and colleagues (2013) suggest that body image is altered in individuals with spinal cord injuries due to changes in body use and experience (e.g., using a wheelchair everyday) and not because of sensorimotor loss. In this study, participants with and without spinal cord injury were presented with an image of a body part (anchor) on a computer screen. They were asked to imagine that this anchor was part of their body. They had to identify where various body parts would be located in reference to the anchor. The results showed that those with spinal cord injuries had an elongated body image. However, the specific elongated body parts were not predicted by the lesion level. The authors argued that the elongated body image may be due to the prolonged effect of changes in body posture; individuals with spinal cord injury typically spend much of their time sitting on a wheelchair or laying. This view suggests that the body image may in fact change due to long-term experience.

Body schema: It is important to note that the changes observed in the body schema have all been found immediately after using a tool; suggesting short-term effects (Cardinali, 2011; Cardinali et al., 2011; Cardinali et al., 2009; Maravita & Iriki, 2004; Martel et al., 2016; Sposito et al., 2012). In fact, it has been argued, that there is no functional benefit for lasting changes to the body schema following tool-use (Cardinali et al., 2012), thus body ownership should rapidly revert to pre-tool use representation. No study has directly explored this proposition. Moreover, if the body schema constantly updates with position and posture of the body, this would suggest that long-term training (in whatever capacity) should not alter this body representation. Otherwise, there is the potential for negative consequences (e.g., not being able to perform a task). No study to my knowledge has investigated if training changes the body schema per se.

Body model: In one study, I investigated the effects of long-term training with a tool on the body model of the hand (Coelho et al., 2019; see appendix 3). In this study, I recruited elite level baseball players (15+ years of experience) and asked them to complete the localization task. I found that compared to age and sex matched controls, their body models were reduced in size. Specifically, the elite baseball players underestimated hand width and finger length significantly more than the controls. I argued that because the elite baseball players spend so much time with their hand inside a baseball glove (physically larger than their actual hand), when they are not wearing their glove, they perceive their hand as physically smaller. This argument is based on the data observed, as well as several of the players comments post-localization task. In particular, one player said, "When I reach out and grab a ball without my glove, my hand feels small and weak." I speculate that this reduction in perceived hand size may also have performance advantages. For example, a conservative estimate of the size of their hand could result in more optimal hand position relative to the incoming ball. In other words, if the baseball player has a smaller estimate of hand size, this will lead to less misses and fumbles. This finding resembles reach-to-grasp literature which has found that the more certain a participant is about the size of an object, the smaller they open their hand (Jackobson & Goodale, 1991).

There is also evidence that long-term training changes the body model, even without a tool (Coelho & Gonzalez, in prep, Mora et al., 2018; 2020). For example, I investigated if compared to controls, expert piano players had different body models of their hands. The results showed that piano players made more accurate judgments of hand width, compared to control participants (Coelho & Gonzalez, in prep; see appendix 6). This might be because expert piano players need an accurate representation of the width of the hand, so they can reach specific keys without looking at their hands or the keys. This finding supports that tool embodiment is not the only type of training that alters the body model and furthermore, suggests that while the body model is a stored body representation, extensive practice can produce changes to the body model. This is supported by other studies that have shown that expert magicians (Cocchni et al., 2019) and sign-language speakers (Mora, 2020) also have altered body models of their hands. Plasticity of the body model has also been observed in other body parts like the face (Mora et al., 2021).

In conclusion, studies on training both with and without a tool show that the body model is particularly sensitive to changes due to long-term experience.

5. Is the body model an independent representation?

The argument for the body model as a distinct representation was first put forward by Longo and Haggard in their original report (2010). In this study, the participants were asked to complete both a localization task (body model) and a visual body image task (template matching task). They found that participants were able to accurately complete the body image task but had systematic distortions in the body model task. They argued that the reason why accurate manual action is possible may be due to the body model and the body schema being functionally independent (Longo & Haggard, 2010). The following section details the differences between the three taxonomies of body representation.

5.1 Differences between the body model, the body schema, and the body image

In a recent study, I asked the same group of participants to complete a body model, a body schema, and a body image tasks regarding finger length (Coelho et al., under review; see appendix 4). I found that participants exhibited distortions in all three tasks; they underestimated finger length in the body model and body image but overestimated it in the body schema task. Moreover, the magnitude of these distortions were all significantly different from one another, suggesting differences between these representations. A closer look at the data showed significant correlations between the body model and body schema; those with larger estimates of body schema, also had larger estimates of their body model. Perhaps, this relationship exists because both representations are relevant to action. While the role of the body schema on action has long been established, we are just starting to learn about the role of the body model on action (Peviani & Bottini, 2018; Peviani, Liotta, & Bottini, 2020). In their work, Peviani and colleagues developed a task for isolating the body model in action; the proprioceptive matching task (PMT). In the PMT, the participants were required to slide their hand (hidden underneath a table) until it matched with a visual target on the top of the table (e.g., slide the base of your index finger to the target location). They found that the PMT produced hand maps with similar distortions to those found in the localization task. Importantly, while distortions were still present in the PMT, they were smaller in magnitude than those produced in the localization task. Of course, it is likely that the PMT task is also measuring the body schema, and since the body schema is 'accurate', the distortions on the body model are reduced. Because in the PMT participants are moving the estimated hand (i.e., the hand is in action), it is likely that kinesthetic feedback reduces the body model distortions. This would be supported by my work showing that haptic feedback reduces body model distortions (Coelho & Gonzalez, 2018). Current work in the lab is being completed to investigate if adding kinesthetic feedback to the localization task modulates body model distortions (See appendix 7). In this study, participants were asked to tap the table with the target finger prior to each estimation. Preliminary results show a more accurate body model in some measures in this condition. If kinesthetic feedback modulates body model distortions, then this would explain why relying on this representation allows us to interact with the environment.

In recent years, a co-construction model has been proposed, in which, the body image and schema are functionally distinct, but they interact to create and reshape each other (Pitron et al., 2018; Pitron & De Vignemont, 2017). It is possible that the body model arises from this interaction. Specifically, we know that position sense is informed by afferent signals that detail the position and angle of the joints, but also relies on a stored representation (body model) to inform us of the size and shape of these segments. Longo suggested that it does not make sense to have two stored representations (the body image and the body model; Longo & Haggard, 2010). Perhaps, the representation informing us about the size and shape of our joint segments *is* the body image, and it is then combined with online signals about the size and shape of the body (body schema), resulting in the body model. This would support the co-construction model and would explain why the body model is involved in both perception and action tasks.

5.2 The body model incorporated into the dyadic, triadic, and PAM taxonomies

The dyadic taxonomy: As we have learned, the body model is informed by both haptics and visual information (Coelho & Gonzalez, 2018, Longo, 2014; Peviani et al., 2020), is more or less stable across the lifespan (Coelho & Gonzalez., 2021), exhibits long-term plasticity (Coelho et al., 2018; Coelho et al., in prep, Mora et al., 2018), is sexually dimorphic (Coelho & Gonzalez, 2019; Longo, 2019), and is necessary for both perception and action tasks (Peviani & Bottini, 2018). These features make the body model incompatible with the dyadic taxonomy. Any update on the dyadic taxonomy of body representation should include the body model as a third independent representation. The need to include a third body representation into the dyadic taxonomy, supports the criticism that this definition is too narrow. Including the body model into this taxonomy could help address limitations/issues that have arisen within this model. For instance, it has been argued that action sometimes requires an offline representation of the body (De Vignemont, 2010; Kanayama & Hiromitsu, 2021). Including the body model into the dyadic taxonomy would bridge the body image and body schema limitations as the body model can be both offline and relied upon during action.

The triadic taxonomy: It is possible to include the body model within the definitions described in this taxonomy. Specifically, the triadic taxonomy features a subsection of the body image described as the "body structural description" (BSD). Past research has identified that the BSD may not be entirely visual but incorporates proprioceptive information as well (Buxbaum & Branch Coslett, 2001). In addition, BSD has been proposed to be responsible for position sense (Corradi-Dell'Acqua, Tomasino, & Fink, 2009), and to feature separate neural correlates from the body schema (Corradi-Dell'Acqua et al., 2009). This set of characteristics is remarkably similar to the body model (however at this stage little is known about neural correlates of the body model). Therefore, perhaps the body model and the BSD are the same representation? While it has been stated that the BSD in healthy individuals is understudied, there is some evidence to support that it also retains information from the somatosensory homunculus (Longo, 2015b; Myga, Ambroziak, Tamè, Farnè, & Longo, 2021). In these studies, participants were asked to localize the position of their knuckles on a silhouette of their hand or on that of another person's hand. The results revealed systematic distortions similar to those found in the body model. The authors argue that the results of the silhouette task provide evidence of conceptual knowledge of our hands that is distorted. However, while the pattern of characteristics of the BSD may be similar to the body model, my previous research found no relationship between body model and body image distortions (Coelho et al., under review; Appendix 4). This suggests that these representations may be separate, or that the BSD should be a subcomponent of the body schema and not of the body image. Future research is needed to dissociate the BSD and the body model.

Another possibility is that the body model is a subcomponent of the body schema, but the triadic taxonomy does not provide a narrow enough definition of the body schema in its current version. The suggestion to split the body schema into further categories has been previously proposed (Medina & Coslett, 2010). In this study, the authors suggested that body schema should be split into primary somatosensory representations (representations on the skin), body form representation (body size and shape), and postural representation (limb position). We know that the body model is the representation that underlies position sense (knowledge of where the limbs are in space). Therefore, based on function, it would appear that postural representation (limb position) and the body model are, at the very least, highly interrelated representations. It is even possible that the body model could be a subcomponent of the postural representation. More research is needed to dissociate these representations.

One more possibility is that the body model is the by-product of all representations in the triadic taxonomy. To be specific, by its very nature the localization task is perceptual and produces a visuospatial map of the body (just as BSD), but it involves movement of the pointing hand (body schema), and lexical knowledge (knowing the names of each of the body parts/locations). Therefore, perhaps the distortions found in the body model arise out of the interaction between these three representations. Research that does not require the participant to point and/or minimizes lexical requirements is necessary to separate the body model from the other representations. In my previous study we found that both the body model and body image feature an underestimation of finger length, but an overestimation in the body schema (Coelho et al., under review; Appendix 4). Curiously, the body model was less underestimated than the body image. Perhaps the severely underestimated body image combined with the overestimated body schema results in more accurate (but still underestimated) representation of the hands (body model). This possibility seems unlikely, however, as my research found that the body model was different from both the schema and image (Coelho et al., under review).

Perception and action model: The PAM dissociates the taxonomies based purely on function (representation for action vs representation for perception). However, the body model appears to be involved in both action and perception tasks (Peviani & Bottini, 2018; Peviani et al., 2020) thus it must have access to both the dorsal and ventral somatosensory streams. This would support de Haan and Dijkerman's current suggestion that the two streams interact with one another (de Haan & Dijkerman, 2020). My recent research, however, has shown that the body model is only related to the body schema (Coelho et al., under review; see appendix 4) suggesting that it is a by-product of the dorsal stream. Imaging studies targeting each of the three representations may help elucidate where each fit with respect to the dorsal and ventral streams.

To summarize, different conclusions about the body model can be drawn depending on dyadic, triadic or PAM models. For example, when considered in relation to the dyadic taxonomy, the body model must be an independent body representation. This is supported by a review which postulated that the body image and model are likely independent because they underly different functions and have different characteristics (Gadsby, 2019). Moreover, my previous work has shown that the magnitude of distortion between the three representations are different. When considering the triadic taxonomy of body representations or the PAM, it is possible to define the body model as a subcomponent of the body schema (Gadsby, 2019). In fact, my research showed correlations between these two representations (Coelho et al., under review). The argument that the body schema and model are interrelated arises out of their shared functional role for action (Gadsby & Williams, 2018). Some have suggested that the body model may be in fact the "short-term body schema", concerned with guiding body location and posture, both of which are constantly updating (Gadsby & Williams, 2018). My research on the plasticity of the body model would suggest that this representation is also long-term (Coelho et al., 2019). More research is needed to fully understand the relationship between the body schema and the body model.

6. Future directions: Where should the field of body representation go?

One of the major limitations to body representation research is the lack of consistent terminology across this research field. A specific problem in describing the body model is that the other taxonomies are not well defined. For example, sometimes the same taxonomy (e.g., body image) is used to refer to different representations, and in some cases with opposite meanings (Gallagher, 2006). For example, early work defined the *body image* as a picture of our bodies in our minds (Schilder, 1936), however, later in the same paper the author refers to the *body schema* as the image of our own body. Clearly, ambiguity in terminology has long inundated this research field. In addition, there has been considerable debate over the characteristics and boundaries of the body image and schema (Gadsby, 2019; Pitron et al., 2018) making the introduction of the body model into such taxonomies extremely difficult. The field would greatly benefit from unifying terminology regarding body representation. Another limitation so far is the lack of studies that have included a within subject's design. Ideally, the same participants would complete a typical measure of body image (line length task), body schema (aperture task), and body model (localization task). This would allow for direct comparisons between the different taxonomies, which may be necessary to clarify these definitions.

Imaging studies provide an avenue to further understand the various taxonomies. Specifically, by focusing on what areas of the brain are involved when referring to body image, body schema, and body model will allow us to understand if these representations are independent or subcomponents of one another. Understanding the neural correlates of these three representations and how they relate to one another could also lead to a better understanding of those with body representation disorders. While previous research has investigated the neural correlates of body image and schema in those with anorexia, no study has investigated how these representations interact, or the body model in this population. Lastly, imaging studies can increase our knowledge on the body model itself. To date, no study has investigated the neural correlates of this representation. Longo postulates that the body model is reflecting the somatosensory representation of the body. He argues that the tactile receptive field geometry is responsible for the distortions in this representation (Longo 2015). However, this is yet to be shown.

An additional factor that should be considered in moving forward the field of body representation, is gender. As stated earlier in the review, there is a plethora of research that has shown sex differences in body representation disorders (Burke et al., 2019; Kanayama & Pope Jr, 2011; Keski-Rahkonen & Mustelin, 2016). Females are overrepresented in anorexic patients (90% of the population) and males in body dysmorphia. Some studies on body image have found women overestimate body width compared to males (D'Amour & Harris, 2019; Schneider, Frieler, Pfeiffer, Lehmkuhl, & Salbach-Andrae, 2009; Urdapilleta, Cheneau, Masse, & Blanchet, 2007), however, other studies have not found sex differences in body representation (Dolan et al., 1987; Keeton et al., 1990; Meneguzzo et al., 2021; Pasman & Thompson, 1988). One possible reason for the discrepancy in these findings, is that none of these studies, have controlled for gender identity (American Psychological Association, 2015). There are virtually no studies investigating gender differences in body representation. Previous research has found that the neural systems for own-body processing align with gender identity rather than biological sex (Majid et al., 2020), meaning that participants who identify as androgenous may have different representations of their bodies (regardless of biological sex). Moreover, previous research has found that gender dysphoria (a mismatch between gender identity and birth-assigned sex) is associated with specific anatomical features in one-body/self-processing circuits (Kilpatrick et al., 2019; Korashad et al., 2021;Moody et al., 2021). For example, gender dysphoric participants had weaker structural and functional connections in the anterior cingulate-precuneus and right occipito-parietal cortex. Importantly, these differences have been shown to be reduced following cross-sex hormone treatment (Kilpatrick et al., 2019). A comprehensive investigation of biological sex *and* gender differences in the various types of body representation is needed. Moreover, sexual orientation may also influence body representations (Meneguzzo et al., 2021). This would be inline with neuropsychological tests that show sexual orientation can affect the outcome in such tests. For example, while females typically outperform males on verbal tasks; homosexual males outperform their heterosexual counterparts, while homosexual females have the lowest scores (Hall & Kimura, 1995). Reports on body dissatisfaction and body image follow a similar trend (Peplau et al., 2009). Heterosexual females and homosexual males score lower than heterosexual males and homosexual females on body image satisfaction. In addition, homosexual males overestimate body width more so than heterosexual males in a visual body image task (Meneguzzo et al., 2021). So perhaps, sexual orientation also affects body representations. An examination of sex, gender, and sexual orientation may lead to explanations regarding the cause(s) of distorted body representations or body dysmorphias (e.g., anorexia, muscle dysmorphia) and the known sex differences in these disorders.

7. Remainder of the thesis

While body representation research has long focused on the body image and schema, we are just beginning to understand the body model. The remainder of this thesis addresses gaps in the literature regarding the characterization of the body model. Using the localization task throughout a set of experiments (Appendies 1-7). I measured the body model in various conditions. Specifically, I show that the body model is enlarged during childhood (Appendix 1), that this representation is sexually dimorphic (Appendix 2), altered by long- but not short-term training (Appendix 3) and that the distortions are different than those in the body image or schema (Appendix 4). I also show that seniors and adults have similar estimates of body model size (Appendix 5), professional piano players have more accurate body models (Appendix 6), and that kinesthetic feedback may modulate the body model (Appendix 7). These findings contribute to the limited collection of studies which have characterized this representation.

8. Conclusion

In this thesis, I reviewed the body image, the body schema, and the newly defined body model. I found that the body model featured several unique characteristics that are not a part of the other two representations. Specifically, it is a long-term, sexually dimorphic representation, that updates only after long-term training, and serves action *and* perception. The results of this thesis suggest that there must be more than just two representations. The dyadic taxonomy theory (in its current state) needs to be revised to encompass the body model. Overall, more refined, and updated definitions regarding the dyadic and triadic taxonomies are needed in the literature.

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Appendix 1: Growing into your hand: The developmental trajectory of the body model.

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Abstract

We rely on accurate body representations to successfully interact with the environment. As adults, we rely on many years of experience with a body that has stayed relatively the same size. Children, however, go through periods of rapid growth and whether or not their body representation matches this physical growth is unknown. To address this question, we examined the developmental trajectory of the body model of the hand. The body model is the representation of our bodies that underlies position sense. We recruited a group of children (8-16yrs) and a control group of young adults (18-26yrs) and asked them to complete the body model task. In this task, participants estimated the location of 10 different landmarks (the tips and metacarpophalangeal joints of each of their five fingers). The position (XY location) of each estimate was tracked using an Optotrak camera. From the XY locations we derived hand width and finger length. Not surprisingly, children's physical hand width and finger length were smaller than adults but remarkably, the body model, was similar for both groups. This result indicates that children overestimate hand size and suggests that the body model is ahead of physical growth. This result contradicts the notion that body representation lags physical growth during puberty, accounting for the clumsy motor behaviour characteristic of teens. We discuss the results in relation to the different taxonomies of body representation and how an enlarged representation of the hand during childhood may influence action.

Introduction

The mental depiction of the size and shape of our body is referred to as body representation (Frédérique De Vignemont, 2011). We rely on an accurate representation of our bodies in order to interact with the environment. For example, reaching to pick up an object would be incredibly difficult without an accurate representation of the length of one's arm. The brain houses several different representations of the body. Two of these representations are the body image and the body schema (Dijkerman & De Haan, 2007). The dyadic taxonomy of body representation defines the body image as the offline visual depiction of the body that is relied on for perceptual tasks (F. De Vignemont, 2010; Gallagher & Cole, 1995; Head & Holmes, 1911; Paillard, 1999). The body schema on the other hand, is the online somatosensory representation of the body that is used for action. These two representations can also be understood as explicit (body image) versus implicit (body schema). Previous research has found that the implicit representation is based off a sensorimotor representation and that it is dissociable from the explicit representation (Frassinetti et al., 2010; Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008). Importantly, this implicit representation is also present in children (Frassinetti et al., 2012; Frassinetti et al., 2008).

As adults, we can rely on many years of experience performing tasks with a body that has remained more or less the same size over years. Children, however, experience rapid growth spurts and therefore cannot fully rely on body-size-experience to accurately perform actions. It has long been observed that children during puberty are clumsy (Hirtz & Starosta, 2002; Tanner, 1962; Visser, Geuze, & Kalverboer, 1998). One possible explanation for their clumsiness is that body image and/or schema do not develop at the same rate as physical growth. In other words, body representation may lag behind physical growth creating a mismatch between body representation and physical size. There is evidence to support this suggestion (Cardinali, Serino, & Gori, 2019; Steinsbekk et al., 2017). For example, Steinsbekk and colleagues (2017) asked children aged four years (and followed up on them at age six and eight) to complete the Children's Body Image Scale. This scale consists of seven photographs of different body sizes. Each body size is designed to correspond with a defined BMI range. The child is asked to select which of the seven images is most similar to their own body size. Discrepancy of body size were calculated by subtracting the BMI of the selected image to the child's real BMI. The authors found that children typically underestimated their BMI, by selecting images that corresponded with a lower BMI than their own. In addition, in a similar body image task Cardinali and colleagues (2019) found that from ages 6-10 years, there was a negative correlation between age and perception of hand size. Older children underestimated hand size to a greater degree than younger children. These studies provide evidence that body image does not keep up with physical growth (in support of a mismatch between perceptual and physical growth). However, other research on the body schema did not find this to be the case (de Haan, Smit, Van der Stigchel, Keyner, & Dijkerman, 2018). These authors tested children on a variety of body representation tasks. For example, in one such task they asked participants to estimate the distance between two tactile stimuli that were applied to their forearm. They were also asked to move their hand through different sized apertures. They found that children's representations did not lag behind their physical growth. The contradictory results from these two separate studies most likely arise out of the different body representations being measured. In Cardinali et al (2019), participants engaged in a body image task. Whereas in de Haan and colleagues (2018), the body schema was the targeted representation. Therefore, it is likely that different body representations develop at different rates.

