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ORIGINAL ARTICLE

A kinematic examination of hand perception

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Abstract Previous research has found that the perception of our hands is inaccurate. This distorted representation has several constant characteristics including an overestimation of hand width and an underestimation of finger length. In this study, we further investigate this phenomenon by exploring the boundaries of hand representation. Participants placed one hand underneath a table top so it was occluded from view. Using their free hand, participants were instructed to point to the location where they believed the tips and bases of each of their fingers were. These ten landmarks were recorded using a motion capture system. One group of participants pointed to the landmarks in a random order (as done in previous studies) while another group pointed to them in a systematic fashion (from the tip of the thumb sequentially through to the pinky). Furthermore, to explore if having a frame of reference facilitates hand perception, some participants initiated each of their estimations directly from the previous landmark while others initiated them from a home spot located outside the span of the hand. Results showed that the participants who pointed in the systematic order made numerous accurate judgments of hand size and were overall more precise than participants who pointed in a random order. Including a frame of reference however, had no effect on the judgments. The results also showed asymmetries in hand perception. These findings are discussed in relation to different possible internal body representations and hemispheric asymmetries in body perception.

Introduction

Body representation (or body schema) is defined as a sensorimotor representation of the body that is constantly updated and functions to register where the body is in space and how the individual parts of the body come together to form a whole body image (Dijkerman & de Haan, 2007; Haggard, Kitadono, Press, & Taylor-Clarke 2006; Keizer et al., 2013). Body representation is important because we often use our bodies as a metric to guide our actions. For example, estimating whether an object is within arm's reach or determining whether the body can fit through a small space are impossible without an accurate representation of arm length or shoulder width (Keizer et al., 2013; Warren & Whang, 1987). Some studies have shown that when participants are asked to estimate the lengths of their own body parts (e.g., arm) these estimates are accurate (Bolognini, Casanova, Maravita, & Vallar, 2012; Guardia et al., 2010; Sposito, Bolognini, Vallar, & Maravita, 2012; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010). Furthermore, the representation of body length has been shown to be more accurate than the representation of extrapersonal objects. For example, in a task where participants estimate the length of their own forearms or a similarly sized cylindrical model, participants are better at estimating their limbs compared to the cylinder (Sposito et al., 2010).

The hand is our main source of contact with the environment (Napier, 1980). Surprisingly, the internal representation of our hands has been shown to be distorted (Longo & Haggard, 2010). In that study, participants were asked to judge the location of the knuckles and tips of each of their fingers while their hands rested underneath a tabletop so participants had no vision of their hand. The results showed a consistently distorted perception of the hand: an overestimation of hand width (measured as the

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distance between knuckle pairings) and an underestimation of finger length (measured as the distance between knuckle and fingertip). The authors concluded that such distortion is evidence of a body model that is not cognisant of its own metric properties.

The result of misperceived hand size is puzzling for at least two reasons. First, other studies have shown accurate estimates of body parts (Sposito et al., 2012) or body size (Warren & Whang, 1987; Wing & Fraser, 1983); and second, one would expect more accurate estimates of body parts that are in constant interaction with the world. After all, it is through our hands that we grasp, manipulate, and identify objects hundreds of times a day. If the internal stored model of our own hands is inaccurate, how are we able to make accurate and consistent grasping movements?

One possibility is that the visuomotor system utilizes a holistic image of the hand rather than isolated landmarks when reaching to grasp an object. Research into the perception of human faces, for example, has shown that we do not process faces as a group of individual facial features but as an integrated perceptual whole (see (Richler & Gauthier, 2014) for a review). In the Longo and Haggard (2010) study, participants were asked to point to the ten locations on their hand in a random order (e.g., from the tip of the index finger, to the base of the ring finger, to the base of the thumb, etc.). Participants were also instructed to return to a home spot (outside the span of the hand) between each trial. It is possible that this "fragmented" methodology prevented participants from using a holistic representation of their hand yielding the much distorted map. In this study, we introduce a systematic methodology and a reference point to increase the likelihood that participants would use a holistic representation when making estimates of hand size.

Participants were asked to point to the ten landmarks of their hands in either the random fashion (random order; e.g., Longo & Haggard, 2010), or in an ordered configuration (i.e., systematic order). Participants with the systematic order pointed at their fingertips and knuckles (the metacarpophalangeal joints) in sequence (i.e., starting at the thumb [digit 1] and continuing sequentially until they pointed to the pinky finger [digit 5]). Because previous research has shown more accurate body perception when given a single joint as a reference point (Neri, 2009) within each order, half of the participants pointed in a continuous pattern. That is, participants did not return to a home spot, instead they used their previous point on their hand as a landmark for their next estimation. The other half of the participants pointed in an interrupted sequence in which they were required to return to a home spot (outside the span of the hand) after each trial (Longo & Haggard, 2010). We hypothesized more accurate hand maps in the systematic group and when participants pointed using a continuous pattern.

Methods

Participants

Forty-eight university students (37 females) participated in exchange for course credit. Handedness was evaluated using modified Edinburgh (Oldfield, 1971) and Waterloo (Brown, Roy, Rohr, & Bryden, 2006) handedness questionnaires. Forty-six participants identified as right-handed and two as left-handed. All participants gave written consent prior to participating.

Materials

An Optotrak Certus sensor (Northern Digital, Waterloo, ON, Canada) recorded the position of an infrared emitting diode that was attached to the end of a stylus. The location of the diode was recorded for 1 s at 200 Hz for each trial.

Procedure

Participants sat in front of a Plexiglas desk (86.5 × 41.0 cm) with a wooden shelf placed 12 cm below the Plexiglas. Participants were asked to place their right or left hand (counterbalanced among participants) palm up underneath the Plexiglas and in contact with it (see Fig. 1). The forearm was supported by a thin pillow. Initially, half of the participants placed their hand palm down against the wooden shelf (10 mm below the Plexiglas; see Fig. 1). However, our primary analysis found that the results did not depend on hand orientation so we continued testing only in the palm up condition. After the participant was comfortable, a black tablecloth was placed over the Plexiglas, which occluded vision of the hand. Trials without vision of the hand are subsequently referred to as the occluded hand trials. Participants kept their target hands in a fixed position. They were then instructed to point with the stylus in their free hands to where they believed the tip (the edge of their finger nail) and the base (the knuckle) of each of their digits were. The tablecloth was removed after the estimation trials and participants were instructed to point to their visible landmarks. These were referred to as the non-occluded hand trials.

The experimental design was a 2 × 2 × 2 mixed design. The factors were Order (systematic, random), and Pattern (continuous, interrupted), and there were 12 participants in each of the four groups (systematic-continuous, systematic-interrupted, random-continuous, random-interrupted). Participants with the systematic order pointed at their fingertips in sequence, from digit 1 (thumb) to digit 5, then to their bases with the same order (half of the participants pointed to their fingertips first and the other half to