In the last decade, a new body representation has been proposed; the body model (Longo & Haggard, 2010). This is the representation of the spatial layout of the body. Specifically, the body model underlies position sense (knowledge of where the body part is in space). When we move our bodies, afferent signals indicate the angle of each joint (Proske & Gandevia, 2012). However, no signal informs us about the size and shape of the body segments between joints, and thus we must rely on a stored mental representation (the body model). In their original study, Longo and Haggard asked their participants to localize 10 different landmarks on their hand which was hidden underneath a tabletop. The resulting representation of the hand had two distinct characteristics: an overestimation of hand width and an underestimation of finger length. The authors argued that position sense is being informed by a distorted body model (Longo & Haggard, 2010). These characteristic distortions have been replicated in multiple studies from different labs (Cocchini, Galligan, Mora, & Kuhn, 2017; Coelho & Gonzalez, 2017, 2018; Coelho, Zaninelli, & Gonzalez, 2016; Longo & Haggard, 2012; Longo, Mattioni, & Ganea, 2015; Peviani & Bottini, 2018; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). There are functional similarities between the body model and the body schema, both are relied on for action. While the body model is used to calculate position sense (Longo & Haggard, 2010), the body schema is relied upon to calculate motor commands (Dijkerman & De Haan, 2007). As previously presented, many studies have investigated the development of the body image and the body schema but only one study has focused on the body model of children (Van der Looven, Deschrijver, Hermans, De Muynck, & Vingerhoets, 2021). In this study, Van der Looven and colleagues asked participants aged 5-23 to complete a body model task (as in Longo & Haggard, 2010) and a body image task. They found that children showed distortions in the body model task that were not present in the body image task. Specifically, they found that underestimation of finger length increased as a function of age. This is a novel finding that requires further investigation. Documenting the developmental trajectory of the body model will inform us: 1) if distortions seen in adults (overestimation of hand width and underestimation of finger length) are also present in children, and 2) if the body model lags behind physical development.

The purpose of the present study was to investigate the body model in children. We recruited a group of children between the ages of 8-16 and a group of young adults (18-26 years of age), for comparison. We hypothesized that if the body model lags behind physical development, then children would underestimate hand size more than the adults. A secondary aim of the study was to document if body model distortions changed as a function of age. This is based on previous work that has found that children's body image and body model of the hand increases with age (Cardinali et al., 2019; Van der Looven et al., 2021). For example, Van der Looven and colleagues (2021) found that finger length underestimation increased with age. The participants completed a modified version of the body model task (Coelho et al., 2016; Longo & Haggard, 2010). In this task, the hand is placed palm up underneath a covered tabletop (no vision of the hand) and participants are asked to localize 10 different landmarks on their unseen hand. Using an Optotrak camera, XY locations of each estimates are recorded. We then convert these XY locations into a map of hand size for each participant.

Methods

Participants

We conducted a power-analysis in G*power (Erdfelder, Faul, & Buchner, 1996) to determine the minimum number of participants needed to determine group differences in a body model study. We used ŋ2p from our previous studies to determine participant number (Coelho & Gonzalez, 2017, 2018; Coelho, Schacher, Scammel, Doan, & Gonzalez, 2019; Coelho et al., 2016). Based off these previous reports we needed anywhere from 38-82 participants. Fifty-eight participants were recruited for the study. All participants self-identified as being right-handed. The participants were split into two groups depending on their age. There were twenty-three participants in the children group; 8-16-year-olds (mean age=11.3±2.0SD; 14 males). Eight years is considered to be the age when multisensory integration (specifically haptic spatial information) occurs (Gori, Del Viva, Sandini, & Burr, 2008; Mackrous & Proteau, 2016), thus we chose this age as a minimum to participate in the study. We chose to include adolescence (between the ages of 13-16) because we wanted to explore how the body model develops into young adulthood. Thirty-five participants were in the adult group; 19-26-year-olds (mean age=20.3±.2.1SD; 15 males). All participants in the adult group were undergraduate students at the University of Lethbridge and were recruited in exchange for a course credit. The participants in the children group volunteered to participate. In accordance with the Declaration of Helsinki, all participants over 18 gave written consent prior to participating in the study. For the participants who were under the age of 18, parental consent was obtained prior to the onset of the study.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diodes (IRED). The IRED was placed at the end of a wooden stylus (19.5 L x 0.5 W x 0.3 H cm). IRED location was recorded for 1000ms at 100 Hz for each trial.

Procedures

A modified version of the hand mapping protocol described in previous studies (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2019; Coelho et al., 2016) was used. In brief, the participant sat in front of a glass tabletop (41.0 L x 86.5 W cm) and were instructed to place their hand palm up against the tabletop and spread their fingers as wide apart as possible. During the occluded hand condition (occluded hand), the tabletop was covered with a black tablecloth so they could not see their hand (see figure 1). Participants were then asked to estimate where the locations of ten different landmarks were on their occluded hand. The ten locations were the tips and metacarpal phalangeal (mp) joints of each of their five fingers. They completed each estimate by placing the wooden stylus (with the IRED attached), on the glass directly over top of each perceived location. The XY location for each estimate were recorded via the Optotrak. After each estimate the participant was required to place the wooden stylus on a "home spot". This was located directly above the participants arm, at the edge of the table. During this occluded hand condition, the estimated body model of the hand is being measured. Immediately following this condition, the black tablecloth was removed, and the protocol was repeated with full vision of the hand (non-occluded hand condition). This condition was completed in order to compare perceived hand dimensions (occluded hand condition) to the real hand size (non-occluded hand condition). This condition measures the participants physical hand size. Both conditions were repeated for the opposite hand. Traditionally, in the hand mapping task we have asked participants to complete 50 trials per condition (5 estimations to each landmark). Due to the fact that the younger children struggled to hold their hand still against the tabletop, we reduced the number of trials. Each condition consisted of ten trials (1 trial per landmark; 10 trials per condition; 20 trials per hand; 40 trials total).

As in our previous reports, there were two dependent variables: great span (hand width), and finger length. We defined the great span as the summed distance between the tip of the thumb to the tip of the pinky. We chose to include the thumb into the measure of hand width due to its relevance in reaching and grasping. For example, a power grasp requires the entire width of the hand (including the thumb). Moreover, we have included the thumb in the great span for all our reports on the body model (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2019; Coelho et al., 2016). We defined finger length as the distance between the tip and the mp joint of each finger averaged together.

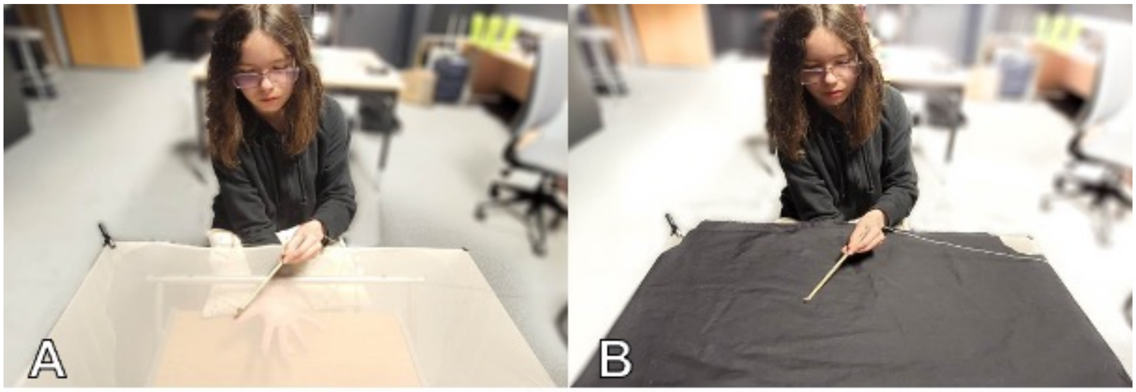

Figure 1

Figure 1: The experimental setup for the body model task. Frame A is the non-occluded hand condition. Here, the participant had full vision of their hand shows the occluded hand condition Frame B is the occluded hand condition. In this condition a black tablecloth was placed on the table, so the participant had no vision of their hand.

Analyses:

To determine if the two groups (children and adults) had distorted estimations of hand size, we ran a 2x2x2 repeated measures ANOVA on the raw estimates (in mm) of hand size. Hand (left, right) and condition (occluded, non-occluded) were the within factors. The between factor was group (children, adults). We were specifically interested in the condition x group interactions to see if there were differences in the characteristic distortions between children and adults.

A second analysis was conducted to investigate if there were significant differences in the magnitude of distortion between age groups, sex, and hand (left, right). Thus, a 2x2x2 repeated measures mixed design ANOVA was conducted on the percent distortion. To account for differences in hand size (children had significantly smaller hands than the adults, p's<.001, as determined by analysis 1 in this study), we expressed the data from the occluded hand estimates as a percentage of the non-occluded hand size. Specifically, the occluded-hand size data were transformed using: ((occluded hand condition – non-occluded hand condition)/non-occluded hand condition)*100 (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2019; Coelho et al., 2016). The between factors were group (children and adults), and sex (male, female); the within factor was hand (left, right).

Our last analyses were a series of Pearson *r* correlations. Based off previous research showing that underestimation of hand size increases with age (Cardinali et al., 2019; Van der Looven et al., 2021), we investigated if there was a relationship between age and perceived hand size in the current study. For this analysis, the variables used were age (expressed in years), the great span, and finger length. As with the mixed design ANOVA, all hand size data were expressed as the percent of the non-occluded hand size. In addition, we also completed these correlations on the raw mm from the occluded hand and non-occluded hand conditions. We expected to see hand size increase as a function of age in the non-occluded hand size.

Results

Mean and standard error is reported for all analyses.

1. **Body Model Distortion (repeated measures ANOVA):**

<u>Great span</u>

There was a main effect of condition [$F(1,54)= 4.8$, $p=.03$, ŋ2p=.08]. The occluded hand condition (192.7mm±3.9, CI[184.7, 200.6]) was overestimated compared to the non-occluded hand condition (182.7±2.9, CI[177, 188.4]). Indicating that the body model was significantly larger than the physical hand size. However, there was also a significant condition by group interaction [$F(1,54)=9.9$, $p=.003$, ŋ2p=.16]. Follow-up pairwise comparisons revealed that while children overestimated the non-occluded hand condition [$t(23)=4$, $p<.01$, occluded hand condition: 187.4±5.8; non-occluded condition: 163.9±3.8], adults had accurate estimates of the occluded-hand condition ($p=.6$; occluded hand condition: 197.5±4.9; non-occluded hand condition: 200.8±4). There was a main effect of group [$F(1,54)=21.9$ $p<.01$, ŋ2p=.29]. Children had smaller hand sizes (in both conditions) compared to the adults. In addition there was a hand x condition x group interaction [$F(1,54)=5.4$, $p=.02$, ŋ2p=.09]. Follow-up one-way ANOVA's revealed that while the occluded hand condition was different between children (179.6±7.1) and adults (200.4±6.2) for the right hand ($F(1,57)=4.8$, $p=.033$), there was no difference between the groups (children =195.3±8.1; adults= 194.4±4.8) for the left hand occluded condition ($F(1,57)=.006$, $p=.94$). As expected, both non-occluded hand conditions were different between the groups) *p*'s<.001). See figure 2.

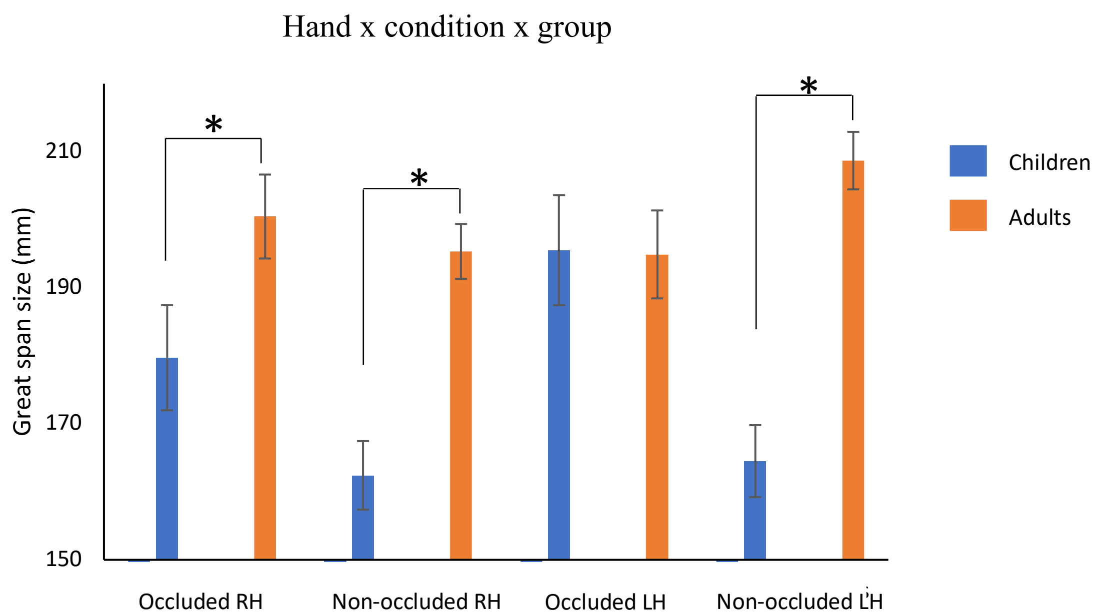

Figure 2: The hand x condition x group interaction. Adults had larger occluded and non-occluded hand size estimations for the right hand. Surprisingly, adults and children had similar estimates of the occluded left hand.

<u>Finger length</u>

There was a main effect of condition [$F(1,54)=25.5$, $p<.01$, ŋ2p =.32]. Finger length was smaller in the occluded hand condition (47±1.1, CI[44.9, 49.2]) compared to the non-occluded hand condition (53.8±1, CI[51.9, 55.7]). This indicates that finger length was significantly underestimated in the body model. Moreover, there was a condition x group interaction [$F(1,54)=8.9$, $p=.004$, ŋ2p =.14]. Follow-up paired sample *t*-tests revealed that children did not underestimated finger length (p=.16). Adults had significantly smaller finger lengths in the occluded hand condition (48.1±1.4) compared to the non-occluded hand condition (58.9±1.2) [$t(35)=-6.5$, $p<.001$]; see figure 3. Lastly, there was a main effect of group [$F(1,54)=19.2$, $p<.01$, ŋ2p =.26]. children had smaller finger length's (47±1.2, CI[44.6, 49.4]) compared to the adults (53.8±.1, CI[51.9, 55.7]).

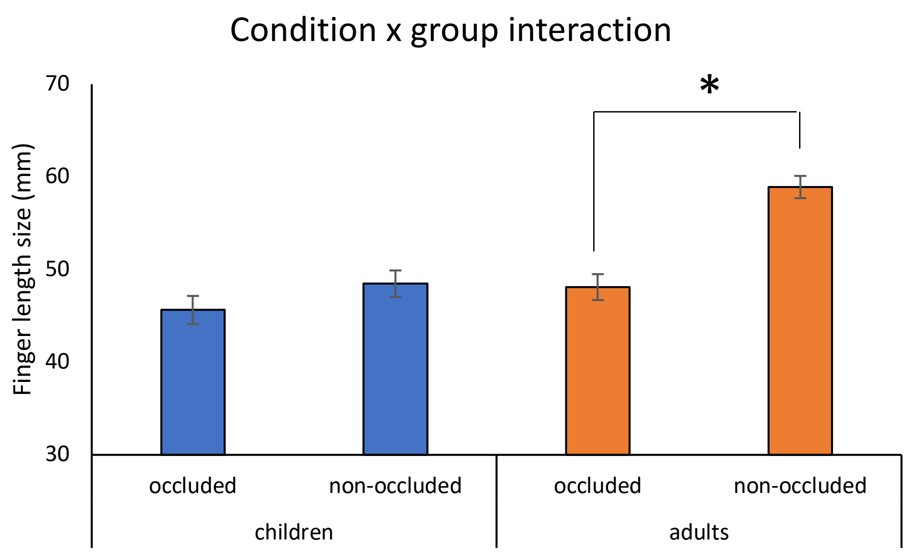

Figure 3: The condition x group interaction for finger length. Children had similar estimates in both the occluded and non-occluded finger length. This indicates that the body model or finger length was not distorted. Adults had smaller estimates in the occluded condition. This aligns with previous research that has found finger length is underestimated in the body model in adults.

3. Age Differences (Repeated measures mixed design ANOVA):

<u>Great span</u>: There was a main effect of group [$F(1,51)=8$, $p<.01$, ŋ2p =.14]. Children had larger overestimations of the great span (15.7% ±3.9, CI [7.7, 23.7]) compared to adults (1.1%±3.2, CI [-5.5, 7.7]).

There was also a group x hand interaction [$F(1,51)=9$, $p<.01$, ŋ2p =.15]. Follow-up pair-wise *t*-tests revealed that the adults overestimated the right hand (7%±4, CI [-.09, 13.9]) significantly more ($t(31)=3$, $p<.01$, d=1.1) than their left hand (-4.1%±3.6, CI [-12.6, 4.0]). For the children there were no differences in overestimation between the two hands ($p=.18$). See Figure 4.

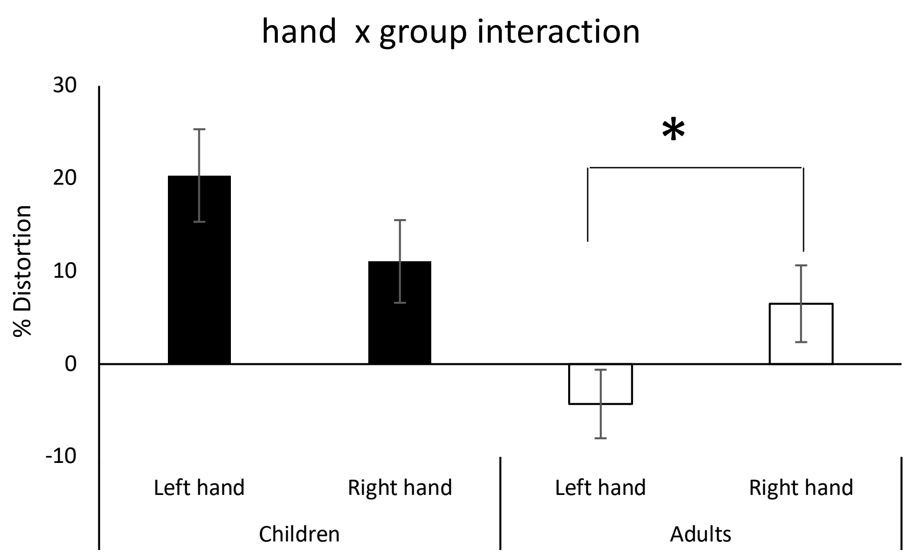

Figure 4: The interaction between hand and group. Adults overestimated the great span of their right hand significantly more than their left. For children there was no difference between hands.

<u>Finger length</u>: There was a main effect of group [$F(1, 52)=9.2$, $p<.01$, ŋ2p =.15]; compared to adults, children had larger estimations of finger length (adults: -18% ±2.9, CI [-23.8, -12.09]; children: -3.4% ±3.6, CI [-11.1, 3.2]). No main effect of sex was found but there was a main effect of hand [$F(1,52)=4$, $p=.05$, ŋ2p =.07]. Participants underestimated finger length on their left hands (-14.1±2.7, CI [-14.1, -8.7]) more than on their right hands (-7.8±2.9, CI [-13.6, -2.1]).

4. Relationship between the Body Model and Age (Correlation analysis):

Great Span: There was a significant negative relationship between age and distortion of the great span [N=55, p<.01, r=-.48]; underestimation of hand width increased with age. See figure 5A.

Finger Length: A significant negative correlation was found between age and finger length distortion [N=56, p<.01, r=-.43]; underestimation of finger length increased with age. See figure 5b.

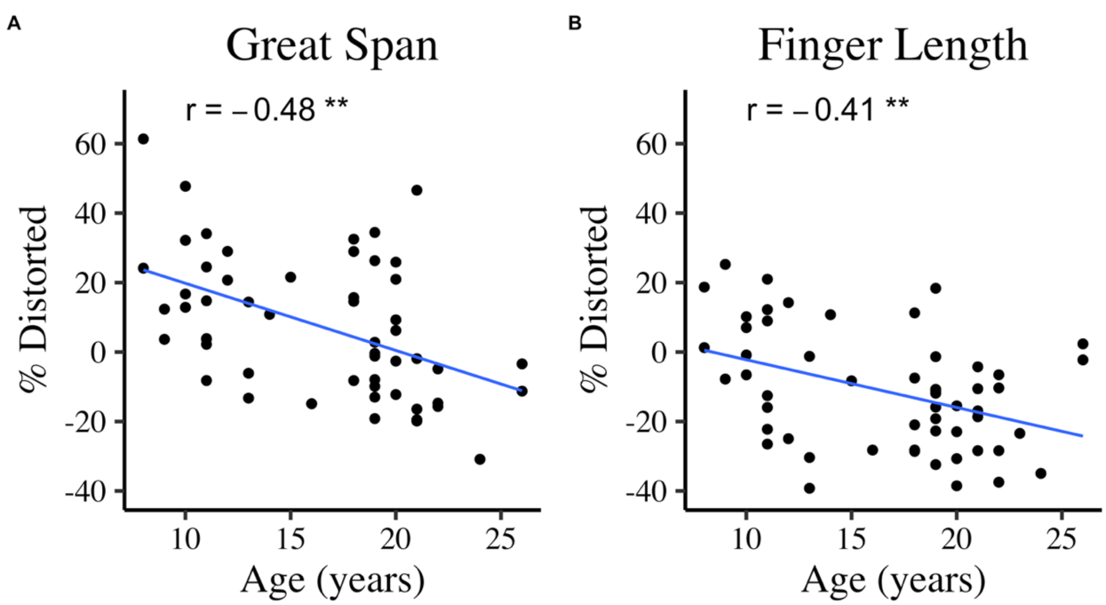

Figure 5: The relationship between % distortion and age for both dependent variables. Frame A shows the great span, Fame B finger length. In both cases as the participants got older great span distortions decreased.

To further understand the origin of the relationship between age and the body model distortions, we also completed these correlations on the raw measurements (in millimeters) from the occluded and non-occluded hand conditions. There were significant relationships between age and non-occluded hand size (as shown in table 2 and figure 6), but no relationship between age and occluded hand size. Statistics are reported in table 2.

Table 2: The descriptive statistics for the correlations between age and estimated hand size condition and age and physical hand size condition. There was a significant relationship between age and estimated hand size for both variables. However, for estimated hand size there were no significant relationships.

		Great span estimated hand size	Great span physical hand size	Finger length estimated hand size	Finger length physical hand size
age	Pearson Correlation	.09	-.72**	.18	.66**
	Sig. (2-tailed)	.48	<.001	.18	<.001
	N	58	58	58	58

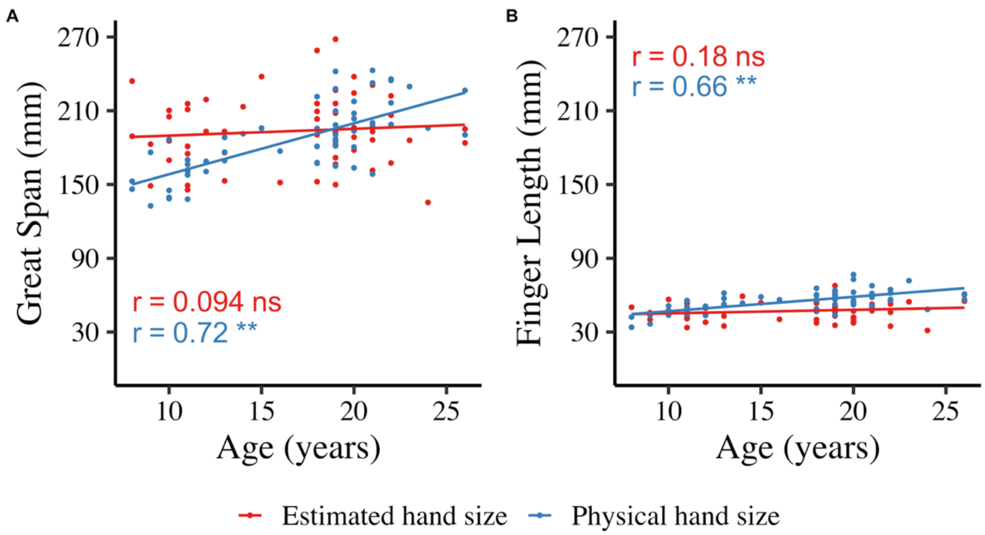

Figure 6: The relationship between age and estimated hand size conditions are in red (for both the great span and finger length). The relationship between age and physical hand condition are in black (for both variables). Note the significant relationships for physical hand size. In both cases hand size increases as a function of age. However, there were no relationships between age and estimated hand size, indicating that children and adults had similar estimates of hand size.

Discussion

Previous research has shown that the body model, this is, the representation of the spatial layout of the body, is distorted in adult participants. The purpose of the present study was to investigate if body model distortions are also present in children. To this end, we recruited a group of children (8-1) as well as a group of young adults (for controls; 18-26). We asked participants to complete a modified version of the hand's body model task that we have used in previous studies (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2019; Coelho et al., 2016). In this task, participants place their hand palm up underneath a glass tabletop that is covered by a black cloth (no vision of the hand). Participants are then asked to indicate the location of the tips and metacarpal phalangeal (mp) joints of each of their fingers. The resulting estimates are then compared to a condition in which the tablecloth is removed and thus participants have full vision of their hand (i.e., physical size).

Based off previous research that has posited that body representation may lag behind physical development, we hypothesized that children would underestimate hand size more than adults. We found that children had large distortions of hand size, but in the opposite direction as hypothesized: they overestimated hand width and had larger estimates of finger length (they were accurate) compared to the adult group. Furthermore, the results of the correlation analysis demonstrated that hand size estimations decrease with age. This finding aligns with a previous study in children 6-10 years of age (Cardinali et al., 2019). In that study, the older the children the more the hand was underestimated. In the present study we found that this trend continues into adulthood. Lastly, we replicated previous findings that adults perceive their right hand as larger than their left for both the great span and finger length. Children showed this asymmetry in finger length as revealed by a main effect of hand but showed no difference between hands for the great span.

Our first finding was that children had larger overestimations of both the great span and finger length compared to the adult group. Moreover, children's estimations of the great span were significantly larger than their physical hand size, but their estimates of finger length were accurate. This last finding is a surprising result as all other reports on the body model have consistently found that participants underestimate finger length (Cocchini et al., 2017; Coelho & Gonzalez, 2017, 2018; Coelho et al., 2016; Longo & Haggard, 2012; Longo et al., 2015; Peviani & Bottini, 2018; Saulton et al., 2015; Saulton et al., 2016). It can be argued that the accurate representation of finger length is in fact an *overestimation* of size, as the norm has been shown to be an underestimation. The results of overestimation of both the great span and finger length are in contrast to previous studies in children that have found body representation to be underestimated (Cardinali et al., 2019; Giurgola, Bolognini, & Nava, 2020; Steinsbekk et al., 2017) or to be accurate (de Haan et al., 2018; Van der Looven et al., 2021). For example, Giurgola and colleagues presented children (aged 4-6) with resized photographs of their hands (bigger, smaller, or their actual hand size). The participants were then asked to indicate if the image matched their physical hand dimensions. Children in this study selected images that were smaller than their physical hand size, indicating that the body image of their hand was underestimated. In a recent study, Van der Looven and colleagues asked participants to complete a body model task and a template matching task (body image). They found distortions in the body model of the hand, but the representation of the hand measured through the template matching task was accurate. Together, these results combined with the finding of the present study strongly suggest a dissociation between the body model and body image.

The result that children overestimate hand size compared to adults adds to recent studies that suggests body representation does not lag behind physical growth (de Haan et al., 2018; Giurgola et al., 2020). These studies however show no difference in body representation between children and adults. For example, de Haan and colleagues asked different aged participants (6-50 years) to complete both, body image and body schema tasks (de Haan et al., 2018). They found that children and adults made similar estimates of body size in both tasks. In addition, a different study found that both children and adults underestimate hand size, to the same degree, in a body image task (Giurgola et al., 2020). These authors argue that body-part perceptual distortions are present in early childhood and are therefore a characteristic of human body representation, and not a result of perceptual growth lagging behind physical growth. Our results also indicate that body-part perceptual distortions are present in youth, however, they suggest that the body model is enlarged in this population. It is possible that this enlarged representation of their limbs in fact contributes to the uncoordinated movements that characterize this age group. In a previous study we suggested that hand size underestimation may result in more accurate manual actions (Coelho et al., 2019). In that study we tested male elite baseball players on the body model task. We found that the baseball players had smaller hand size estimates than sex- and age-matched controls. We argued that having a smaller hand estimate may actually help the players optimize the position of their hands when catching a ball thus leading to fewer misses and fumbles. Having a larger estimate of hand size would actually cause them to miss catching the object. Moreover, studies have shown that when vision is occluded, participants increase the size of their hand aperture to increase the margin of error during grasping when they are unsure about object size (Flindall, 2017; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000; Jakobson & Goodale, 1991). Coming back to the results of the current study, by overestimating hand size children could be increasing their margin of error for a task that they are unsure of, that is, how big their hands are. Another possibility (not mutually exclusive) is that the body model, and not the body image (i.e., the perceptual representation), is used when planning and executing manual actions, therefore overestimation of hand size results in clumsy behaviour. This suggestion would be supported by work from Peviani and colleagues (2018), who demonstrated that the body model is relied on for both perception and action tasks. Importantly, they suggested that the distortions in the body model may be partially responsible for motor accuracy issues.

One last possible interpretation as to why children had larger distortions in the body model, is an over reliance on non-informative vision. Previous research has shown that during spatial tasks children rely more on visual information compared to adults (Petrini, Caradonna, Foster, Burgess, & Nardini, 2016). In our previous work we explored the contributions of vision and haptics to the body model (Coelho & Gonzalez, 2017). In that study, we asked participants to complete the body model task in one of three conditions: 1) with vision and haptics; 2) with haptics only; and 3) with vision only. We found that when participants could only rely on vision (of the tabletop) their body models were the most distorted. Therefore, if the children rely more on visual information to complete the body model task, this could contribute to the large distortions found in this group. Further research is needed to address how haptics and vision influence the development of the body model.

Although in the present study children showed an overestimation of both the great span and finger length when compared to adults, an important point to make is that children's representations were in fact not different from that of adults; the overestimation arises because children have smaller hands. The finding that children and adults have comparable body models suggests that estimates of hand size do not change throughout development. This finding aligns to the results of a study by de Haan et al (2018). In this study, children and adults were required to estimate the distance between two tactically presented stimuli on their forearms. The results showed no difference on the estimations between children and adults even though children's forearms were shorter. The authors argued that body representation does not lag behind physical development. Our results support this argument, and in fact suggest that the body model is ahead of physical growth. Longitudinal studies are needed to investigate this possibility.

Another finding of the current study was the main effect of hand for finger length. All participants estimated the fingers to be longer on their right versus their left hand. There was also a hand by group interaction for the great span. Adults overestimated their right more than their left hands. These findings replicate our previous studies (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2016) in which we found that the right hand was perceived as larger than the left. We have argued that this hand difference exists because right-handed participants view their right hand as being more skilled than their left. Evidence for this suggestion comes from a previous study on the body image of the hand (Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009). In this study participants were presented with different sized blocks and were asked to estimate if they were able to grasp the block placed in front of them. Participants overestimated the grasping ability of their right hands. The authors argued that this result occurs because participants view their right hand as being more capable for action. Moreover, it has been shown that compared to the left hand, there is a larger cortical representation for the right hand (Sörös et al., 1999). It has been suggested that the body model is a reflection of the cortical representation of the hand (Longo & Haggard, 2010). The finding of hand asymmetries in the body model supports this view and the current results suggest that this asymmetry might develop during childhood. Children overestimated the finger length of their right hand. However, the question remains as to why children did not show this asymmetry for the great span. Perhaps the cortical representations are not fully established yet, or children perceive both hands as being equally capable (or incapable). More research is needed because if children perceive both hands as equally capable, why then do they prefer to use the right hand for grasping and manipulating objects (Nelson et al., 2017; Sacrey, Arnold, Whishaw, & Gonzalez, 2013); this would suggest a mismatch between perception and action.

There was a significant relationship between age and hand size distortion: Underestimation increased as a function of age. This finding replicates previous studies in children that found that underestimation in hand size (Cardinali et al., 2019) and finger length (Van der Looven et al., 2021) increase with age. For example, in Cardinali et al., children were asked to identify if a model of a 3D hand was larger or smaller than their physical hand. They found that all children underestimated hand size, however, the underestimation was greater in the older children. Our findings of the body model demonstrate that the representation of both finger length and hand width continues to decrease at least into young adulthood, but this is due to changes in physical hand size (children have smaller hands than adults). Children's estimates of hand dimensions were the same size (in mm) as those in the adults. This finding suggests that the body model has reached "adult size" before the physical size of the hand. Based off this suggestion, we predict that the relationship between age and body model distortion will stabilize after the hand stops growing. Future research that includes older adults is necessary to address this prediction.

As mentioned in the introduction, this is not the first study to investigate the body model in children. A recent study investigated the effect of handedness and age on the development of hand size representation (Van der Looven et al., 2021). These authors used a body model task as well as an explicit body image task to test hand size representation in four different age groups (5-8 years, 9-10 years, 11-16 years and 17-23 years). These authors found that even the youngest children showed the characteristic distortions in the body model as reported by Longo & Haggard, 2010; overestimation of hand width, and underestimation of finger length. Our results do not completely align with Van der Looven's (2021). For instance, we found that children (<18 years) overestimated finger length. The different results are likely due to the different methodologies used between the studies. For example, in the present study we asked participants to estimate the palmar side of the hand, whereas Van der Looven had participants estimate the dorsal side. However, both studies found that finger length underestimation increases with age and that hand width is overestimated. More research is needed to establish if children's representation of the dorsal and palmar develop at different rates.

The results from our study indicate that children have an enlarged body model compared to adults. It is tempting to speculate that disorders such as Developmental Coordination Disorder (DCD) is due in part, to this enlarged representation. DCD is characterized by uncoordinated movements and poor motor skill that emerges during the primary school years (age 6+; (Missiuna, Rivard, & Bartlett, 2003). Deficits in position sense, which informs the body model, have been described in DCD (Chen, Pan, Chu, Tsai, & Tseng, 2020; Tseng, Tsai, Chen, & Konczak, 2018, 2019). These studies have suggested that proprioceptive issues likely contribute to the fine motor problems in children with DCD. As the body model is the representation that underlies position sense, perhaps differences in this representation result in childhood clumsiness. Future research characterizing the body model in this population may provide insight into its origins.

A corollary of the current study is the feasibility of using a shorter version of the body task to study body representation. In our previous reports on the body model, the task has consisted of five estimations to each of the ten locations, per hand, per condition;

200 trials total (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2019; Coelho et al., 2016). With this many repetitions, some participants have reported discomfort and/or boredom during the task. Moreover, one possible caveat to the longer version is that sensory adaptation may occur. Sensory adaptation is the decrease in neuronal responsivity that occurs after prolonged exposure to a stimulus (Wark, Lundstrom, & Fairhall, 2007). Specific to haptics, previous research has shown that sensory adaptation can occur as early as 14 seconds after the presentation of a stimulus (Weill-Duflos, Sakr, Haliyo, & Régnier, 2020). In our original hand mapping task, each condition takes between 10-15 minutes to complete. As the participant cannot move their hand for the duration of each condition, it is likely that sensory adaptation occurs. An in-depth analysis on how the body model changes over the full-length of the experiment is needed to address if sensory adaptation alters this representation. The results of the current abbreviated version are similar to those found in the full version which might be useful when testing special populations (e.g. children, seniors, and people with neurological/mental health conditions).

In conclusion, we found that children had enlarged representation of their hand compared to adult participants. Furthermore, we found that while children had smaller physical hand size compared to adults, their estimates are at par with them. This seriously challenges the suggestion that uncoordinated behaviour during adolescence is the result of the body model lagging behind physical growth. We argue that clumsy manual actions may in fact arise out of an enlarged representation of the hand during youth. Lastly, our results support the view that hand representation distortions decrease as a function of age and that this trend continues into adulthood. Together, our results strongly suggest that body model growth occurs before physical changes in hand size. Longitudinal studies are needed to address this possibility.

Conflict of interest statement: On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability statement: Data will be made available upon reasonable request.

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Appendix 2: Chubby hands or little fingers: Sex differences in hand representation

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Abstract

Disturbed body representation is a condition defined by the perception that one's body size is different from their anatomical size. While equal amounts of males and females suffer from disturbed body representation, there appear to be differences in the direction of this distortion. Females will typically overestimate, whereas males will typically underestimate body size. One part of the body that has been consistently misperceived is the hands. This misrepresentation consists of two distinct characteristics: an overestimation of hand width, and an underestimation of finger length. Many of these studies, however, have used predominately female participants, allowing for the possibility that women are driving this distortion. The aim of the present study was to examine possible sex differences in hand perception. To this end, participants estimated the location of ten landmarks on their hands when their hands were hidden from view. Our results indicate that females follow the characteristic distortion, whereas males only underestimate finger length (albeit more than females). These findings are surprising, because the hands are not an area of concern for weight gain/loss. We discuss these findings in relation to body dysmorphia literature.

Introduction

Over 90% of anorexia and bulimia patients are female (Fairburn & Beglin, 1990; Hoek & Van Hoeken, 2003). One diagnostic criteria of these two disorders is a disturbed body representation (Grant & Phillips, 2004). Many studies that have investigated body perception in anorexic patients have found that they overestimate the size of their bodies (Cornelissen, Johns, & Tovée, 2013; Gutiérrez-Maldonado, Ferrer-García, Caqueo-Urízar, & Moreno, 2010; Hagman et al., 2015; Mohr et al., 2010; Schneider, Frieler, Pfeiffer, Lehmkuhl, & Salbach-Andrae, 2009; Urdapilleta, Cheneau, Masse, & Blanchet, 2007). For example, one study asked female participants, both anorexic and controls, to judge if a photograph of their frontal profile was either too wide or too thin (Hagman et al., 2015). These photographs were distorted between 20-30% in either direction. The results showed that the anorexic participants overestimated body size significantly more than the controls suggesting that they believe they are larger than their own body size.

While most of the research on body perception in anorexic patients has focused on females, there is some evidence that anorexic males also overestimate the size of their bodies (Gila, Castro, Cesena, & Toro, 2005). However, males who have a disturbed representation of their body, are more likely to underestimate than overestimate their body size (McCreary & Sasse, 2000; Weltzin et al., 2005). This tendency to underestimate body size is a subtype of body dysmorphia referred to as muscle dysmorphia. This disorder is characterized by a belief that your body is not muscular enough or that it is too small (Olivardia, 2001; Olivardia, Pope Jr, & Hudson, 2000). This has been described as "reverse anorexia" (Pope, Katz, & Hudson, 1993) and it is more prevalent in males than females (Grieve, 2007). So, while the incidence of body dysmorphia is similar between the sexes, the direction of the dysmorphia is different with females tending to be more likely to desire a thinner body, and males wishing they had a larger body (McCreary & Sasse, 2000). These differences highlight that body dysmorphia presents itself in different directions in males and females.

Interestingly, healthy controls have also demonstrated a distorted representation of their bodies. One study asked female participants to modify photos (using a computer) of their own bodies by adjusting its dimensions to the point where they believed it was accurate (Urdapilleta et al., 2007). They found that both anorexic and healthy controls significantly overestimated the size of their body. Thus, it is possible that even healthy females have inaccurate body representation. One area of the body that has been consistently misrepresented by healthy participants is the hands (Coelho & Gonzalez, 2017; Coelho, Zaninelli, & Gonzalez, 2016; Longo, 2014, 2015; Longo & Haggard, 2010, 2011, 2012a, 2012b; Longo, Mancini, & Haggard, 2015; Longo, Mattioni, & Ganea, 2015; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). In these studies, participants were asked to place their hand underneath a tabletop (so it was hidden from view), and then localize ten different landmarks on their hands (the tips and metacarpal phalangeal joints (mp joints). The results show a stereotypical pattern of distortion, which features participants overestimating hand width and underestimating finger length. Crucially, the majority of the previous studies of hand representation included more females than males. For example, in the original experiment by Longo and Haggard (2010) there were 15 females and 3 males, and in a study (which replicated Longo and Haggard's results) from our lab there were 15 females and 2 males (Coelho et al., 2016). It is possible therefore, that the characteristic distortion was primarily driven by the female participants. The direction of the distortion in terms of width would be consistent with previously discussed studies on body dysmorphia where females are more likely to overestimate body width. But if body dysmorphia affects females and males differently, it is possible that hand representation in males would have a very different pattern; one of underestimation.

The aim of the present study was to investigate sex differences in hand representation in healthy neurotypical participants. While previous research has investigated sex differences in body perception (Grieve, 2007; Sand, Lask, Høie, & Stormark, 2011; Sisson, Franco, Carlin, & Mitchell, 1997), these studies have focused on key areas such as the waist or thigh. By focusing on the hand, we intend to investigate if the perceptual patterns of body dysmorphia could affect perception of a body part that is not a primary concern for weight change. If this happens to be the case, an argument can be made regarding why females are more likely to suffer from anorexia and males to suffer from muscle dysmorphia. We split our participants into a male and female group and asked them to complete a similar task to Coelho et al, 2016. With their hands hidden from view, each participant was required to estimate where they believed ten different landmarks (the tips and mp joints of each of the five fingers) on their hands were located. Furthermore, we decided to include an analysis of both the left and the right hand as previous work from our lab (Coelho et al, 2016; Coelho & Gonzalez, 2017) as well as others (Linkenauger et al, 2009) have identified differences in perception between the hands. All these studies have found that the right hand is perceived as larger than the left hand. It has been proposed that these differences in hand perception are due to the fact that the right hand is perceived as being more capable than the left hand (Linkenauger et al, 2009). If this is the case, then we expect to see an overall difference of hand, with the right hand as being perceived larger than the left, for both males and females.

Methods

Participants

59 university students (25 males and 34 females) participated in the study in exchange for course credit. All participants were right-handed. Handedness was assessed using a modified version of the Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires. We conducted a power analysis using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) which revealed that in order to find sex differences with a 95% certainty a total of 46 participants (23 of each sex) were required.

Materials

An Optotrak certrus camera (Northern Digital, Waterloo, ON, Canada) recorded the position of an iRED marker that was attached to the end of a wooden stylus. The position of the stylus was recorded for 1000ms at 100 HZ for each trial.

Procedure

The participants sat in front of a glass table (41 L X 86.5 W CM) with a wooden shelf located 12 cm below the glass top (see figure 7). They placed the palm of their hand (with their fingers spread apart) underneath the glass table, while their forearm rested on a thin pillow. The pillow was incorporated into our setup, to help ensure that the participants hand remained in a stable hand position for the duration of the study. Once they were comfortable a black tablecloth was placed over the table, occluding the participants hands from view (occluded hand condition). We then asked participants to estimate where they believed ten different locations on their hands (the tips and mp joints of their fingers) were located. The order of trials was pseudorandomized. The participants pointed by touching the top of the glass with the wooden stylus. After each trial, the participants returned the wooden stylus to a home spot that was located directly above the participants forearm (as in Coelho et al, 2016). Each location was pointed to five times for a total of 50 trials per condition. After the occluded hand condition was completed, the tablecloth was removed and then the participant repeated the same task, but with full vision of their hands (non-occluded hand trials). The non-occluded condition was completed so the estimation trials (occluded hand condition), could be compared to the actual size of the participant's hand. This task was repeated for both the participant's right and left hands (for a total of 200 trials, 50 per condition), with the starting hand being counterbalanced across participants. In order to investigate how sex affects the representation of our hands, we split our participants into two groups (male and female) depending on their sex.