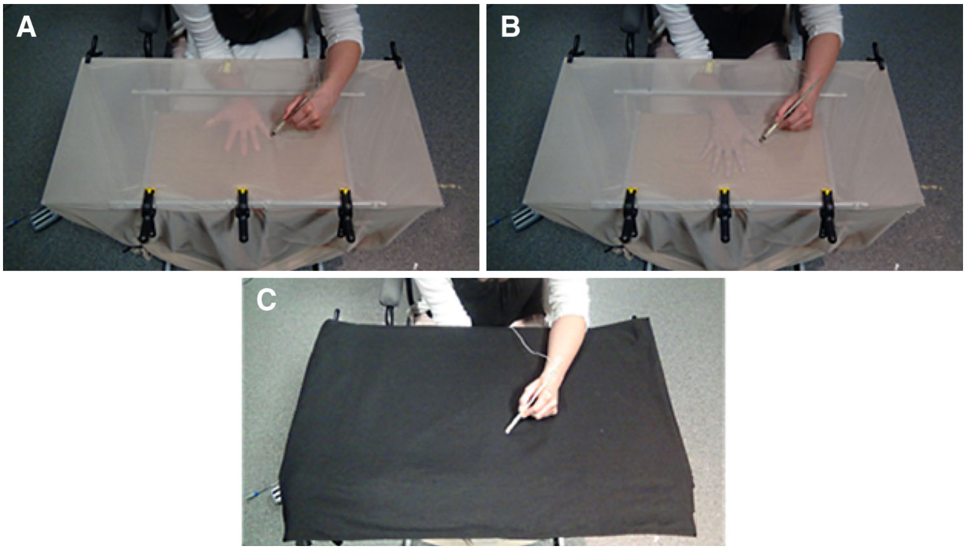

Fig. 1 Schematic of the experimental setup. **a** Demonstrates the Palm Up condition. **b** Demonstrates the Palm Down condition. **c** Demonstrates the without vision part of the experiment

their bases). Participants with the random order followed Longo and Haggard's design, in which they randomly pointed to the ten locations on their hand. Participants with the continuous pattern pointed to a target location and then moved to the next target location. Participants with the interrupted pattern returned to a "home spot" that was situated directly above the participant's fixed forearm [as per Longo & Haggard, 2010]. In all cases the experimenter verbally instructed the participant where to point on each trial.

Analyses

Each participant completed 200 trials. There were 50 occluded hand trials (five to each of the ten locations on the hand) and 50 non-occluded hand trials and this was repeated for each hand. We conducted two analyses on the data. The first (occluded vs. non-occluded) was conducted to investigate whether the perceived hand (width and finger length) was different from the real one. A series of paired-samples *t* tests were conducted on the raw values (expressed in mm) of the occluded versus non-occluded hand dimensions (Longo & Haggard, 2010).

The second analysis (effects of Order, Pattern, and Hand) a 2 × 2 × 2 mixed design ANOVA included Order (systematic, random), Pattern (continuous, interrupted), and Hand (left, right) as factors. Order and Pattern were between participants factors and Hand was the within participant measure. For the analyses we normalized the data by expressing the estimated values as a percentage of the real-hand values [(occluded hand/non-occluded hand) × 100]. For instance, if the perceived distance between the tip of digits 1 and 2 was 120 mm and the real distance was 111 mm, the normalized value would be 109 %, a 9 % overestimation. We made this transformation to account for individual differences in hand size.[1]

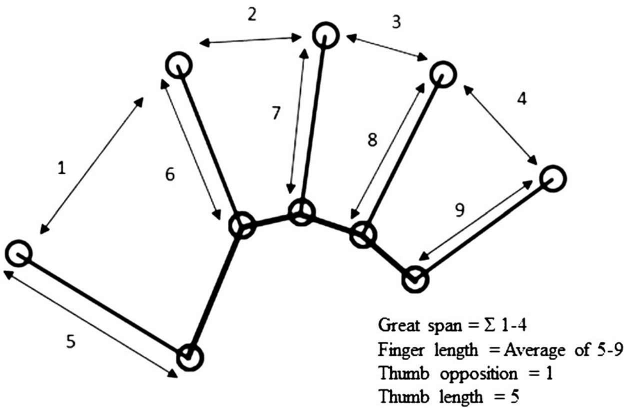

Fig. 2 Representation of the measures used to analyze hand size

The two analyses were repeated for four dependent variables: hand width, finger length, thumb length, and opposition. 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 (Fig. 2). Finger length was calculated by averaging the distance from the tip to the base of each digit for all five digits, including the thumb. Two measures were used to investigate the perception of the thumb: length, the distance from the tip to the base of digit 1; and opposition, the distance between digits 1 and 2. We introduced the great span and opposition measures as they are of particular relevance with respect to power (using the whole hand) and pincer grasps (using the

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[1] We also conducted a repeated measures ANOVA using the standard deviation of the five repetitions to each landmark to assess if hand differences were related to the hand employed to point to the landmarks. No significant differences were found between the right and left hands.

index finger and thumb). Means and standard error of the mean are reported below.