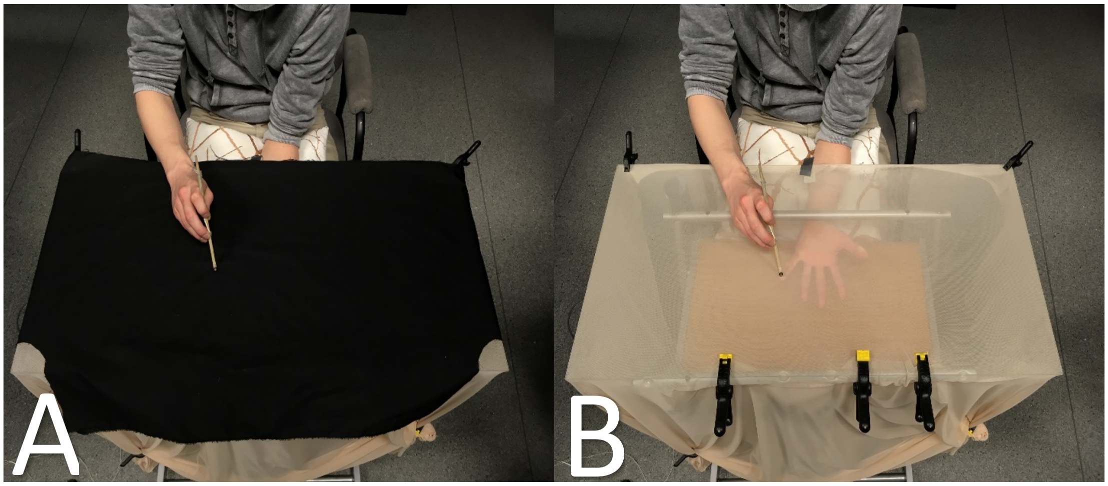

Figure 7
View of the experimental set up. In figure 1A. The occluded hand condition is shown. Participants placed their hands underneath the glass table-top and rested their forearm on a thin pillow. A black tablecloth was placed over top of the table and participants had to estimate where they believed the different landmarks were on the table. Figure 7B. Shows the non-occluded hand condition. Participants in this condition sat in the same position but were allowed to

Analyses

We conducted two main analyses on the data. The first analysis (Occluded vs non-occluded hand) was a series of a-priori t-tests conducted on the raw values (expressed in mm). This was conducted in order to determine if the estimated values (occluded hand condition) were different from the physical metrics of the hand (non-occluded hand condition). We modeled this analysis after the analysis used in the original report (Longo & Haggard, 2010), and it was identical to the analysis used by Coelho et al, 2016.

The second analysis (effects of hand and sex) was a 2 X 2 repeated measures ANOVA, where hand (left, right) was the within factor, and sex (male, female) was the between factor. For this analysis data were expressed as the percent of the real value ((occluded - non-occluded) / (non-occluded) *100). This analysis was included as it allowed us to compare directly between individuals, as it takes into account individual hand size differences.

The two analyses were repeated for two different variables: hand width (the great span), and finger length. The great span was calculated as being the summed distance between the tip of digit 1 to the tip of digit 5. We calculated finger length as the average between the tip and base of each of the five digits. These variables were identical to those used by Coelho et al, 2016.

Data processing

Trials were excluded if participants moved the stylus before the 1000ms recording was finished, or if the participant pointed to the incorrect landmark (<5% of all trials).
All data were analyzed using Matlab R2015a (Mathworks, Natick, MA), and statistics were completed using SPSS 23.

Results

Analysis one: Occluded vs non-occluded hand

Only significant results are reported. All values are Bonferroni corrected.

Females

Great span: Female participants significantly overestimated the width of their right ($t(33) = 3$, $p=.02$, $d=1$; occluded hand 200.93±6.4mm, non-occluded hand 181±3.5mm) and left ($t(33) = 2.9$, $p=.02$, $d=1$; occluded hand 201.1±5.7mm, non-occluded hand 186.9±3.7mm) hands.

Finger length: Finger length was underestimated by female participants for both the right ($t(33) = -6.2$, $p<.01$, $d=2.1$; occluded hand 44.4±1.6mm, non-occluded hand 54±.6mm) and left (t (33) = -7.8, p<.01, d=2.7; occluded hand 45±1.3mm, non-occluded hand 54±.7mm) hands.

<u>Males</u>

Great span: Male participants accurately estimated the width of both their right and left hands (p's>.4)

Finger length: Male participants underestimated finger length for both the right (t(24) = -11, p<.01, d=4.5; occluded hand 43.3±.9mm, non-occluded hand 56.8±.9mm) and left (t(24)= -6.5, p<.01, d=2.6; occluded hand 43.7±1.2mm, non-occluded hand 60±2mm) hands.

Analysis two: Effects of hand and sex

Great span: There was a significant main effect of hand [f(1,57)=5.8, p=.02, partial eta^2=.09], where the right hand (7±2.5%) was significantly more overestimated than the left hand(2.4±1.8%). There was also a main effect of sex [f(1,57)=6.8, p=.01, partial eta^2=.11], where females (9.9±2.5%) overestimated the width of their hands, while males (-0.2±2.5%) made accurate estimations. See figure 8.

Finger length: There was a main effect of sex [f(1,57)=5.6, p=.02, partial eta^2=.09], where male participants (-24.6±2.4%) underestimated finger length more than the female participants (-17.2±2%). See figure 9.

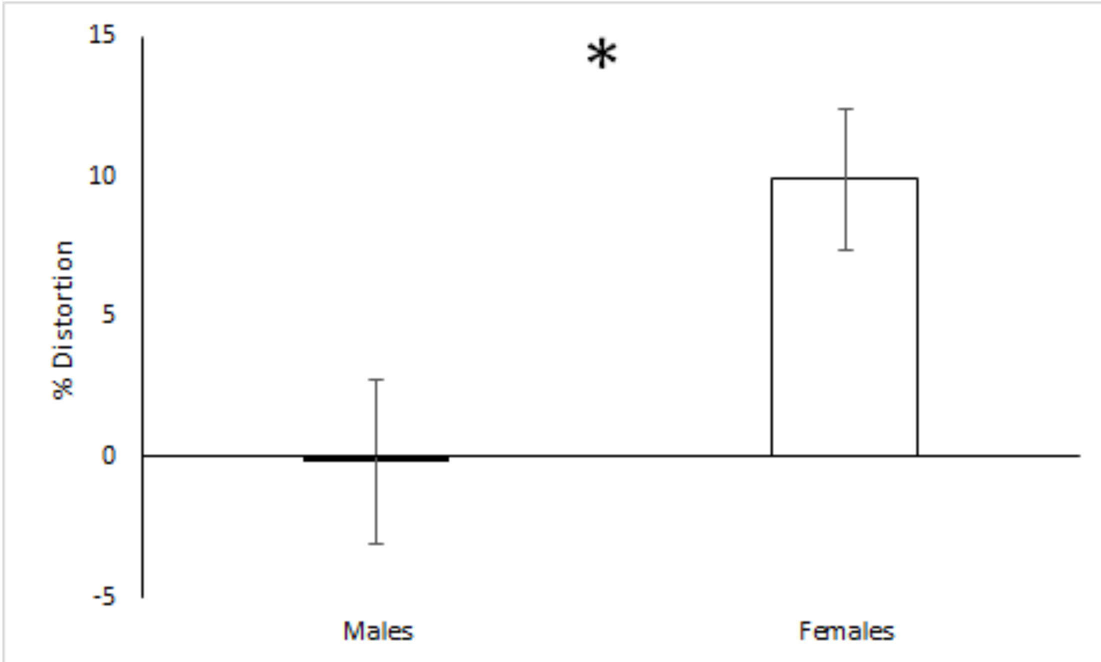

Figure 8: Main effect of sex for the great span. Females overestimated the width of their hands, while males made accurate estimations.

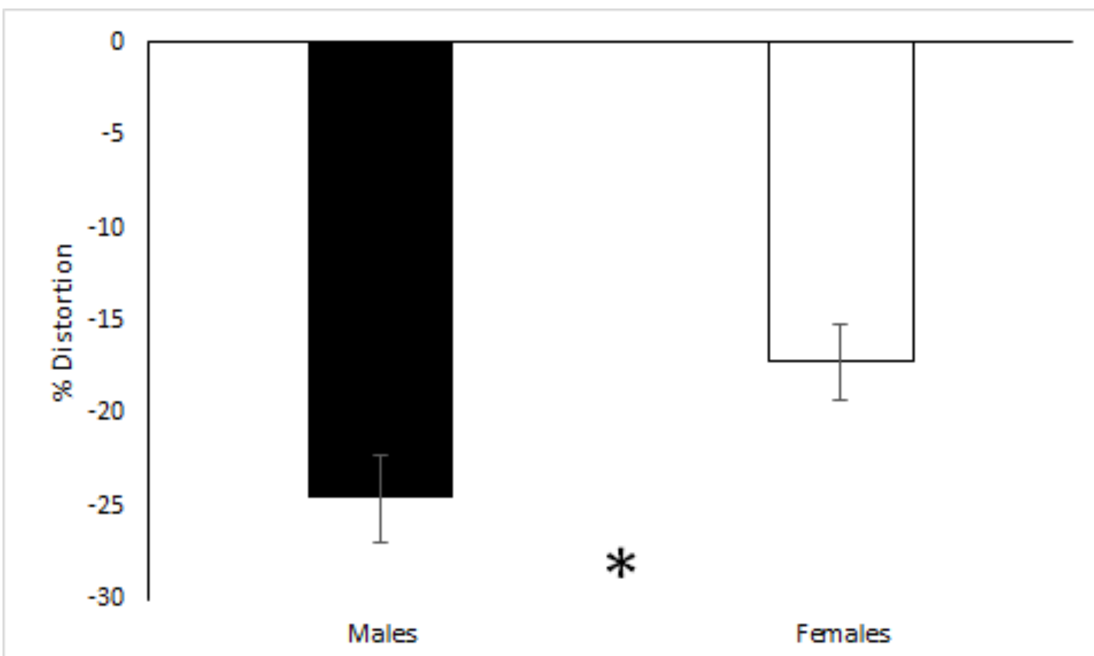

Figure 9:Main effect of sex for finger length. Males underestimated finger length significantly more than females did.

Discussion

The purpose of the present study was to investigate possible sex differences in body perception in healthy individuals. The hand was chosen as a model because studies have consistently documented misrepresentation of this body part. Female and male participants completed a hand perception task. For this, participants placed their hands underneath a tabletop (the hands were occluded from view), and were asked to localize ten landmarks on their hands (the tips and mp joints of their fingers). Using 3D motion capture technology, the width of the hands and length of the fingers were derived from XY coordinates. The results showed significant differences between the sexes for both hand width and finger length. Our hypothesis was partially supported in that females overestimated hand width. Males however, did not underestimate width but instead had accurate representations. With respect to finger length the prediction was less straight forward as studies of body dysmorphia have focused mostly on width. We found that both groups underestimated finger length but more so in the male group. The results suggest that representation of the hands is different for females and males.

One of the diagnostic criteria for anorexia is an overestimation of body size (Cornelissen et al., 2013). This disorder predominately affects females with over 90% of all clinical anorexic patients being female (Fairburn & Beglin, 1990; Hoek & Van Hoeken, 2003). In the present study, we found that healthy females overestimated the width of their hands. This is in line with previous research that has found that healthy females also overestimate body size (Schneider et al., 2009; Urdapilleta et al., 2007). For example, Schneider et al asked participants to estimate the size of their waist, thighs, and arms. Participants estimated the circumference of each of these body parts by adjusting a string. They found that while the eating disorder participants overestimated circumferences significantly more than the healthy controls, the healthy controls still overestimated these body parts by 8-16%. In the current study overestimation of hand width by the female group fell exactly within this range (13.6%). It is puzzling that the hand would follow the results observed on the waist and thigh, because one could argue that hand width is not usually a body part that women (including those with eating disorders) are concerned about (Berscheid, Walster, & Bohrnstedt, 1973; Petrie, Tripp, & Harvey, 2002). This is probably due to the fact that diet and exercise would not result in big changes regarding hand shape/size (as it would to say the stomach or the thighs). In particular, the distance between the thumb and the pinky would seldom be affected by gain/loss of body fat. The finding that females overestimate hand width suggest that females have a tendency to overestimate width of all their body parts. Disturbed body representations are one of the diagnostic criteria for anorexia and bulimia, and these are female dominated disorders. It is possible that females are more likely to develop these disorders because they overestimate the width of all body parts.

With respect to males, they underestimated finger length more than females. This finding is also in line with the common type of body dysmorphia experienced by males. While body dysmorphia rates are similar between males and females, males are more likely to underestimate body size (Sand et al., 2011; Sisson et al., 1997). Males have self-reported that they feel their bodies to be small, and that they wished their bodies were bigger (McCreary & Sasse, 2000; Olivardia, 2001; Olivardia et al., 2000). One study investigated how youth (aged 12-15) perceive their own body size. Participants were asked to adjust a distorted photograph of themselves on a computer screen until it reflected what they believed to be their body metrics (Sand et al., 2011). They found that males at risk of developing an eating disorder underestimated body size. Although in the present study we did not collect information about eating habits, it is possible that males in general underestimate the size of all body parts including, as we found, finger length. Future research is needed to elucidate if body perception changes as a function of body mass index (BMI), eating habits, and/or exercise regimens.

While previous research has identified that there are sex differences in body perception disorders (Grieve, 2007; Sand et al., 2011; Sisson et al., 1997), a puzzle remains as to why these sex differences exist. One possibility is that sex differences are driven by the different biopsychosocial influences that females and males experience (McCabe, Ricciardelli, Sitaram, & Mikhail, 2006). McCabe et al, investigated the predictors of body size accuracy, and found that female's predictors included depression levels, and media/peer influences. Although studies have shown strong links between body dysmorphia and depression (Olivardia, Pope Jr, Borowiecki III, & Cohane, 2004; Otto, Wilhelm, Cohen, & Harlow, 2001) for both males and females. For females the two seem to comorbid more often in males (Stice, Hayward, Cameron, Killen, & Taylor, 2000; Vaughan & Halpern, 2010). Future research on body perception, including that of the hand could include a measure of depression as a covariate.

Interestingly, depression was not a predictor of body dysmorphia in males, but instead peer influence and BMI were predictors. Males with greater BMI had more distorted body representation. Puzzling, BMI was not a predictor in females, indicating that body perception is similar regardless of body composition. This is important as it suggests that females who suffer from body dysmorphia may place more importance on the social factors (such as media and peer pressure) than on their real weight (i.e. BMI). Furthermore, an additional study found that only females linked body dissatisfaction with their self-esteem (Furnham, Badmin, & Sneade, 2002) supporting the view that social factors influence body representation particularly in females. Because our females were inaccurate in both width and length, this would suggest that social cues may have greater influence on body perception.

Another possible explanation for the sex differences found in the current study pertains the visuospatial nature of the task. It is known that males outperform females in some visuospatial tasks (Bull, Cleland, & Mitchell, 2013; Delgado & Prieto, 1996; Kramer, Ellenberg, Leonard, & Share, 1996; Postma, Jager, Kessels, Koppeschaar, & van Honk, 2004; Voyer & Jansen, 2016; Weiss, Kemmler, Deisenhammer, Fleischhacker, & Delazer, 2003). For example, Delgado and Prieto (1996) asked participants to complete two visuospatial tasks (a rotation of solid figures task and a 3D mental rotation task). They tested a large number of participants (621 males and 821 females), and found that males were more accurate than females in both measures of visuospatial ability. It is possible that males made accurate estimates of hand width, because our task requires mental visualization and perhaps some degree of mental rotation (although we did not measure this). A visuospatial advantage cannot however, explain why males underestimated finger length significantly more than females. Furthermore, a recent study has found similar results to the ones described here (Walk & Heller, 2014). The experiment required participants to estimate the size of their hands when the hand was magnified, reduced, or with no added distortion (control condition). These authors found that males underestimated hand size significantly more than females when judging their hands with normal vision. Perhaps there is a clear asymmetry in the way males and females perceive their hands, with males underestimating length and females tending overestimating width.

Lastly, the left and the right hand were not perceived to be the same size. The right hand was perceived larger than the left in both females and males. This result has been found on several other occasions (Buchner, Kauert, & Radermacher, 1995; Coelho et al., 2016; Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009). One reason that could explain a larger representation for the right hand is that there is more cortical area devoted to this hand when compared to the left (Buchner et al., 1995). It is also possible, that this asymmetry exists because we perceive the right hand as being more capable than the left hand. Evidence for this comes from a study that asked participants to estimate their hand size, as well as the largest object (from an array) that they thought they could grasp with each hand (Linkenauger et al., 2009). These authors showed that participants not only estimated their right hands as larger than their left hands, but they also estimated that they could grasp larger objects with their right hand. Thus, the larger representation of the right hand could be due to the fact that this hand is perceived as more capable than the left hand. Our results indicate that the difference in perceived hand size is well-conserved across sexes. It is puzzling however that hand differences only appears in measures of hand width; there were no differences between the hands in terms of finger length ($p=.78$) for either males or females. It is possible that we did not find finger length differences between the hands because participants pointed to the landmarks of their hands in a random fashion (tip of the thumb followed by base of the middle finger, followed by tip of the pinky etc). In a previous study (Coelho et al, 2016), we found that when participants pointed in a systematic fashion (moving from one location to the nearest adjacent digit pairing), perception of finger length for the left hand was that of being shorter than for the fingers of the right hand. We argued in that paper that when the hand is perceived in a holistic manner (in the systematic fashion) differences between the hands occur for both hand width and finger length. A different possibility is that because we collapsed across the fingers, any difference between the hands (in relation to a specific digit) was washed out. In order to ensure this was not the case, we conducted an additional analysis were we looked at individual digit length, and found no main effect of hand (p=.66), and importantly no hand by digit interaction (p=.33).

To conclude, we investigated sex differences in a hand perception task. The results showed significant effects of sex for both hand width and finger length. Females overestimated width while males made accurate judgements. Males underestimated finger length significantly more than females. We propose that the characteristic distortion of hand perception described previously may only be present in females. The sex differences found in this study align with the body dysmorphia literature which finds that females are more likely to overestimate the width of their bodies whereas males are more likely to underestimate its size. Further research is needed to investigate a possible link between hand perception and overall body perception.

Data availability

The data set used and analyzed in this study are available from the corresponding author upon request.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent: Informed consent was obtained from all individual participants included in the study.

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Appendix 3: Long- but not short-term tool-use changes hand representation

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Abstract

Tool-use has been found to change body representation. For example, participants who briefly used a mechanical grabber to pick up objects perceived their forearms to be longer immediately after its use (e.g., Cardinali et al, 2009; they incorporated the tool into their perceived arm size). While some studies have investigated the long-term effects of tool-use on body representation, none of these studies have used a tool that encapsulates the entire body part (e.g., a glove). Moreover, the relationship between tool-use and the body model (the representation of the body's spatial characteristics) has yet to be explored. To test this, we recruited 19 elite baseball players (EBP) and 18 age matched controls to participate in a hand representation task. We included EBP because of their many years (8+) of training with a tool (baseball glove). The task required participants to place their hands underneath a covered glass tabletop (no vision of their hands), and to point to where they believed 10 locations (the tips and bases of each finger) were on their hands (Coelho et al., 2017). Each point's XY coordinates was tracked using an Optotrak camera. From these coordinates, we mapped out the participants perceived hand size. The results showed that when compared to the controls, EBP underestimated hand width and finger length of both hands. This indicates that long-term tool use produces changes in the body model for both, the trained and untrained hands. We conducted a follow-up study to examine if 15 minutes of glove use would change perceived hand size in control participants. Novice baseball players (participants without baseball experience: NBP) were recruited and hand maps were derived before and after 15 minutes of active catching with a glove. Results showed no significant differences between the pre and post hand maps. When we compared between the two experiments, the EBP showed smaller hand

representation for both hand width and finger length, than the NBP. We discuss these results in relation to theories of altered body ownership.

Introduction

We rely on proprioceptive signals to interact with our surroundings. The proprioceptive receptors are located in the skin, muscles, and joints of our limbs. Afferent signals generated during a movement are processed to code for an endpoint position of the limb. The term proprioception has been used loosely to describe several conscious sensations. These include the senses involved with limb position and movement, the sense of tension or force, the sense of effort, and the sense of balance (Proske & Gandevia, 2012). For the purpose of the present study we will be focusing on a subdivision of proprioception; position sense (Sherrington, 1910). Position sense refers to the ability to perceive the location of our limbs in space, even when we cannot see them. Much of the research on position sense focuses on disorders that feature misrepresentations of the body, including eating disorders (Gadsby, 2017; Guardia et al., 2012; Keizer et al., 2013; Metral et al., 2014; Treasure et al., 2010). Traditionally, the studies that have investigated position sense in healthy individuals focused on how position sense relates to bodily movement (Goble & Anguera, 2010). These studies assumed that healthy adults have an integrated and accurate body representation of their limbs in space. However, recent evidence has shown otherwise (Longo and Haggard, 2010). In a procedure to isolate and measure position sense in healthy adults, Longo & Haggard found that the representation of the hand is distorted. They referred to this type of representation as implicit body representation (or the body model). This body model is the representation of the body's spatial characteristics. This is different from the body schema which forms a representation from constantly updating sensory information from afferent signals. Longo and Haggard asked their participants to place their hands underneath a covered tabletop (no vision of their hand), and to point to where they believed ten locations were on their hand. They found that healthy adults consistently and significantly overestimate the width of their hands and, underestimate the length of their fingers (Longo & Haggard, 2010). This result has been replicated on numerous occasions, and in various different conditions (Coelho, Zaninelli & Gonzalez, 2017; Coelho & Gonzalez, 2018; Longo, 2014, 2015; Longo & Haggard, 2011, 2012a, 2012b; Longo, Mancini, & Haggard, 2015; Longo, Mattioni, & Ganea, 2015; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016).

Changes to the body schema following tool-use have been documented. A tool can be defined as an object that is a physical extension of the body (Iriki, Tanaka, & Iwamura, 1996). Many studies have shown that after tool use, there are measureable perceptual changes in the body schema (Cardinali, 2011; Cardinali et al., 2009; Cardinali et al., 2012; Carlson, Alvarez, Wu, & Verstraten, 2010; Iriki et al., 1996; Maravita & Iriki, 2004; Sposito, Bolognini, Vallar, & Maravita, 2012). For example, Cardinali asked participants to perform a reach and grasp movement using a mechanical grabber (2011). The participants were required to estimate the length of their arms before and after the grasping task. Interestingly, it was found that participants perceived their arms to be longer after they had performed the grasping task with the grabber. This result suggests that after its use, tools become integrated with the subject's own body schema, as if the tool is a physical extension of the body. Long-term tool use has also been shown to change peripersonal space representation (Serino, Bassolino, Farne, & Ladavas, 2007) and the neural representation of the body (Fourkas, Bonavolontà, Avenanti, & Aglioti, 2008). For example, peripersonal space plasticity was investigated in a group of blind subjects (many years of experience using a cane), and in a group of sighted participants (no experience using a cane; (Serino, Bassolino, Farne, & Ladavas, 2007). They found that the blind individual's peripersonal space extended when they held the cane, but not when they held a short handle. These authors argue that long-term exposure to a tool results in a unique representation of peripersonal space.

The effects of tool-use on the body schema, and peripersonal space have been explored previously, but what about the body model (as identified by Longo & Haggard, 2010)? One previous study found that extensive practice with the hands caused the hand's body model to be more accurate (Cocchini, Galligan, Mora, & Kuhn, 2017). This study recruited expert magicians and a group of control participants and used the same experimental protocol as Longo & Haggard (2010) to isolate the body model of the hand. They found that the magicians had more accurate representations of the lengths of their fingers. Although, this study showed that training leads to changes in the body model, it remains to be shown if tool-use also produces these changes.

The aim of the current study therefore was to investigate if long-term exposure to a tool would change the body model of the hand. Rather than asking participants to train with a tool for an extended period of time (likely unfeasible), we recruited a population with long-term experience using a tool; elite baseball players (EBP). EBP have many years of practice using a tool that extends the capability of their hand: a baseball glove. Based on the results of previous studies on the effects of tool use on the body schema and peripersonal space (Cardinali, 2011; Cardinali et al., 2012; Carlson et al., 2010; Cocchini et al., 2017; Maravita & Iriki, 2004; Schaefer et al., 2004; Sposito et al., 2012) we hypothesized changes in the body model of the hand of EBP. We present two alternate hypotheses: 1) EBP will incorporate the glove into their implicit representation of their hands and will therefore perceive their glove hand as *larger* than their non-glove hand, and larger than both hands of a control group; 2) EBP would have a *smaller* implicit representation of their glove hand because when they are not wearing it their hand appears smaller. There is also the possibility that long-term use of the glove results in no measurable changes in the body model. This would be consistent with the suggestion that experience-induced plasticity should not last in the long-term, as there would be no functional benefit to a lasting change in body representation (Cardinali et al, 2012). These authors argued that "disembodiment" of the tool should occur fast and without consequence.

Methods

Participants

Nineteen right-handed male baseball players from Prairie Baseball Academy voluntarily participated, and 18 male age matched controls from the University of Lethbridge participated in exchange for course credit. Handedness was assessed using a modified Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaire. All but one participant self-reported as being right-handed (one baseball player reported as being ambidextrous). The baseball players also completed a questionnaire on their playing history. This questionnaire asked the players how long they had been playing, how many times a week they practice, and what hand they wore their glove on. EBP glove hand preference was consistent with being right-handed (ie. glove being worn on the left hand by all players). We made the a priori decision to test 19 participants per group (38 total), as there were 19 elite baseball players who volunteered to participate, and we wanted to have a close number of participants in each group. We had to exclude one participant from the control group due to hand movement during testing.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode attached to the tip of a stylus. The location of the diode was recorded for 1s at 100 Hz for each trial.

Design and Procedure

Design and procedures closely followed our previous work (Coelho & Gonzalez, 2018; Coelho et al., 2017). Briefly, participants were instructed to sit and place their hand palm up underneath a glass tabletop (86.5 x 41.0 cm), see figure 1. The original paradigm by Longo & Haggard (2010) had participants place their hands palm down against the wooden shelf (situated below the glass). However, in our original report (Coelho et al., 2017) we found no differences in distortion between a palm-up group and a palm-down group, and to keep it consistent with our own research we decided to have all our participants place their hands up against the glass. Their forearm rested on a pillow that was situated on a shelf located 12 cm below the glass. We asked participants to have their fingers spread to the maximal width that was comfortable, and we informed them that the positioned hand was to be fixed in one location for the entirety of the set of trials. When the participant was ready to begin the experiment, a black tablecloth was placed over the table, occluding the hand from the participants view (occluded hand condition). With the unrestricted hand, participants were asked to place the tip of the stylus (with the diode attached) directly above (while contacting the top of the glass) where they believed 10 individual hand landmarks were. These landmarks consisted of the tips and the metacarpal phalangeal (mp) joints of each finger. In all cases the experimenter verbally instructed the participants as to which landmark to point to on each trial. Trials were pseudorandomized for each condition and for each participant. Following each trial participants were asked to return to a “home spot” situated directly above the participants fixed forearm. After the set of trials was completed, the black tablecloth was removed from the table and the experiment was repeated again but with full vision of the hand (non-occluded hand condition). The participants repeated the experiment for both their left and right hands. Each participant completed 100 trials for each hand (200 trials total). Each set was further broken into 2 x 50 trial subsets (5 points to each landmark). The first pseudorandomized set of trials was the occluded hand condition, immediately followed by the non-occluded hand condition. This procedure was identical to that used in previous studies.

Analysis

We conducted two analyses on the data. Each of the analyses were repeated for two dependent variables: hand width, and finger length. Hand width was determined by the great span, which was defined as the sum of the distances between the tips of each digit, including the thumb. Finger length was calculated by averaging the distance from the tip to the base of each digit for all five digits.

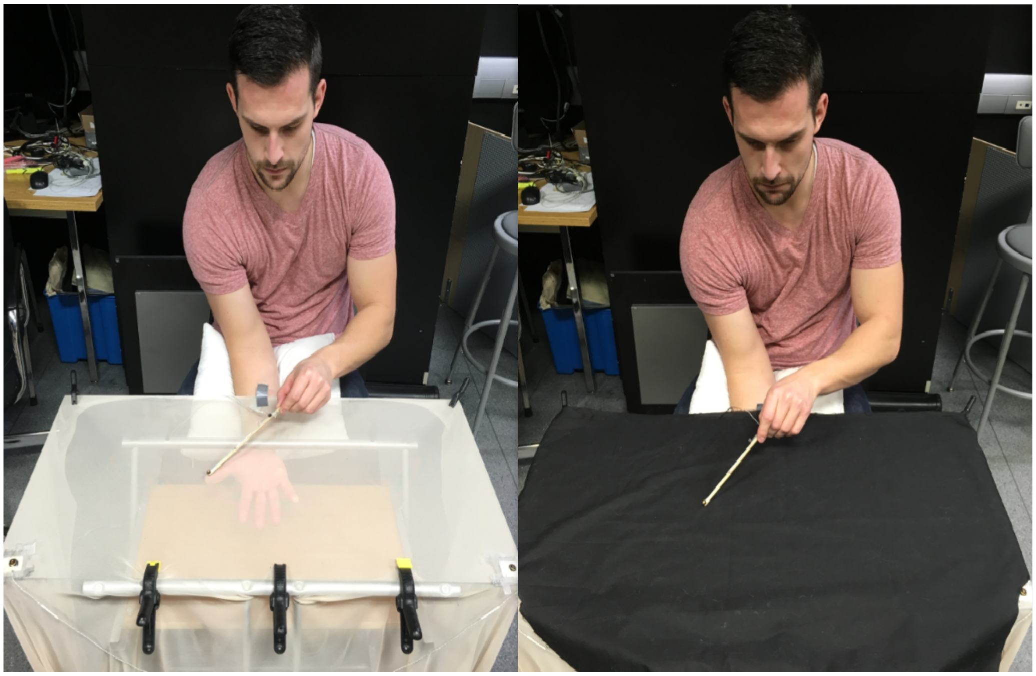

Figure 10: This was the experimental set up. The participants sat with their hand pressed up against the glass tabletop. They pointed using the wooden stylus. The black tablecloth restricted vision of the participant's hand in the occluded trials.

The first analysis (occluded vs non-occluded hand) was a series of paired samples t tests conducted on the raw data (expressed in mm). For this analysis, we compared the occluded versus the non-occluded conditions for both measures to investigate if the perceived hand dimensions (occluded hand condition) were significantly different from the real hand dimensions (non-occluded condition).

The second analysis (effects of hand and group) was a 2 X 2 repeated measures ANOVA. The within variable was hand (left, right), and the between variable was group (EBP, control). This analysis was conducted on the data expressed as a percent of the non-occluded value ((occluded - non-occluded) / (non-occluded*100)). This normalization was done to account for any individual differences in hand size (Coelho et al., 2017).

Data processing

Trials were excluded if participants moved the stylus before the 1s recording was finished, or if the participant pointed to the incorrect landmark (<5% of all trials).

All data were analyzed using Matlab R2015a (Mathworks, Natick, MA), and statistics were completed using SPSS 23.

Results

Means and standard errors are reported. The analysis of occluded vs non-occluded hand was Bonferroni corrected for multiple comparisons.

Handedness questionnaires

Both groups had an average score that was consistent with being right-handed (EBP 26.6±1.5, and the control group 30.5±1.7). A one-way ANOVA revealed there was not a significant difference between groups (p=.1).

Baseball questionnaire

The EBP had been playing baseball for an average of 12.9±.48 years, and they were playing baseball 5.1±.52 days per week at the time of testing. There were no significant correlations between the amount of time spent playing baseball and the magnitude of distortion of their hands (p's>.17).

Analysis one: Occluded vs non-occluded hand

Control group: The great span of both the right and left hands was accurate [right hand t(17)=.68, p=.51, d=.33; left hand t(17)=-.24, p=.8, d= .12]. Finger length however, was significantly underestimated for both their right [t(17)=-8.1, p<.01, d=3.98, CI:[-16.6, -9.7] ; occluded hand = 42.9±1.1, non-occluded hand = 56.22±1.2] and left hands [t(17)=-

7.8, $p<.01$, $d=3.64$, CI[-16.5,-7.8]; occluded hand = 44.57±1.4, non-occluded hand = 57.3±1.1].

EBP: Baseball players significantly underestimated the great span of their right hands [$t(18)=-3.5$, $p<.01$, $d=1.65$, CI[-36.6, -9.2]; occluded hand = 175.1±5.4, non-occluded hand = 198.1±4.45]. The great span estimations of the left hand approached significance, when compared to the non-occluded condition [$t(18)=-2.51$, $p=.09$, $d=1.83$, CI:[-23.3, -2.0]; occluded hand = 180.3±4.5, non-occluded hand = 93±4.5]. Finger length was also significantly underestimated for both the right [$t(18)=-11$, $p<.01$, $d=5.19$, CI[-23.6, -16.0]; occluded hand = 37.23±1.8, non-occluded hand = 57.04±1] and left hands [$t(18)= -7.5$, $p<.01$, $d=3.54$, CI:[-22.8, -12.8]; occluded hand = 40.1±1.93, non-occluded hand = 57.92±1.1].

Analysis two: Effects of hand and group:

Great span

There was a main effect of group [$f(1, 35)= 6.4$, $p=.02$, partial $e^2=.15$], where the EBP (-8.4±2.8, CI:[-14.1, -2.7]) estimated the width of their hands to be significantly smaller than those of the control group (1.72±2.9, CI:[-4.1, 7.6]). The effect of hand was non-significant [$f(1,35)=.00$, $p=.99$, partial $e^2=.00$], as was the hand*group interaction [$f(1,35)=3.2$, $p=.09$, partial $e^2=.08$].

Finger length

There was a main effect of group [$f(1, 35)= 6.8$, $p=.01$, partial $e^2=.16$], where the EBP (-32.38±2.6, CI:[-37.8, -27.0]) estimated their finger length to be significantly smaller than that of the control group (-22.53±2.7, CI:[-28.0, -17.0]). The effect of hand was not significant [$f(1,35)=1.6$, $p=.21$, partial $e^2=.05$], as was the hand*group interaction [$f(1,35)=.91$, $p=.35$, partial $e^2=.03$].

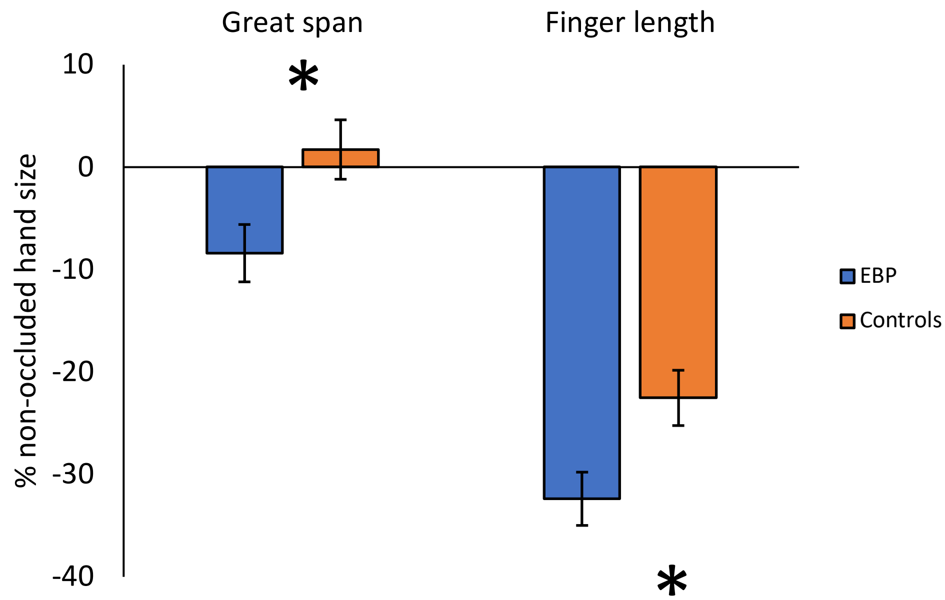

Figure 11: Differences between the EBP and controls for both the great span and finger length. The EBP significantly underestimated both the great span and finger length in comparison to the control group.

The results indicate that long-term use of a tool changes the representation of our hands. This is in line with one study that found that compared to naïve participants, experienced magicians, when compared to controls, had different representations of their hands (Cocchini et al, 2017). Previous research has found that after using a tool (for as little as 15 minutes), the tool becomes embodied; participant's body representation changes to incorporate (literally) that tool (Cardinali, 2011; Cardinali et al., 2012; Maravita & Iriki, 2004; Schaefer et al., 2004; Sposito et al., 2012). Would short-term tool use change hand representation? A follow up study investigated if 15 minutes of using a baseball glove would also produce measurable changes to the participants hand maps. To test this, we recruited a group of novice baseball players (NBP; no experience playing baseball) and asked them to complete the hand mapping task both before (pre-tool use) and after 15 minutes (post-tool use) of catching a baseball using the glove.

Follow up: Short-term effects of tool-use on hand representation

Method

Participants: Eighteen male undergraduate students participated in this study. All participants received a course credit in exchange for participation. All participants self-reported as right-handed, which was confirmed via the modified version of the Waterloo-Edinburgh handedness questionnaire (mean score: 28.3±1.6). We made the a priori decision to stop testing after 18 participants, so that our group sizes were the same between study 1 and study 2.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode attached to the tip of a stylus. The location of the diode was recorded for 1s at 100 Hz for each trial.

Design and Procedure

Our experimental design was similar to that used in the first study. Participants were asked to complete the hand mapping task (pre-tool use), followed by 15 minutes of playing catch using a baseball glove, which was immediately followed by a repeat of the hand mapping task (post-tool use). All participants played catch with an EBP, who pitched at a steady pace and placed the balls in easy-to-catch positions. All participants wore the glove on their left hand during the practice trials. There was one key change to the hand mapping process; instead of having the participants complete 50 trial subsets (5 estimations to each location, as in the first study), the participants completed 10 trial subsets (1 estimation to each location; 20 trials per hand, 40 trials in total). We decided to make this change in our protocol for sake of brevity. In none of our previous work (Coelho & Gonzalez, 2018, in press; Coelho et al., 2017) nor in the first study have we found differences between the maps derived from the first 10 points to each location, and any of the other 4 subsets (points #11-50). Importantly, the hand map results from control participants (first study) and from the NBP (pre-tool use) were not significantly different from each other, (p's >.6) indicating that the abbreviated version of the hand-mapping task yields the same results as the full version.

Analysis

We conducted three analyses on the data. Each of the analyses were repeated for two dependent variables: hand width, and finger length. These were calculated using the same methods as in the first study.

The first analysis (occluded vs non-occluded hand) was a series of paired samples t-tests conducted on the raw data (expressed in mm). We conducted this analysis to examine whether the pre- and post-occluded-hand values were significantly different from the non-occluded hand values both before and after the 15 min of training.

The second analysis (pre- vs post-tool use) was a 2x2 within subjects repeated measures ANOVA. Hand (left, right) and time (pre-, post-tool use), were the 2-within variables. As in the first study, the data was expressed as a percent of the non-occluded hand value (occluded - non-occluded) / (non-occluded*100). We chose to use this normalization to account for any differences in hand size or posture between participants. With this analysis we aimed to examine if using the baseball glove significantly changed the representation of the participant's hands.

Lastly, we included one final analysis to compare if our EBP and our NBP had different representations of their hands. To test this possibility, we conducted a 2 X 2 mixed design repeated measures ANOVA. Our within variable was hand (left, right), and the between variable was group (EBP, NBP post-tool use). All the values here were expressed as a percent of the non-occluded hand value (as in our second analysis).

Data processing

Trials were excluded if participants moved the stylus before the 1s recording was finished, or if the participant pointed to the incorrect landmark (<1% of all trials).

All data were analyzed using Matlab R2015a (Mathworks, Natick, MA), and statistics were completed using SPSS 23.

Results

Analysis one: occluded vs non-occluded hand

<u>Great span:</u>

There were no significant differences between the occluded and non-occluded hand for either the pre- [right hand $t(17)=1.6$, $p=.13$, $d=.78$; left hand $t(17)=-1.03$, $p=.32$, $d= .5$]or post-[right hand $t(17)= .23$, $p=.82$, $d=.11$; left hand $t(17)=.31$, $p=.76$, $d=.15$] tool-use.

<u>Finger length:</u>

Pre-tool use: The participants significantly underestimated the finger lengths on their right [$t(17)=-7$, $p<.01$, $d=-2.23$, CI: [-17.8, -9.5]]; and left hands [$t(17)=-6.3$, $p<.01$, $d=-1.96$, CI:[-18.9, -9.4]; see table A.3.1 for summary of means and standard errors.

Post-tool use: The participants significantly underestimated the finger lengths on their right [t(17)=-4.3, p<.01, d=-1.16, CI:[-16.63, -5.71]; and left hands [t(17)=-7, p<.01, d=-1.65, CI:[-18.3, -9.87]]; see table 3 for summary of means and standard errors.

Table 3: Means and standard deviations of pre-and post-tool use finger length estimations (occluded) and actual (non-occluded) finger lengths.

	Pre-tool use				Post-tool use			
	RH		LH		RH		LH	
	Occluded	Non-occluded	Occluded	Non-occluded	Occluded	Non-occluded	Occluded	Non-occluded
Great span	216.3±7.2	206.3±5.1	211.2±10.1	221.1±6.7	211.1±11.6	208.6±5	220.6±9.6	217.9±5.5
Finger length	46.3±1.7	59.9±1.2	46.9±2.3	61±1.2	47.6±2.8	58.7±1.4	45.6±2.4	59.7±1.4

Analysis two: Pre- vs post-tool use

<u>Great span:</u>

No significant effects were found (see figure 12).

<u>Finger length:</u>

No significant effects were found (see figure 12).

Analysis three: EBP vs NBP

<u>Great span:</u>

There was a main effect of group [F(1,35)= 4.4, p=.04, partial e^2=.11], where the estimates of the EBP group (-8.4±3.3, CI:[-15.2, -1.7]) were significantly smaller than those of the NBP group (1.6± 3.4, CI:[-5.4, 8.5]). See figure 13.

<u>Finger length:</u>

There was a main effect of group [F(1,35)= 5.4, p=.03, partial e^2=.14], where the estimates of the EBP group (-32.4±3.3, CI:[-38.98, -25.8]) were significantly smaller than those of the NBP group (-21.45± 3.4, CI:[-28.2, -14.7]). See figure 13.

The group X hand interaction approached significance [F(1,35)=4.1, p=.05, partial e^2=.12]. Follow-up one-way ANOVA's revealed that the estimated finger length of the EBP's right hand was significantly smaller than those of the NBP [F(1,36)=8.9, p<.01]. This was not the case for the left hand (p=.2). See figure 14.

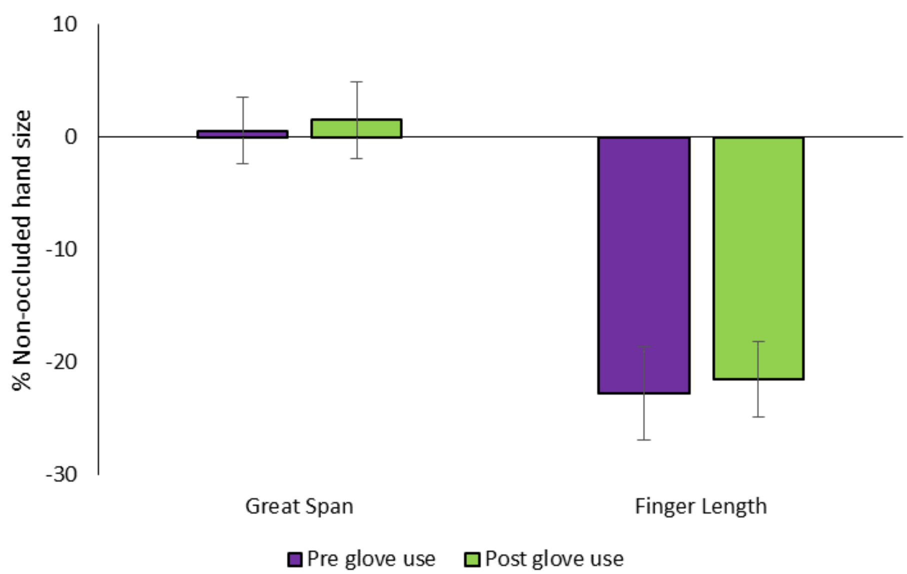

Figure 12: This figure compares the pre-tool use to the post-tool use perceived hand size. There were no differences in hand representation pre- and post-tool use.