Data processing

All trials were visually inspected and extreme outliers (i.e., mistakes; when an estimate of a specific landmark was 5 or more centimeters away from its non-occluded location) were excluded (<1 % of the trials).

Results

Analyses included all participants but they were also conducted without the two left-handed individuals to ensure that their inclusion did not have an effect on the results. Results from every measure were similar with and without the left handers so we opted to include them.

Hand width

Occluded vs non-occluded hand

Participants with the systematic order accurately estimated the width of their hands as the non-occluded and occluded values were not significantly different from each other, $p > .1$. In the random order, however, there was a significant overestimation of the left and right hands [left hand estimated 210.65 ± 6.32, left hand non-occluded 193.51 ± 4.22; $t(23) = -2.58$, $p = .02$, $d = .65$, right hand occluded 211.23 ± 8.11, right hand non-occluded 185.36 ± 4.13; $t(23) = -2.58$, $p = .02$, $t(23) = -2.95$, $p < .01$, $d = .81$].

Effects of order, pattern, and hand

There was a main effect of order, $F(1,44) = 10.7$, $p < .01$, $\eta^2 = .196$. Participants with the random order overestimated hand width more than the participants with the systematic order (12.4 ± 3.3 % versus −2.98 ± 3.3 %, respectively). An effect of hand approached significance $F(1,44) = 3$, $p = .09$, $\eta^2 = .064$, where the right hand (6.9 ± 2.9 %) was overestimated more than the left hand (2.5 ± 2.4 %). There were no other significant main effects or interactions. F's $< .124$, p's $> .14$, $\eta^2 < .05$.

Finger length

Occluded vs non-occluded hand

When participants pointed using the systematic order, finger lengths for the right hand were accurate ($p > .1$), but estimates for the left hand were significantly underestimated, [left hand occluded 48.9 ± 2.1, left hand non-occluded 56.2 ± .9, $t(23) = 3.9$, $p < .01$, $d = .94$]. Participants in the random order, however, underestimated the length of their fingers in both hands, [left hand occluded 46.8 ± 1.7, left hand non-occluded 56.7 ± 2.2, $t(23) = 3.3$, $p < .01$ $d = .81$: right hand occluded 44.6 ± 1.3, right hand non-occluded 54.2 ± .7, $t(23) = 7.3$, $p < .01$, $d = 1.8$].

Effects of order, pattern, and hand

There was a main effect of order, $F(1,44) = 6.4$, $p = .02$, $\eta^2 = .127$]. Participants assigned to the random order underestimated the finger length (−16.6 ± 2.6 %) more than those assigned in the systematic order (−7.3 ± 2.6 %). The order by hand interaction was also significant [$F(1,44) = 4.7$, $p = .04$, partial $\eta^2 = .135$]. Follow up t tests showed that in the systematic group, finger length on the left hand was underestimated when compared to the right $t(23) = -2.4$, $p = .02$. The same was not the case in the random group $t(23) = .5$, $p = .6$, which underestimated finger length of their hands to the same extent (see Fig. 3). There were no other main effects or interactions, F's < 2.3, p's $> .137$, $\eta^2 < .05$.

Thumb length

Occluded vs non-occluded hand

No main effects were found.

Effects of order, pattern, and hand

There was a significant main effect of hand, $F(1,44) = 4.2$, $p = .05$, $\eta^2 = .087$, where length of the left thumb (−8.9 ± 4.1 %) was underestimated more than of the right thumb (1.6 ± 4.1 %). There were no other main effects or interactions, F's $< .1.4$, p's $> .24$, $\eta^2 < .03$.

Thumb opposition

Occluded vs non-occluded hand

Opposition in both hands and both orders was underestimated [systematic order left hand: $t(23) = -5.7$, $p < .01$, $d = 1.42$: right hand: $t(23) = -8$, $p < .01$, $d = 2.1$; random order left hand: $t(23) = -2.4$, $p = .02$, $d = .62$; right hand: $t(23) = -2.9$, $p < .01$, $d = .57$].