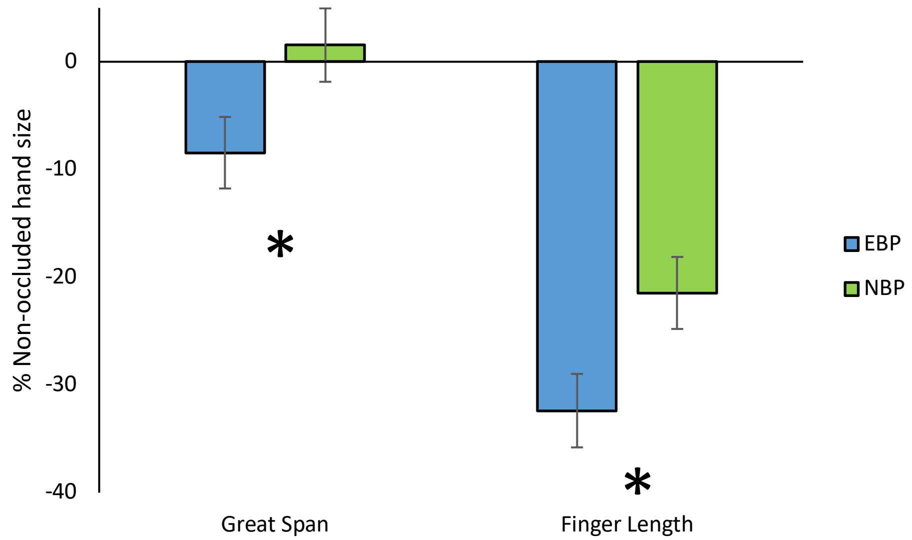

Figure 13: This figure compares the perceived hand size of the EBP and the NBP (post-tool use). The EBP made significantly smaller estimates of both hand width and finger length compared to the NBP.

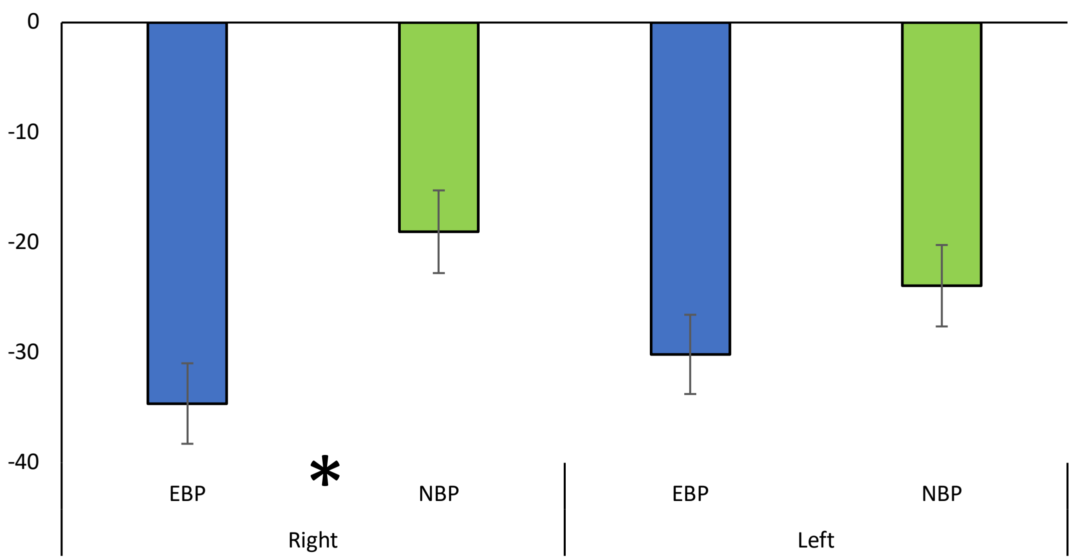

Figure 14: The group X hand interaction. EBP made significantly smaller estimates of finger length on the right hand. However, there were no differences in perceived finger length between the EBP and NBP for the left hand.

Discussion

The present studies were designed to examine if long- and short-term exposure to a tool (baseball glove) changes the body model of the hand. To investigate long-term effects, we recruited a group of male elite baseball players (EBP) and a group of age matched male controls. We asked all participants to complete a hand mapping task. This task involved participants pointing to ten landmarks (the tips and mp joints of their fingers), when their hands were occluded from view. XY coordinates from each point were tracked using an Optotrak camera. From the XY coordinates of these ten landmarks we created a map of how the participants perceived their hands (Coelho & Gonzalez, 2018, in press; Coelho et al., 2017). The results demonstrated that long-term practice with a tool (i.e. the glove) changed the body model. The results supported our second hypothesis, as the EBP significantly underestimated the width of their hands, while the male controls made accurate estimates. The EBP also underestimated the length of their fingers significantly more than the controls did.

To investigate the short-term effects of tool use, we recruited a group of novice male baseball players (NBP, no experience playing baseball). They were asked to complete the hand mapping task both before and after 15 minutes of ball catching using the glove. While previous research has found changes in the body schema immediately after tool-use (Cardinali, 2011; Cardinali et al., 2012; Carlson et al., 2010; Maravita & Iriki, 2004; Sposito et al., 2012) our results for the body model did not align with these findings. There were no significant differences between the pre- and post-tool use hand maps. This suggests that participants did not embody the baseball glove during the 15 minutes of training. When we compared the results of the two studies, we found that EBP had significantly smaller estimates of hand width and finger length than NBP. Together the results suggest lasting changes in the body model of the hand after long- but not short-term tool use.

Previous studies have demonstrated that the body model is distorted; this distortion is characterized by an overestimation of hand width and underestimation of finger length (Coelho & Gonzalez, 2018; Coelho, Zaninelli, & Gonzalez, 2017; Longo, 2014, 2015; Longo & Haggard, 2010, 2011, 2012a, 2012b; Longo, Mancini, & Haggard, 2015; Longo, Mattioni, & Ganea, 2015; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). The results of the EBP in the current study did not adhere to this distortion. When compared to the non-occluded hand maps, both hand width and finger length were underestimated. This is the first report documenting an underestimation of hand width. Moreover, when compared to the maps of controls, finger length was further underestimated in the EBP. These results suggest that, after long-term training with the glove, the participants' hand perception is that of being overall smaller. This finding is somewhat surprising, and we discuss it later in more detail.

The male controls in the first study and the NBP also failed to follow the characteristic distortion, with respect to hand width. Control participants and NBP made accurate estimates of hand width, while underestimating finger length. We have recently reported similar results of hand width in controls (Coelho & Gonzalez, in press). That study found that while females overestimated width, males made accurate estimates. We argued that this is in line with body dysmorphia literature which has found that females overestimate body width whereas males underestimate body size (Fairburn & Beglin, 1990; Hoek & Van Hoeken, 2003; McCreary & Sasse, 2000; Weltzin et al., 2005). We proposed that females and males have different underlying perceptions of their bodies (including the hands). The results from the male controls and from the NBP in the present study provide further support that males do not adhere to the previously described distortion of hand width reported when using female and male participants together. Most of the previous studies on the body model have featured predominantly female participants, which could have hidden these sex differences. It would be interesting to investigate how long-term tool use changes hand representation in females, for example by testing softball players.

Behavioural studies have documented measurable perceptual changes in the participants' body schema following the use of a tool (Cardinali, 2011; Cardinali et al., 2009; Cardinali et al., 2012; Carlson et al., 2010; Iriki et al., 1996; Maravita & Iriki, 2004; Sposito, Bolognini, Vallar, & Maravita, 2012). These studies have shown an expansion of the body schema, one that includes the tool into its representation. Surprisingly, in the present study we find that the body model of the hand is reduced in the EBP. A possible explanation for this reduction is the mechanisms of catching itself. It has been stated that the act of catching relies on visual cues and the ability to predict the path of the incoming ball (Fischman & Schneider, 1985). As catching is made up of a series of complex coordinated movements involving precision and accurate timing of the limbs, the perception of having a smaller hand may in fact provide an advantage. This smaller representation could optimize hand positioning, by creating a more central position of the hand relative to the incoming ball. A conservative estimate of catching the ball, would lead to less misses and fumbles (if you perceive your hand bigger than it really is, then you are more likely to miss catching an object). Indirect evidence for this argument can be found in reach-to-grasp literature, which has found larger hand apertures, when vision is restricted or a delay is introduced (Flindall, 2017; Hu, Eagleson, & Goodale, 1999; Hu &

Goodale, 2000). It has been argued that when the participant is uncertain about the target (i.e. no vision) the larger hand aperture is a way of increasing the margin of error (Jakobson & Goodale, 1991). Thus, the more certain a participant is about the task, the more likely they are to reduce their hand aperture. So by perceiving their hands as smaller, the EBP would be reducing their margin of error for catching. This explanation could also address why we find differing results to another study that investigated how long-term training impacted the implicit representations of the hands (Cocchini et al., 2018). In this study, expert magicians completed a hand mapping task. The results showed that the magicians were more accurate at estimating the lengths of their fingers. Our result from the current study show that while extensive training lead to changes in the body model, it actually caused a reduction in perceived hand size. We attribute the differing results between these two studies to the unique skillsets of the two groups (magicians and EBP). For example, magicians rely on sleight of hand tricks that require them to pretend an action, while they are actually performing a different one. This 'illusion' has been argued to require a representation of their own hand that reflects its anatomical shape and size (Cocchini et al., 2018; Cavina-Pratesi et al., 2011). EBP in contrast, would benefit from a smaller hand representation as this could lead to more accuracy in catching.

Alternatively, it is possible that the smaller hand representation found in the EBP is a result of the fact that when they are not wearing the glove it creates the perceptual illusion that their hand is smaller. In other words, the extensive usage of the glove produces its embodiment so that when the glove is absent their hand feels incomplete. Here we quote one of the EBP who mentioned to one of the authors that "when I reach out to pick up a ball without my glove, I feel my hand is tiny and useless". In their review, Cardinali et al (2012), argue that there is no functional benefit for lasting changes in body representation following tool use. Moreover, they state that following tool-use body ownership should rapidly revert to normal and without negative consequences (disembodiment). Our results argue otherwise, as they demonstrate that after long-term practice using a baseball glove there are lasting changes to hand representation. The relationship between tool use and the conditions upon which it is embodied and disembodied needs further investigation.

One last explanation involves the cortical representation of the hand. It has been suggested that the body model preserves characteristics of the somatosensory homunculus for both the hand (Longo& Haggard, 2010) and the face (Mora, Cowie, Banissy, & Cocchini, 2018). Although is tempting to speculate that long-term use of the glove changes the neural representation of the hand, only future neurostimulation or imaging research could directly address this question. Nevertheless, the result that EBP have an underestimated body model of the hand could be explained in terms of changes in cortical representation. Previous work has documented that extensive training leads to less cortical activation in musicians (Janke et al, 2000) and in athletes (Naito & Hirose, 2014). For example, Naito and Hirose (2014) found reduced recruitment in motor areas when professional soccer players rotated their feet, compared to controls (Naito & Hirose, 2014) These authors argued that the long-term training controlling the ball, may have led to plastic changes in the foot's motor representation of soccer players. These studies however, did not measure body representation, so it is impossible to assert that the reduced recruitment of cortical areas leads to changes in the body model. Further research is needed to investigate this possibility.

A puzzle remains as to why we found perceptual changes in both hands if EBP consistently wear the glove on their left hand. We are unaware of any studies that have found that tool-use with one limb leads to changes in both limbs. However, one study asked participants to use (15 min) a rake with both their dominant right hand and their non-dominant left hand. They showed that training with a tool changes body representation for both the dominant and non-dominant arms (Sposito et al., 2012). It was argued that even though the dominant arm is more dexterous and trained in using tools, the left hand is equally susceptible to changes in body representation after tool use. The fact that EBP showed changes in the representation of both hands even though they wear the glove only on the left hand, suggests that extensive training using a tool in one hand could lead to a carry-over effect to the other hand. This is reminiscent of behavioural studies that have shown that motor skills learned with one hand transfer to the other (e.g.(Parlow & Kinsbourne, 1989; Sainburg & Wang, 2002; Schulze, Lüders, & Jäncke, 2002). For example, Schulze and colleagues asked participants to train for four weeks on a pegboard task (pegs of different sizes had to be inserted into the appropriate holes). Some participants trained with the right hand, others with the left, and yet another group trained with both hands simultaneously. The main finding was that training had reduced the time of inserting the pegs on both the trained and the untrained hand (regardless of group). So even though only one hand did the training, movement times by the untrained hand were also faster after the training. The authors suggested that interhemispheric transfer must occur, and they further discuss the possible neural mechanisms supporting this transfer. Based on these studies, we speculate extensive training with the glove (EBP) changes the body model of the hand and this effect can be seen in both hands.

Lastly, we found that short-term tool use with the glove did not change implicit hand representation. One likely possibility is that participants did not embody the glove during the short 15 minutes of active catching. As catching is a skilled movement, and using the glove requires practice, perhaps these participants did not treat the glove as something that aided their performance. This is different from the classic paradigm (mechanical grabber for example), in which the task could not be completed without the incorporation of the tool into the body schema. One previous study found similar results to ours (Biggio, Bisio, Avanzino, Ruggeri, & Bove, 2017). The authors investigated if peripersonal space was modulated by tool-use (tennis racket) and found that holding onto the tennis racket only altered peripersonal space elite tennis players, but not in novices. In other words, only elite tennis players embodied the racket. The authors argue that this result means that plasticity of peripersonal space depends on familiarity with the tool, and this is gained over years of practice. Our results suggest that the same could be true for the body model, as our NBP did not demonstrate a change in the hand maps following 15 minutes of catching. Additionally, a study investigated the neural correlates of body representation changes in elite tennis players and controls (Fourkas et al., 2008). The authors used TMS to measure forearm and hand muscles in these groups while they mentally practiced a tennis forehand, table tennis forehand, and a golf drive. The elite tennis players showed increased corticospinal facilitation during the imagined tennis forehand but were not different from the novices in the other two conditions. The authors argue that their results indicate that long-term experience is crucial in modulating sensorimotor body representations. Our results suggest that long-term experience with a tool is necessary for changes in the body model. Perhaps, testing a group of participants who had played elite level baseball for some years but did not continue playing, would yield similar results to the EBP or to other studies demonstrating changes in body representation after short-term training. It would be important to also identify how much training is necessary to see the long-term changes in hand representation; is one year enough? Or does it take 5+ years? Further research is needed to answer these questions.

To conclude, we investigated the long- and short-term effects of experience-based plasticity on the body model of the hand. A group of EBP (many years of baseball experience; long-term effects of tool use), a group of NBP (no experience playing baseball; short-term effects of tool use), and a group of male controls, completed an implicit hand representation task. The results show that EBP underestimated hand width and finger length more so than the NBP or controls. This result suggests that prolonged tool use produces long-lasting changes in the body model.

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Appendix 4: Taxonomies of body representation: The body model, body schema and body image.

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Abstract

The dyadic taxonomy of body representation postulates that the body schema is the sensorimotor representation of the body that serves action, whereas the body image is the visual representation of the body that serves perceptual tasks. In the past 10 years, a new body representation has been investigated: the body model. This is the representation of our bodies that underlies position sense. It is unknown if the body model is a separate representation or a subtype of the body schema or the body image. To investigate how the body model fits into the dyadic taxonomy of body representation, participants completed body model, schema, and image tasks that were focused on the hand. The results showed that all three representations were distorted and furthermore, the distortions for each representation were different from one another. This result suggests that the body model is an independent body representation and thus we propose a future revision to the dyadic taxonomy, one that includes the body model as a third and separate representation.

Key words: Hand, anchor effect, independent body representations, finger length, position sense

Public significance statement: This study provides evidence that the body model, body schema, and body image are independent representations of the body. This suggests that motor commands and position sense rely on different representations of the body.

Introduction

Body representations are defined as the cognitive structures that are concerned with encoding and tracking the state of the body (De Vignemont, 2018). These representations inform us about the shape and size of our bodies. We rely on these representations to successfully interact with our environments. For example, reaching out and picking up a glass requires an understanding of the length of one's arm and the size of our hand. The brain houses several mental depictions of the body. Traditionally, literature has documented two unique representations: the body schema and the body image (Dijkerman & De Haan, 2007; Gallagher, 2006; Paillard, 1999). The dyadic taxonomy of body representations postulates that the body schema is the constantly updating sensorimotor representation that serves action (de Vignemont, 2010; Gallagher & Cole, 1995; Head & Holmes, 1911; Paillard, 1999); while the body image is the stable visual representation of the body that serves all other functions (e.g. perceptual, body concept). In recent years, it has been proposed that body representation pathways and networks are multimodal in nature and less independent from one another (De Haan & Dijkerman, 2020). Which suggests that the dyadic taxonomy may be too restrictive.

A third representation has been proposed in recent years; the body model (Longo & Haggard, 2010). This is the representation of the body's spatial content, which serves position sense (Longo & Haggard, 2010). To clarify, we gain knowledge of the position of our bodies in space (position sense) through various afferent signals from the somatosensory periphery. These signals provide information about joint angles only, therefore, the body model is the representation of the distances between these joints.

Without this additional information, localizing a body part in space would be impossible (Longo, 2015b). In their original report, Longo and Haggard (2010) asked participants to localize where they believed 10 landmarks (the tips and metacarpal phalangeal joints) were located on their unseen hand. The results showed that the body model of the hand was systematically distorted. Participants overestimated hand width and underestimated finger length. This finding has been replicated in numerous studies from different labs (Cocchini, Galligan, Mora, & Kuhn, 2017; Coelho & Gonzalez, 2017, 2018; Coelho, Zaninelli, & Gonzalez, 2016; Longo, 2014; Longo & Haggard, 2012a, 2012b; Peviani & Bottini, 2018; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Van der Looven, Deschrijver, Hermans, De Muynck, & Vingerhoets, 2021).

At this point it is unclear where the body model fits into the dyadic taxonomy of body representation. The systematic distortions found in the body model have not been reported in body schema or body image studies even though the body model shares functions with both representations (body schema and body image). For example, self-initiated movement (body schema) relies on the knowledge of where our body parts are in space (body model). Furthermore, similarly to the body image, the body model necessitates a stored mental depiction of the body. Nevertheless, there is evidence, to suggest that the body model is a unique representation. First, in Longo and Haggard (Longo & Haggard, 2010) asked participants to complete both a body image and the previously described body model task. For the body image task, the participants were presented with an array of photographs of their hand. They were asked to select the photograph that best represented the size and shape of their hand. The images presented were either distorted (smaller or larger) or the participant's exact hand size. The participants were able to correctly identify the photograph that was the same size as their hand. Therefore, although there were no distortions in the body image of the hand, the body model was distorted. The authors argued that the body model and the body image do not share the same stored body representation. However, it should be noted that in that study the body model task was only concerned with landmarks on the fingers, whereas in the body image task, participants were presented with images of their full hands. Perhaps if the body image task required participants to estimate the size of their fingers alone, this would result in similar distortions as those seen in the body model. We address this possibility in the current study.

The relationship between the body model and body schema is still somewhat unclear. There is evidence that purposeful movement relies on the body model. (Paviani et al., 2018; 2020). In these studies, participants executed two tasks: 1) the body model as previously described, and 2) a similar task but with added movement. For this, participants were asked to move their hand underneath a tabletop until the tip or MP joint of their finger aligned with a visual cue on the top of the table. They found that although distortions were still present in both tasks, the resulting representation was more accurate when participants moved their hand. The authors argued that the body model informs our actions (at least to some degree). If both the body model and body schema underlie action, perhaps the body model is a sub-representation of the body schema? Afterall, the calculation of motor commands (body schema; Dijkerman & De Haan, 2007) and position sense (body model; Longo & Haggard, 2010) are both necessary for movement. The primary goal of the present study was to investigate if the body model of the fingers was more closely related to the body schema or the body image.

In this study we provide a comprehensive examination of the three body representations using the hand, and specifically the fingers, as a model. Participants were asked to complete: body model, body schema, and body image tasks. In the body model task, we used the same hand mapping technique as in our previous studies (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2016). For this task, the participant placed their hand palm up underneath a covered tabletop and were asked to estimate the location of 11 different landmarks on their hidden hand (similar to Longo & Haggard, 2010). In the body schema, we modified a task used by Martel and colleagues (2019). We blindfolded participants (no vision) and asked them to slide their index finger on the surface of a table until it traced the perceived length of each of their fingers and the full length of the hand. Prior to the onset of this task we tapped and named the base and tip of each target finger with a wooden stylus. This has been considered a body schema task because it is an estimation based on sensorimotor information that involves movement. Lastly, in the body image task we used a computerized version of the line length task (Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009; Longo, 2015a; Martel et al., 2019). Here participants were required to estimate when a vertical line on a computer screen reached the length of their fingers. We hypothesized that because the body model and body schema serve similar functions (i.e. action) these representations would share the most similarities. We predicted that estimations of the body model and body schema would be significantly different from the body image.

In order to compare the three different types of body representations we considered one important factor: Movement direction. All the studies that have investigated the body model have asked participants to make their estimates moving away from their body (proximal-distal direction). It is possible that has led to the underestimation of finger length characteristic of the body model or to the inconsistent results between the body model, image, and schema. Asking some participants to make their estimates towards the body would more closely align to the methodologies used in the line length task (Linkenauger et al., 2009; Longo, 2015a; Martel et al., 2019). In this body image task, it is common practice to have some participants make their estimates in a proximal-distal fashion and others in a distal-proximal manner. Proximal-distal refers to when the line is getting longer (starts small, moves away from the body), whereas in distal-proximal the line gets shorter (starts long, moves toward the body). The belief is that when the line starts from a "small position", this biases the participant into believing their body part is smaller (Gardner & Boice, 2004; Probst, Van Coppenolle, Vandereycken, & Goris, 1992), therefore estimates in the proximo-distal direction might be underestimated. Whereas, starting the line from its "largest position" will result in larger estimates of body size. This is referred to as the anchor effect (Probst et al., 1992). To investigate if the anchor effect influences body representations, we asked half the participants in the current study, to complete all tasks with the anchor proximal to the body (move away; proximal-anchor group) and the other half with the anchor distal to the body (move toward; distal-anchor group). We hypothesized that finger length would be subjected to the anchor effect thus underestimation would be more pronounced in the proximal-anchor group.

Methods

Participants

We conducted an a priori power analysis using G*power (Faul, Erdfelder, Buchner, & Lang, 2009) to determine the required sample size. We used Cohen's *d* from our previous studies (Coelho & Gonzalez, 2017, 2018; Coelho et al., 2016) for this calculation. We specifically entered effect sizes from our previous *F* tests that determined group differences for the finger length variable. Based off this analysis the minimum number of participants needed was 32. We recruited forty-eight female undergraduate students (mean age 20.6) to participate in the study in exchange for a course credit. All individuals self-reported that they were right-handed. Prior to commencing the study, all participants gave written consent in compliance with the Declaration of Helsinki.

Materials

An Optotrak Certrus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of two infrared emitting diodes (IRED). The first IRED was placed at the end of a wooden stylus (19.5 L x 0.5 W x 0.3 H cm). This was used during the body model task. For the body schema task, the IRED was attached to the end of the participants finger. In both cases IRED location was recorded for 1000ms at 100 Hz for each trial.

Procedures

All participants completed three tasks: body model, body schema, and body image tasks. Each task was repeated for both the right and left hand. The task order and starting hand was counterbalanced between participants. To test for an anchor effect, we split our participants into two groups: proximal anchor group and a distal anchor group. The proximal anchor group performed each task starting close to the body (proximal) and moving away from it. Whereas the participants in the distal group started in front of the body (distal) and moved towards it. The details of each task are below:

Body model task:

The participant sat in front of a glass table-top (41.0 L x 86.5 W cm). We asked the participant to place their hand palm up underneath the tabletop, so that the palm of their hand was in contact with the glass. They were required to spread their fingers as wide as possible. Their hand remained in the fixed position for the duration of the conditions completed for that hand. The participants forearm rested on a thin pillow for support during the task. We then covered the table with a black tablecloth so the participant could not view their hand (occluded-hand condition; see figure 1). We asked the participant to estimate where they believed 11 landmarks were located on their fixed hand. These landmarks included the tips of each of their fingers (5), and the metacarpal phalangeal joints (MP joints) of each of their fingers (5). The last landmark was on the wrist (base of the hand), it was situated between the triquetral and scaphoid bones directly on the crease at the bottom of the palm (see figure 1). The participant estimated the landmarks using the wooden stylus with the IRED attached. This action was completed by using their non-occluded hand to grasp the stylus and place it on the tabletop, directly above their unseen hand. For each estimate, we recorded the XY locations of the IRED marker. After each estimate the participant was required to place the stylus on top of a home spot. For the proximal anchor group, the home spot was located on the edge of the table, directly above the participants forearm. This ensured that the participant started every estimate from a position close to the body (proximal) and ended by pointing away from the body (distal). For the distal anchor group, the home spot was located at the far edge of the table, directly in front of the participants target hand (see figure 15). At the end of the occluded hand condition, the tablecloth was removed, and the task was repeated but this time with full-vision of the hand (non-occluded hand condition). This condition was completed so we could obtain the actual hand size dimensions for each participant. The entire task was then repeated for the opposite hand. For each condition the participant completed 3 estimations to each of the 11 landmarks (33 trials per condition; 132 trials in total).

The two dependent variables were finger length and hand length. Finger length was measured as the distance between the tip and the MP joint of the finger. Each individual finger length was averaged together for one variable. Hand length was measured as the distance between the tip of the middle finger and the base of the hand.

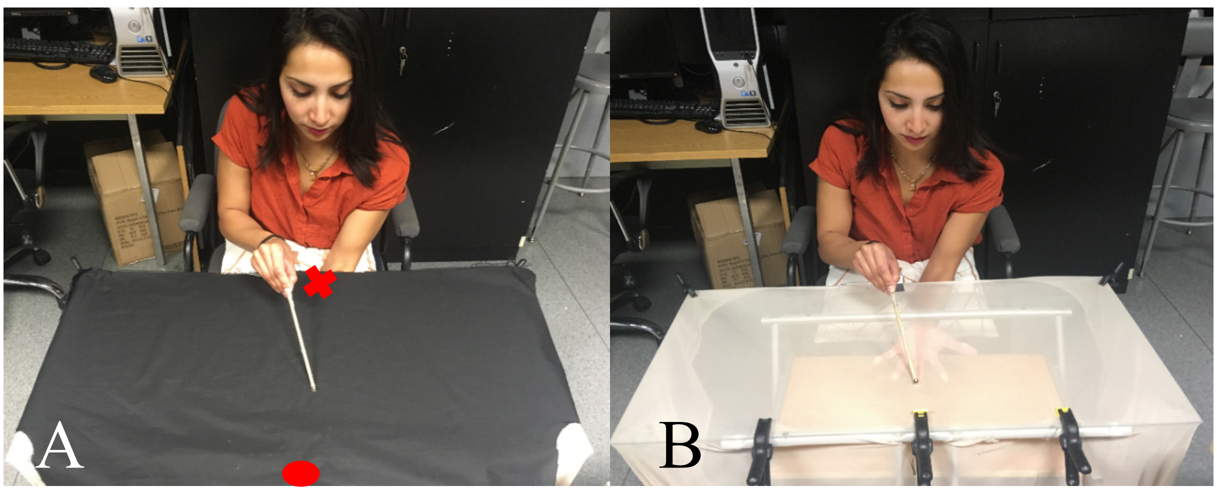

Figure 15: The experimental setup of the body model task. Frame A shows the occluded-hand condition, whereas frame B shows the non-occluded condition. In frame A the proximal anchor group's home landmark is noted by a red x. The distal anchor groups landmark is indicated by a red circle.

<u>Body schema task:</u>

For the body schema, we modified a task from Martel et al (2019). In this task, the participants remained seated in front of the glass tabletop. The participant was blindfolded, so they could only rely on haptic feedback to inform their estimates. We asked them to estimate how long they believe 6 target body parts were. These targets included the length of the five fingers (thumb, pointer, middle, ring, and pinky) from the tip to the MP joint, as well as the total length of the hand, from the tip of the middle finger to the wrist. Prior to the onset of the task, we tapped and named the tip and MP joint of each of the target body parts. For each trial, the participant was required to slide their index finger from a starting position (same as home base in the body model task) across the tabletop, until they believed it had reached the length of the target (as shown in figure 16). The proximal anchor group moved their hand away from the body, whereas the distal anchor group moved their hand towards the body. As the body schema is constantly updating, we asked participants to keep their fingers spread as they moved their hand across the tabletop (as if they curled their fingers it may result in shorter estimations of finger length). We attached an IRED marker to the tip of the participants index finger and took two recordings per estimation; one at the start (on home position) and one when the participant had reached the length, they believed their target was (end position). This was done so we could calculate the length of every target's estimation. We compared the perceive length of the fingers in the body schema to the actual hand size dimensions measured in the non-occluded hand condition of the body model task. The body schema task was repeated for both the left and right hands. Each of the 6 targets were estimated 3 times (18 trials per condition, 36 trials total).

Finger length and hand length was measured as the distance between the starting position and end position for each of the 6 targets. As in the body model, the average of the 5 finger lengths was used to calculate the finger length DV.

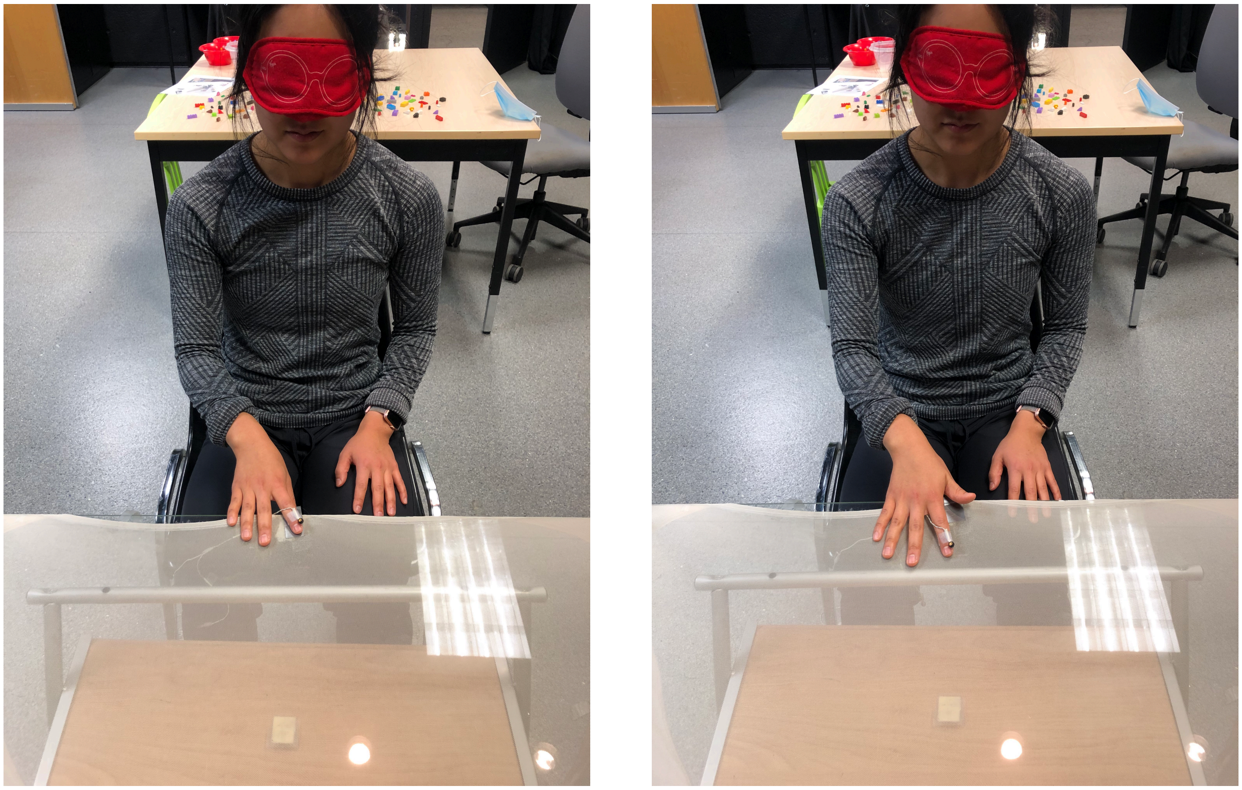

Figure 16: The body schema task. Participants started with their hand either on the proximal home spot (proximal anchor group; as shown on the left) or on the distal homespot (distal anchor group as shown on the right). They were then asked to trace with their index finger their estimated target finger size.

Body image task:

This was a modified version of the line length task (Linkenauger et al., 2009; Longo, 2015a; Martel et al., 2019). The participant was seated in front of a computer screen. We asked them to sit with their hands behind their backs, so that they could not see their hand for the duration of the task. A line would appear on either the bottom (proximal anchor group) or the top (distal anchor group) of the screen. The line would increase by .2mm per slide. Power point was used to present the line to participants. The participant verbally indicated when the line had reached the same length as each one of 6 possible targets. The same 6 targets (thumb, pointer, middle, ring, pinky, hand) were used as in the body schema task. For consistency between tasks, each of the 6 targets were estimated 3 times (18 trials per condition, 36 trials total). Please see figure 17 for a visual description of the task.

The length of each of the targets was derived from the length in mm of the line when the participant stopped each trial. As in the previous tasks, finger length was measured as the average of the length of the five fingers.

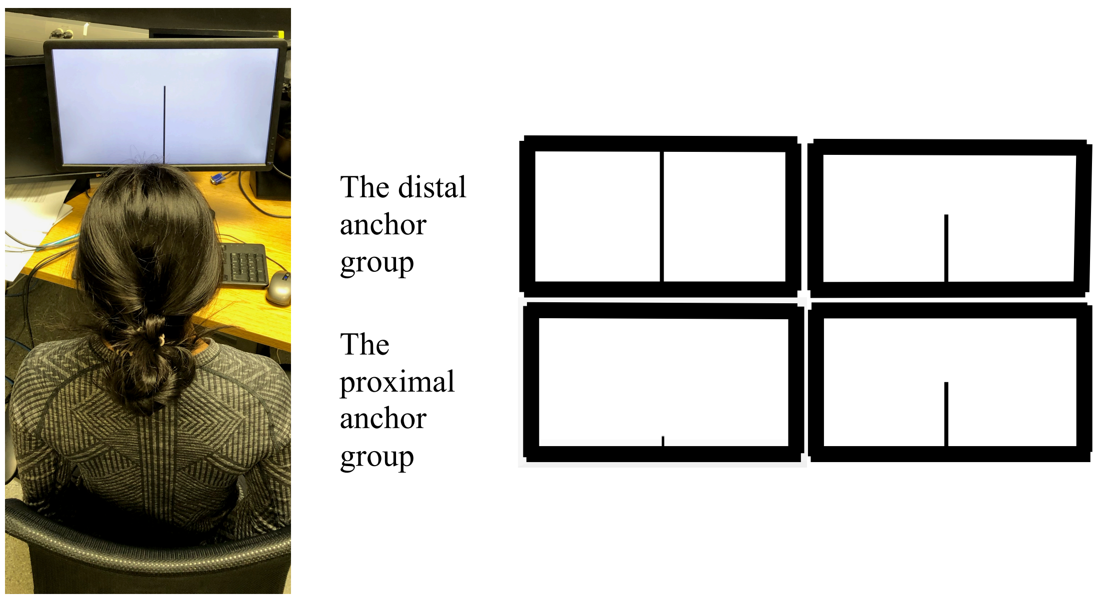

Figure 17: The body image task. Participants sat in front of the screen with their hands behing their back (no vision of their hands for the duration of the task). The line on the screen either started long and got gradually smaller (distal anchor group). Or started small and gradually got longer (proximal anchor group). The participant was required to inform the experimenter when the line reached the length of their target hand/finger.

Analyses

To determine if there were different magnitudes of distortions between the body representations, hands, body parts, and groups our first analysis was a 3x2x2x2 mixed design ANOVA. The within factors were body representation (body model, body schema, body image) x hand (right, left) x body part (finger length, hand length) and the between factor was anchor (proximal, distal). To account for any possible difference in hand size we used the percentage of the non-occluded hand (for both finger and hand length) for data analysis purposes. This was calculated for each body representation as (body representation estimation - non-occluded) / (non-occluded))*100.

To identify which variables were significantly distorted, the second analysis was a series of one samples t-tests. As in analysis one, we used the percentage of the non-occluded hand and compared that value to 0 (i.e., no distortion (accurate)). This analysis was repeated for every dependent variable in the analysis (finger and hand length of the right and left hands for each of the body model, body schema, and body image; total of 12 DVs).

We ran a series of Pearson r correlations between the three representations to see if there were relationships between the different types of body representations. We used the same measurement (% of the non-occluded hand size) as in the first analysis. Here we only report significant correlations that occurred across the body representations (e.g., body model and body schema) and between the same dependent variable (referred to as a dyad). To be specific, if there was a relationship between right hand finger length of the body model and right-hand finger length of the body image this was reported. We were not concerned with significant relationships that occurred within each body representation (e.g., right hand finger length of the body model and left hand finger length of the body model) or significant relationships that occurred across the body representations but did not occur with the same dyad of dependent variables (e.g. right hand finger length of the body model and left-hand hand-length of the body schema). Instead, we were interested in relationships between body representations of the same body part.

All data are available upon request from the corresponding author. The study was not pre-registered.

Results

1. Mixed design ANOVA

There was a main effect of body representation [$F(2,92)=82.2$, $p<.001$, partial $e^2=.64$]. Follow-up pair wise comparisons revealed that all representations were different from one another (p's=<.001). Body model estimates were underestimated by 15%±1.4, whereas the body schema was overestimated by 2.03%±2.6, and finally the body image was underestimated by 31.4%±1.2. See figure 2. The accuracy of the body schema is due to finger length being overestimated, but hand length was underestimated. To illustrate this point, a breakdown by body part (finger length, hand length) is included, see figure's 18 and 19.

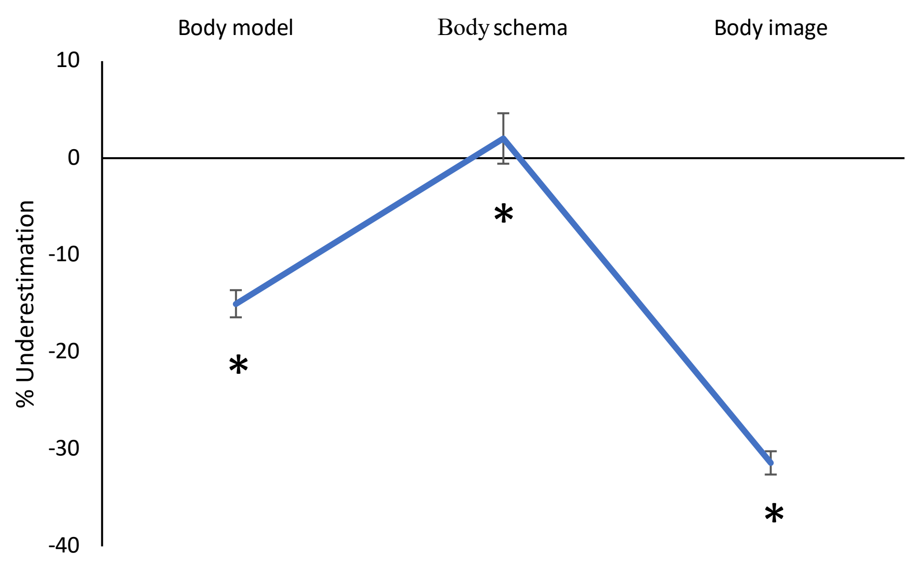

Figure 18:
All three body representations were significantly different from one another. The body image was underestimated by the greatest amount. The body schema was slightly overestimated. * Denotes significance from the other body representation.

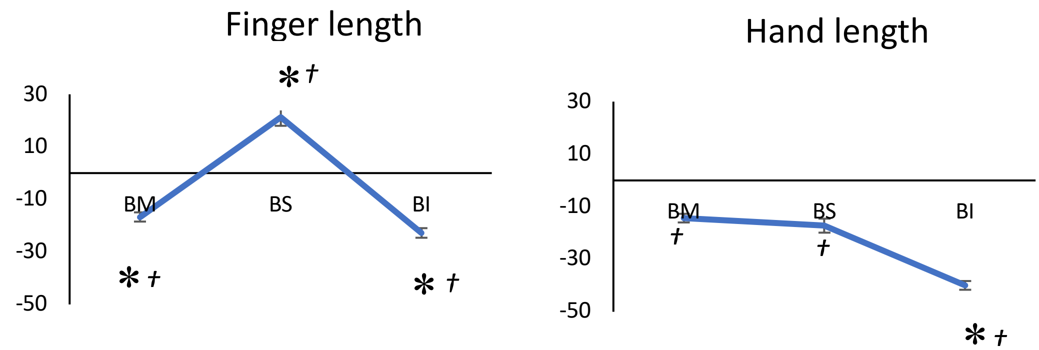

Figure 19: The effect of body representation (BM = body model, BS = body schema, BI= Body image) split by variable. For finger length all three representations were different from one another. For hand length only body image was different from the other two representations.† Indicates that the values were different from 0. * Indicates that the values were significantly different from the other representations.

Additionally, we found a main effect of body part [$F(1,46)=97.2$, $p<.001$, partial $e^2=.68$]. Participants underestimated the lengths of their hands (mean = -23.84%±1.3) significantly more than the lengths of their fingers (mean = -6.07±1.5).

There was a main effect of anchor [$F(1,46)=8$, $p=.007$, partial $e^2=.15$]. Participants with the proximal anchor underestimated significantly more (mean= -18.1%±1.6) than those with the distal anchor (mean= -11.8%±1.6).

We also found a significant body representation by body part interaction [$F(2,92)=108.3$, $p<.001$, partial $e^2=.7$]. Follow up pair wise comparisons revealed that for the body model there was no difference in the magnitude of distortions between finger length and hand length ($p=.16$). However, for both the body schema and body image, hand length was underestimated more than finger length (p<.001). See figure 20.