Effects of order, pattern, and hand

There was a significant main effect of order, $F(1,44) = 5.6$, $p = .02$, $\eta^2 = .113$. Participants assigned to the systematic order underestimated (−23.9 ± 3.6 %) the distance between digits 1 and 2 more than those

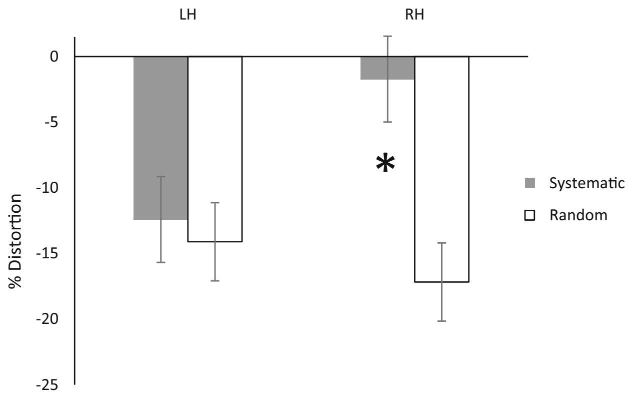

Fig. 3 Finger length order × hand interaction. Systematic order is in *gray*, and the random order is depicted in *white*. There was a significant difference between the left and right hand in the systematic order; the left hand was underestimated significantly more than the right. The random group, however, underestimated both hands to the same extent

participants assigned to the random order (−11.8 ± 3.6 %). No other main effects or interactions were found, F's $< .6$, p's $> .45$, $\eta^2 < .01$.

Discussion

In this study, participants placed one hand underneath a tabletop and pointed at the location where they thought their knuckles and fingertips were located. One group of participants pointed at these landmarks in a systematic fashion (Digit 1, 2, 3…), while the other group indicated the location of the landmarks in a random order. Half of the participants pointed in a continuous pattern (moved directly from one landmark to the next), the other half pointed in an interrupted pattern, returning the stylus to a home spot between trials. Hand maps were constructed from coordinates acquired with a 3D motion capture system. The effects of order (systematic, random), pattern (continuous, interrupted), and hand (left, right) were investigated for hand span, digit length, thumb length, and thumb opposition. The results showed several significant differences for order and hand, but not for pattern (see Table 1). These results are discussed below.

Longo and Haggard (2010) reported a distorted body model of the hands. They described the distortion as an overestimation of hand width and an underestimation of finger length. The results from the random-interrupted group replicate those found by Longo and Haggard; participants overestimated the width of their hands but underestimated the length of their fingers (see Table 1). When participants pointed to the landmarks of their hands in a systematic order, however, hand perception was less distorted. Sequential pointing allowed for many accurate estimations of hand size, particularly in terms of width. Surprisingly, there were no differences between those participants who completed the task in a continuous pattern and those who used an interrupted pattern. These results suggest that the more accurate estimates made by participants in the systematic order was not because they used a reference point within the hand to make their estimates, otherwise those in the continuous pattern would have been more accurate. We offer three (non-mutually exclusive) possible explanations to account for the greater accuracy found in the systematic order.

First, it has been argued that body representation utilizes a stored body model, as well as a model that uses online sensory information for constant updating (de Vignemont, Ehrsson, & Haggard, 2005). It is possible that participants in the systematic order had access to *both* representations; the stored body model plus the continuously updating one. In this case, the constantly updating visual information which provided an anatomical reference of adjacent landmarks could be combined with the stored model to update the representation of the hand. In contrast, participants in the random order would be less likely to base their estimates off of the constantly updating visual information, as this information had little value given that the order of estimations was not sequential (it is harder to form a holistic representation).

Second, a "neighbouring effect" could also explain the more accurate estimates made by the systematic order. A recent study examining toe representation found more accurate identification between neighboring toes (Cicmil, Meyer, & Stein, 2015). For example, identification of digit 2 (toe 2) was more accurate following stimulation of digit 1 but not digit 4. This result suggests that in a body localization task, moving sequentially through body parts (as it was done in the systematic order) could enhance their representation.