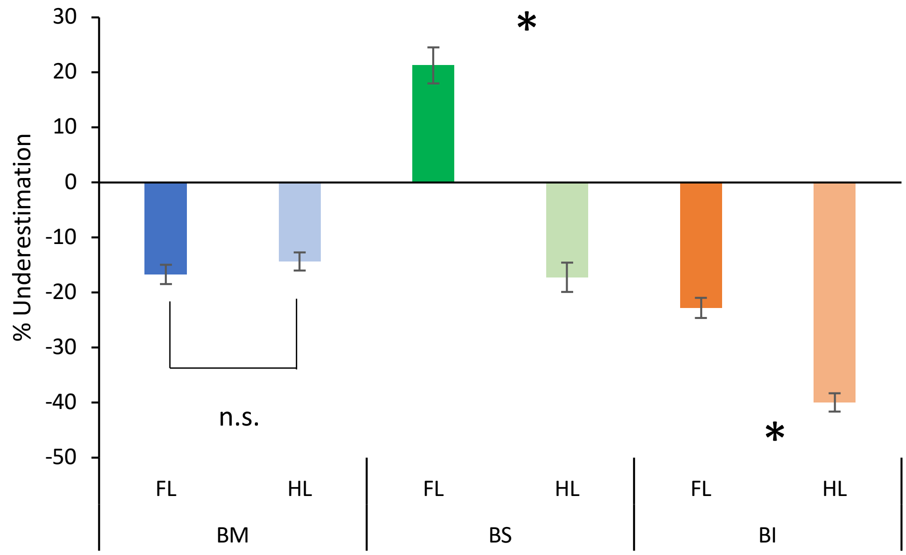

Figure 20: The interaction between body representation and body part (FL= finger length, HL= hand length). For both the BS and the BI, participants underestimated hand length significantly more than finger length (denoted by *). However, the participants underestimated both finger and hand lengths in the BM to the same degree (not significantly different (n.s.)).

Lastly, there was a body representation by hand interaction [$F(2, 92)=3.6$, $p=.03$, partial $e^2=.07$]. Follow-up pair wise comparisons demonstrated that in the body image task, estimates of the right hand were less distorted (-30.1%±1.5) than those of the left hand (-32.6%±1.3), however after adjusting for multiple comparisons this effect did not reach significance ($p=.09$).

2. One-sample t-tests

This was to investigate if there were distortions in each of the three representations of finger and hand length. The results from these tests are shown in table 3. The participants in both groups had significantly distorted estimates of every dependent variable.

Table 4: The descriptive statistics of the one-samples t-tests. Importantly all dependent variables in the three body representations were significantly different from 0. This indicates that all representations are distorted.

	Proximal anchor			
	DV	mean	t	*p* value
Body model	RH finger length	-19.3	-6.5	<0.001
	LH finger length	-16.8	-6.1	<0.001
	RH hand length	-18.2	-5.9	<0.001
	LH hand length	-14.8	-5.2	<0.001
Body schema	RH finger length	16.3	3.2	0.004
	LH finger length	16.2	2.7	0.014
	RH hand length	-24.6	-8.6	<0.001
	LH hand length	-21.1	-6.4	<0.001
Body image	RH finger length	-25.3	-9.4	<0.001
	LH finger length	-25.9	-10.4	<0.001
	RH hand length	-40.4	-13.5	<0.001
	LH hand length	-43.3	-21.1	<0.001
	Distal anchor			
Body model	RH finger length	-15.3	-5.1	<0.001
	LH finger length	-15.4	-5.8	<0.001
	RH hand length	-13.6	-4.5	<0.001
	LH hand length	-10.8	-5.9	<0.001
Body schema	RH finger length	25.6	6.7	<0.001

	LH finger length	27	5.8	<0.001
	RH hand length	-11	-2.4	0.025
	LH hand length	-12.1	-2.5	0.019
Body image	RH finger length	-18.1	-6.8	<0.001
	LH finger length	-21.8	-7.4	<0.001
	RH hand length	-36.5	-13.4	<0.001
	LH hand length	-39.7	-17.1	<0.001

3. Correlational analysis

Proximal anchor

There was a significant relationship between the body model and the body schema for finger length of the right (r=.45, *p*=.03; figure 7).

Distal anchor

There was a significant relationship between body model right hand finger length and body schema right hand finger length (r=.49, *p*=.02; figure 7). There was also a significant correlation between body model right hand length and body schema right hand length (r=.48, *p*=.02; figure 8). There were no other significant correlations between dyads.

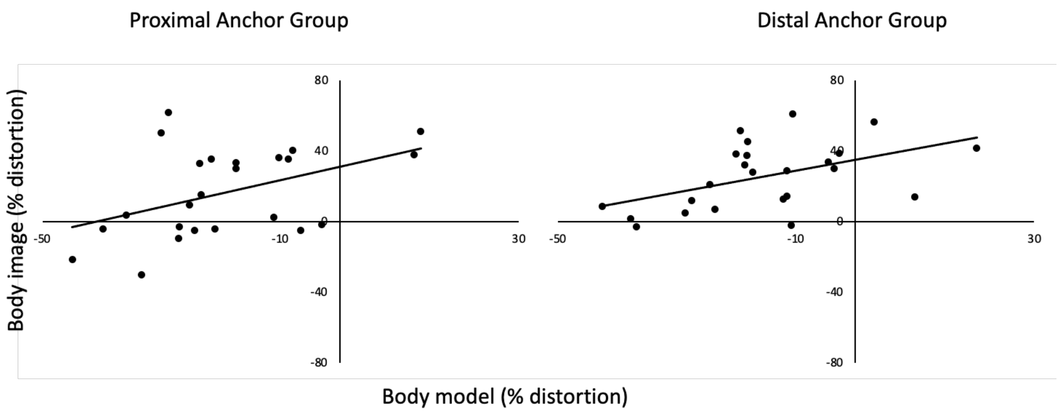

Figure 21:The relationship between finger length of the body model and schema for the right-hand split by anchor group. In both cases as body image distortion increases so does the body model distortion. Finger length size is expressed in % distortion.

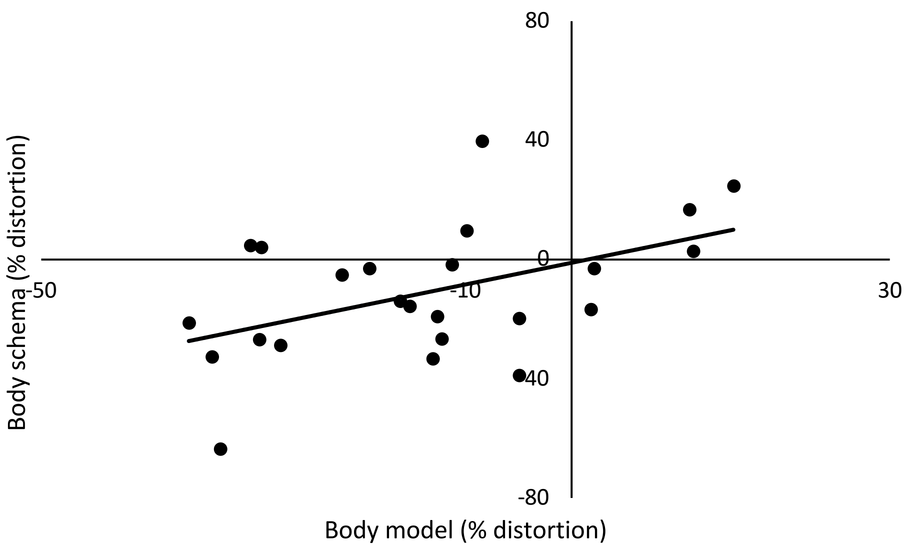

Figure 22: The relationship between body model and body schema for right-hand length in the distal group. An increase in distortion in the body model results in an increase in distortion in the body schema.

Discussion

In the present study we investigated three body representations of the hand. Specifically, we asked participants to complete body model, body schema, and body image tasks. We found that participants exhibited distortions in all three of the representations. Finger and hand length were underestimated in both the body model and body image tasks. In the body schema task, participants overestimated finger length but underestimated hand length. The magnitude of distortion in all three representations were different suggesting that they are independent from one another.

An important goal of this study was to establish whether the body model was an independent representation or a subtype of the body schema or the body image. Our first hypothesis, was that the body model and body schema would share the most similarities because both are used for action. This hypothesis was partially supported, as we did find correlations between the two representations, however, the distortions between these two representations were different in terms of magnitude and direction. In addition, we predicted that both representations would be different from the body image, that prediction was supported. A second objective of the current study was to investigate possible anchor effects, specifically if movement direction during body estimates affects the resulting representation. We hypothesized that an anchor effect would cause participants in the proximal-anchor group (moving away from their body) to underestimate hand size to a greater degree when compared to distal anchor group (moving toward their body). This hypothesis was supported.

It has long been established through double dissociation studies that the body schema and body image are separate representations of the body (Anema et al., 2009; Dijkerman & De Haan, 2007; Gallagher & Cole, 1995; Head & Holmes, 1911; Paillard, 1999). For example, one such study asked two stroke patients to complete a tactile localization task (Anema et al., 2009). In this task, a tactile stimulus was presented on the back of the participant's hand. They were asked to indicate the location of the tactile stimulus either by reaching out with their other hand and touching the location (body schema), or by pointing to the location on a drawing of a hand (body image). One patient (patient KE) exhibited body schema related impairments: KE failed to localize the position where they had been touched using their own hand. However, KE was able to accurately identify the stimulus location on the drawing of the hand. The other patient (patient JO) displayed the opposite pattern. JO was able to use their hand to indicate where they had been touched (body schema), but was unable to identify this location on the drawing of the hand (body image). This study highlights that the body schema and body image are two distinct representations. Our results align with this finding, as we found differences in perceptual distortions between the body schema and the body image. Together, the results of the previous studies described in this paragraph and our findings, support the dyadic taxonomy of body representation; specifically, that the body image and body schema are separate representations.

With respect to the body model, it has been unclear whether it is an independent representation, or if it falls within the body image or schema. The results of the current study clearly demonstrate that the body model is a unique representation. With respect to finger length, estimates of the body model and the body schema were in opposite directions; the body model was underestimated whereas the body schema was overetstimated. We believe this is the first report to directly compare between the body schema and body model of the hand. The body model and the body image were also different from each other, the underestimation was more pronounced in the body image than the body model. That the body model and body image had different magnitudes of distortions is in line with previous research that has argued that the body model and body image use distinct stored mental representation (Longo & Haggard, 2010; Van der

Looven et al., 2021). Van der Looven and collegues tested both the body model and the body image of the hand in a group of participants spanning multiple age groups. They found that while the participants displayed systematic distortions in the body model task (same task as Longo & Haggard, 2010), they were accurate at estimating the body image of the hand when presented in pictures. Participants were able to correctly select an image that corresponded to the physical size of their hand. Taken together, the results of the current and past investigations support the view that the body model is a unique representation. Therefore, we propose that future versions of the dyadic taxonomy of body representation should include a third representation, the body model. In fact, it has been argued that the dyadic taxonomy might be too restrictive (De Haan & Dijkerman, 2020) and it has been proposed that there are more than two pathways (i.e., body schema and body image) of somatosensation for body representation. Our results align with this proposal, as we found three independent representations of the hand.

Not all studies have reported an accurate body image of the hand. A previous study found, as we did, that the body image of the hand is underestimated (Giurgola, Bolognini, & Nava, 2020). In that study participants were presented with an array of different sized 3D hand models and were asked to select the model hand that best represented the physical size of their hand. Participants consistently selected model hands that were smaller than their physical hand size. The authors argued that body-part perceptual distortions are a characteristic of human body representation. The results from our study align with this, as we also found underestimation of hand size (in both finger length and hand length) in the body image task.

One puzzle is the finding that finger length was overestimated in the body schema task. The few studies that have investigated the body schema of the hand have not found consistent distortions (de Haan, Smit, Van der Stigchel, Keyner, & Dijkerman, 2018; Lopez, Schreyer, Preuss, & Mast, 2012; Taylor-Clarke, Jacobsen, & Haggard, 2004). However, one study found that the distance between two tactile stimuli were perceived as farther apart when they were presented on the fingers compared to the same stimuli being presented on the forearm (Taylor-Clarke et al., 2004). In this study, participants were touched on two body parts (finger and forearm) by two small spheres. In 81% of the trials participants perceived the distance to be closer when the stimuli touched their forearms compared to when it tourched their fingers, eventhough it was the same distance. It is unclear from that study, if this result was because people overestimate finger length, or because they underestimate forearm length. Our results would support the former speculation. Moreover, overestimation of body schema in other body parts (e.g. shoulders, hips) have been well documented in anorexic patients, and in some studies this result has also been found in healthy controls (Keizer et al., 2013; Rubo & Gamer, 2019; Wignall, Thomas, & Nicholls, 2017). Keizer and colleagues (2013) asked anorexic and healthy participants to walk through door-like openings. The distance between each opening varied from trial to trial. Anorexics started rotating their bodies when the aperture of the doorway was 40% wider than their shoulders, indicating that they believed they would not go through the door unless they rotated their shoulders. A similar overestimation of shoulder width was seen in the healthy controls, although to a lesser degree (25% overestimation). Furthermore, one study suggested that overestimation of body schema may not be pathological but rather influenced by both normal perceptual biases and societal body ideals (Wignall et al., 2017). In our current study, we find further evidence of overestimation of body schema to include the finger length of the hand.

Although the current study clearly shows that the three body representations are different from each other, we found a significant positive correlation between the body model and the body schema. Previous studies have shown a relationship between these two representations (Cardinali, Brozzoli, Luauté, Roy, & Farnè, 2016; Gallagher & Cole, 1995). For example, one case study featured a patient who had no proprioceptive function below the neck (Gallagher & Cole, 1995). This study showed that the patient could not sit up or move their limbs in any controllable way, even when visual information regarding the position of their limbs was available. The authors in this article highlighted the importance of proprioception in the development of the body schema, and we would add, to the development of the body model. We speculate that the relationship between these two representations is likely due to shared functional similarities; both representations are required for action. While the body model is used to calculate position sense (Longo & Haggard, 2010), the body schema is used to calculate motor commands (Dijkerman & De Haan, 2007), both of which are necessary for completing an action. If both the body schema and body model are needed to reach out and pick up a glass, it would make sense that they are related to one another. Interestingly, the correlation between the body model and body schema was only found in the right hand. One could argue that this is related to the right-hand dominance seen in the human population; most right-handers prefer to use their right hand for reaching, grasping, and manipulating objects (Flindall, Doan, & Gonzalez, 2014; Gooderham & Bryden, 2014; Stone, Bryant, & Gonzalez, 2013; Stone & Gonzalez, 2015) which might result in a more intertwined representation of body model and schema.

As stated in the introduction, the body model is the stored representation of the body's spatial content (e.g., the distance between each joint) that serves position sense

(Longo & Haggard, 2010). While body schema is the online-sensorimotor representation of the body that guides our movements (de Vignemont, 2010; Gallagher & Cole, 1995; Head & Holmes, 1911; Paillard, 1999). An important critique (de Vignemont, 2010) of most body model and body schema tasks is that includes an effector hand (the hand making the estimations) and the target hand (the hand being estimated). Asking participants to perform an action to estimate each location in the body model task by definition would result in the body schema (of the pointing hand) also being measured (or at least influencing the measurement of the body model). Therefore, it is possible that in the current format of the body model task both representations (body model of the goal hand and body schema of the effector hand) are influencing each other, and this leads to the correlations between the two representations. Some studies have tried to reduce hand movement in the body model task, by having participants use a cursor to indicate landmark location (Saulton et al., 2015; Stone, Keizer, & Dijkerman, 2018). However, in order to fully account for this possibility we would need to design a body model task that did not require the participant to point. We are currently conducting a study in the lab using eye-tracking software to address this question. Regardless, our results demonstrate the distortions in each of these two representations although related, they are different from one another.

Lastly, we found a main effect of anchor. Participants who moved from a proximal anchor (proximal-distal movement) had smaller estimates of hand representation than the participants who moved from a distal anchor (distal-proximal movement). Previous research has shown that the starting position could bias participants estimates in body image tasks like the line length task (Gardner & Boice, 2004; Probst et al., 1992). In one study, participants were shown a distorted image of their own bodies

(Probst et al., 1992). They were asked to "reconstruct" the image until it reflected their own body size. Participants that were shown a larger body at the beginning of the trial had larger estimates of body size than the participants who were shown a smaller body. The authors argued that the initial body size that is shown to participants is an anchor that influences their final judgment of body size. Our results include a main effect of anchor, which indicates that this effect is not isolated to the body image (it is also present in body schema and body model tasks). Underestimation of finger length is a characteristic of the body model as has been shown by many studies (Cocchini et al., 2017; Coelho & Gonzalez, 2017, 2018; Coelho et al., 2016; Longo, 2014; Longo & Haggard, 2012a, 2012b; Peviani & Bottini, 2018; Saulton et al., 2015; Van der Looven et al., 2021). We found underestimation of finger length in both anchor groups (proximal and distal), however underestimation of finger and hand length was more pronounced in the proximal anchor group. Because this is the first study to include a group that made their estimates in a distal-proximal fashion, it is possible that the ubiquitous finding of underestimation of finger length, it is the result (at least in part) of an anchor effect. Perhaps, future work on the body model should mix the location of the anchor so that some trials start close to the body, and others further away from the body.

In summary, the present study investigated three different representations of the hand: the body model, body schema, and body image. We found that while all three of these representations were distorted, the magnitude of distortion was different between all representations. This indicates that there are at least three independent representations of the hand. We found positive relationships between the body model and body schema for the participants dominant (right) hand. Both representations share functional similarities (help guide movement), which is a possible explanation as to why these relationships exist. Lastly, we found a main effect of anchor. Participants in the proximal-anchor group had smaller estimates of finger and hand length. This suggests that the starting position biases body representations. Overall, the results from this study suggest that self-initiated movement relies on two independent but related representations of the body, the body model and the body schema.

Author's statement: All data used in the manuscript are available upon request from the corresponding author. This study was not pre-registered.

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Appendix 5: Older adults

Overview

In this study, I recruited children (age 8-16yrs) and young (age 18-26yrs) and older adult (age 50+yrs) participants. To examine how gaining affects the body model of the hand, I asked participants to complete a modified version of the localization task, as this was a follow-up study to Coelho & Gonzalez, 2021 (appendix 1).

Results

Repeated measures ANOVA:

We found a main effect of group [$F(1,65)=8.7$, $p<.01$, partial e= .21]. Follow up pair-wise comparisons revealed that the children were significantly different from both the young ($p<.01$) and older adults ($p<.01$). We also found a group x hand interaction. Children overestimated the left hand more than the right, young adults showed the opposite pattern, and seniors showed that both hands were perceived the same. Finger length results were similar. Children had different hand maps than both young ($p<.01$) and older adults ($p<.01$).

Correlations:

In addition, we found that the relationship between age and hand size continued into adulthood, but only for hand width (hand width: $r^2=-.31$, $p=.03$; finger length: $r^2=-.07$ $p=.64$).

Appendix 6: Piano players

Overview

To test if long-term training without a tool affected body model representations of the hand, I recruited expert piano players and asked them to complete the localization task. We compared their results to healthy controls. Playing the piano necessitates an accurate position sense of each of the fingers. Thus perhaps, years of training, reduces body model distortions.

Results

Repeated measures ANOVA

Great span: There was a main effect of hand [$F(1,66)=9.24$, $p=.001$, e=.123]. Participants overestimated right hand (5.1%±2.3) compared to the left hand (-1.2%±1.5). I also found a main effect of group [$F(1,66)=5.2$, $p=.026$, e=.073]. Piano players estimated the great span more accurately (-1.82%±2.84) compared to the controls (5.7%±1.7). Lastly, there was a main effect of sex [$F(1,66)=5$, $p=.03$, e=.07]; males (-1.75%±2.31) were more accurate than females (5.69%±2.39).

Finger length: There was a main effect of sex [$F(1,66)=5.7$, $p=.01$, e=.08]. Males (-23.7%±2.1) underestimated more than females (-16.5%±2.16).

T-tests:

The piano players (both sexes) had accurate estimations of hand width (p's>.34). They underestimated finger length on both right [t((18)=-5.9, p<.01] and the left [t(18)=-6.73, p<.01].

Appendix 7: Kinesthetic feedback and the body model

Overview: To examine if kinesthetic feedback mediates body model distortions, I designed a modified version of the localization task. In this task, undergraduate participants were required to tap to the beat of a metronome prior to each estimation. The tapping allows for kinesthetic feedback prior to each trial. In addition, sensory adaptation would be controlled in this method. We compared these results to a group of participants who listened to the metronome prior to each estimation (but did not tap).

Results:

Repeated measures ANOVA:

Great span*:* There was a main effect of hand [$F(1,63)=8.3$, $p=.006$, partial $e^2=.12$] where participants estimated their right hand (11.7%±2.78) as being significantly larger than their left hand(6.6%±2.15). There was also a main effect of group [$F(1,63)=4.52$, $p=.04$, partial $e^2=.07$]. Participants in the tapping group made significantly more accurate estimates of the great span (5.9%±2.16) compared to the control group (12.4%±2.78).

Finger Length*:* The participants in the tapping group (-23.9±2.92) underestimated finger length significantly more than those in the control group (-15.99±2.52)[$F(1,63)=5.44$, $p=.023$, partial $e^2=.08$].

T-tests:

Kinesthetic feedback participants

Great span: The participants in the tapping group significantly overestimated the great span of their right hand [$t(32)= 3.73$, $p<.001$, $d^2=.65$; occluded hand condition= 205.3±5.33, non-occluded hand condition= 188.93±2.52]. The left hand was accurately estimated.

Finger length: The participants in this group significantly underestimated finger length for both the right [$t(32)=-7.35$, $p<.001$, $d^2=-1.3$; occluded hand condition= 40.34±2, non-occluded hand condition= 52.75±0.82] and the left-hands[$t(32)=-9.18$, $d^2=-1.6$; occluded hand condition= 40.66±1.58, non-occluded hand condition=53.4±.95].

Control participants

Great span: The participants in the control group overestimated the great span of both the right [$t(31)=4.5$, $p<.001$, $d^{2=}.9$; occluded hand condition=204.8±6.03, non-occluded hand condition= 179.3±3.42] and the left hands[$t(31)=4.33$, $p<.001$, $d^2=.77$; occluded hand condition= 205.23±5.3, non-occluded hand condition=186.95±3.9].

Finger length: Control group participants significantly underestimated the lengths of their fingers on both the right [$t(31)=-5.66$, $p<.001$, $d^2=-1.0$; occluded hand condition= 45.19±1.6, non-occluded hand condition=54.18±.066] and the left hands[$t(31)=-7.3$, $p<.001$, $d^2=-1.3$; occluded hand condition= 45.76±1.22, non-occluded hand condition= 54.25±0.8].