Third, it is also possible that participants who completed the task in the systematic order had access to a more "holistic" representation of their hand. Research has shown that when learning about spatial layouts, two independent representations can be formed (Saulton, Dodds, Bulthoff, & de la Rosa, 2015; Shelton & McNamara, 2004). One of these representations is analytical and relies on the relationship *between* individual landmarks (i.e., distance), while the other relies on a holistic image accessed by memory. Importantly, research has found that human faces and body parts are processed holistically and not only analytically (Farah, Wilson, Drain, & Tanaka, 1998; Reed, Stone, Bozova, & Tanaka, 2003; Seitz, 2002; Tanaka & Farah, 1993). So it is possible that the group that pointed to the landmarks systematically was accessing a holistic representation of the hand that facilitated its representation. The random order, however, would still have

Table 1 List of distortion seen by order and pattern. A ↑ indicates a significant overestimation, a ↓ indicates a significant underestimation, and a – indicates no change

Systematic order	Continuous		Interrupted		Random order	Continuous		Interrupted	
	LH	RH	LH	RH		LH	RH	LH	RH
Width	–	–	–	–	Width	–	↑	↑	↑
Finger length	↓	–	↓	–	Finger length	↓	↓	↓	↓
Thumb length	–	–	–	–	Thumb length	–	–	–	–
Thumb opposition	↓	↓	↓	↓	Thumb opposition	–	↓	↓	–

access to a holistic representation, but it would be less relevant. In other words, the adjacent finger tips and knuckles share a functional relationship, while nonadjacent landmarks (such as the tip of the index finger and the knuckle of the ring finger) do not share this functionality. This possibility offers an explanation as to how we are able to effectively grasp objects even with a distorted body model of the hand; when we grasp an object we are likely accessing a holistic representation of the hand and not relying on where individual landmarks are located in space. Previous research has suggested that when grasping the movements of each of the digits are programmed and controlled independently (Smeets & Brenner, 2001). The current findings would suggest, however, that a holistic representation of the hand would yield more accurate grasping movements. This speculation warrants further research.

Another finding of the current investigation is that hand perception is different across hands. We found that when compared to their left hand, participants overestimated the width of their right hands to a greater extent. In addition, underestimation of finger length was greater for the left hand than for the right hand. In fact, when estimating the right hand, participants in the systematic order were accurate. This result could be because we have a more accurate holistic representation of the right hand, or because we believe this hand to be more capable. Previous research has also found asymmetries in hand perception (Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009). In that study participants were asked to indicate on a tape measure the width and length of their left and right hands. The results showed that the left hand was underestimated when compared to the right hand. The same study also found that participants perceived their right hands as being capable of grasping larger objects than their left hands (Linkenauger et al., 2009). It is possible that because right-handers prefer to use their dominant hands for a multitude of actions including grasping, object manipulation, and tool use (Corey, Hurley, & Foundas, 2001; Gonzalez & Goodale, 2009; Janssen & Steenbergen, 2011; Porac, Coren, Steiger, & Duncan, 1980; Steenhuis, Bryden, Schwartz, & Lawson, 1990; Stone & Gonzalez, 2014) they may perceive their right hand as being more capable of performing actions. This, in turn, would lead to a smaller representation of the left hand as it affords fewer possibilities than the right hand. Current studies in the lab aim at addressing this possibility.

In their paper, Longo and Haggard (2010) argue that the misrepresentation of the hands shares similar characteristics with that of the homunculus such as an accentuation of the medio-lateral over the proximo-distal axis. A larger representation of the right hand could also be explained in terms of homuncular representation. It has been shown that in right-handers the cortical somatosensory representation of the hand is larger for the right than for the left hand (Buchner, Kauert, & Radermacher, 1995; Soros et al., 1999). If the homunculus provides a mental map of the hand and the somatosensory representation of the right hand is larger than of the left, this would explain why we found hand differences. Future studies are needed to characterize the conditions in which such asymmetries in hand representation arise.

One last finding worth noting is regarding the estimates of thumb length and opposition. The thumb was the only digit for which length was estimated accurately in *every* condition and in both hands suggesting a more conserved representation of this digit. It has been argued that the evolution of the thumb allowed for upright posture, tool making, and tool use, all of which led to an enlarged brain (Napier, 1980). Mapping studies of the primary somatosensory cortex (S1) using electrophysiological methods showed that the area for the thumb is larger than the area representing the other digits (Penfield & Boldrey, 1937; Sutherling, Levesque, & Baumgartner, 1992). A recent neuroimaging study used 7T fMRI to precisely map the cortical representation of single digits in human S1 (Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014). For the study, participants laid inside the scanner while each one of their fingers was stimulated by touch. The results showed that the thumb has a much larger cortical representation than the representation of the other fingers. The authors discuss that because such magnification has not been shown in nonhuman primates, the enlargement is likely reflective of the increased tactile function in humans due to thumb opposition and precision grip. Perhaps because of its evolutionary relevance and

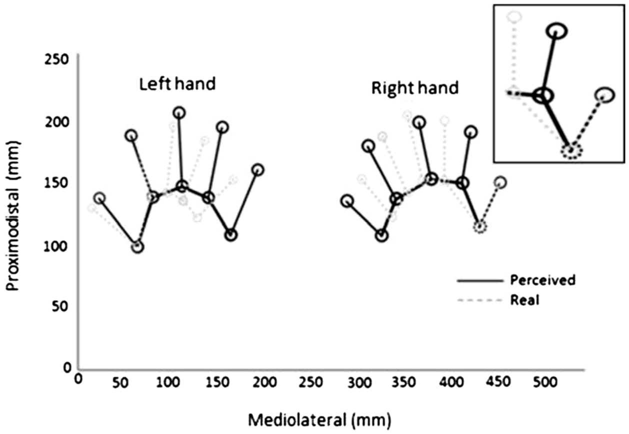

Fig. 4 Representation of the distortion seen between both hands. The close up to the right focuses on how the thumb is situated as "Side on" compared to the rest of the digits which are located as "Front on". The representation of the right hand was overall larger than the representation of the left hand

greater somatosensory cortical representation, the perceptual estimates of the thumb were not underestimated as it was the case for the other digits. With respect to thumb opposition, our results showed an underestimation of the distance between thumb and index finger for both hands in both orders. Previous research has shown that the perception of the thumb is that of being nearer to the index finger (Margolis & Longo, 2015), which aligns with the current findings. Margolis and Longo argue that this is caused by the thumb being orientated "side-on" (when all the fingers are spread out) whereas, the rest of the fingers are orientated as "front-on." So it is possible that participants tried to align the thumb more like a finger, and thus its representation would be of being closer to the index finger (see Fig. 4). Another possibility is that the representation of the distance between thumb and index finger follows too, the somatosensory map of S1. Puzzling, the distance between adjacent digits has been shown to be only different between dyads D1-D2 and D4-D5 (Martuzzi et al., 2014). In other words, somatotopically, the distance between thumb and index finger is not different from the distance between index finger and middle finger or middle finger and ring finger. This might explain why we found the distance between D1 and D2 to be underestimated.

In conclusion, this study confirms the notion that the perception of the human hand is inaccurate, but demonstrates that when pointing to each finger in succession, the magnitude of the distortion decreases substantially. In the case of the width of the hands, the distortion was eliminated completely. The study also found that the right hand has a larger representation than the left, and that the only digit not underestimated was the thumb which enjoyed accurate representation. Taken together, these results suggest that the perception of our hand is dynamic, and that it seems to resemble the somatotopic representation in S1.

Compliance with ethical standards

Funding This study was funded by a discovery grant awarded to Claudia LR Gonzalez from the Natural Sciences and Engineering Research Council of Canada.

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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