Sex Differences in Perceptual Hand Maps: A Meta-Analysis

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Abstract

A large body of research has suggested that localisation of the hand in external space relies on distorted representations of the hand. We developed a paradigm for measuring implicit perceptual maps of the hand (Longo & Haggard, 2010, *Proc Natl Acad Sci USA, 107*, 11727–11732), which show systematic deviation from actual hand shape, including overestimation of hand width and underestimation of finger length. Recently, Coelho and Gonzalez (in press, *Psychol Res*) reported sex differences in these perceptual hand maps, with women showing greater overestimation of hand width, but less underestimation of finger length than men. In the current study, I conducted a meta-analysis of 19 experiments using this paradigm by myself and my colleagues. The results replicated the sex differences reported by Coelho and Gonzalez. Importantly, however, these sex differences were not apparent when actual hand size was included as a covariate in analyses, suggesting that they may, at least in part, be due to women having smaller hands on average than men.

Distortions and misperceptions of the body are a conspicuous part of a number of serious neurological and psychiatric disorders, which have historically attracted widespread interest due to their dramatic contrast with the seeming immediacy of our ordinary experience of our body (Longo, Azañón, & Haggard, 2010). Within neurology, examples include phantom experiences of amputated limbs (Henderson & Smyth, 1948; Melzack, 1990; Ramachandran & Hirstein, 1998); anosognosia, in which patients deny serious motor impairments (Berti et al., 2005; Fotopoulou et al., 2008; Moro et al., 2016); somatoparaphrenia, in which patients insist that one of their limbs belongs to somebody else (Fotopoulou et al., 2011; Romano, Gandola, Bottini, & Maravita, 2014; Vallar & Ronchi, 2009), or even becomes evil (Critchley, 1974); asomatagnosia, in which patients claim that the left side of their body has vanished (Critchley, 1953); and autoscopic illusions and out-of-body experiences, in which the experienced and actual locations of the body become dissociated (Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Metzinger, 2009; Brugger, Regard, & Landis, 1997). Within psychiatry, examples include the strange body image disturbances seen in eating disorders in which emaciated patients insist that they are fat (Bruch, 1978; Gaudio & Quattrocchi, 2012; Smolek & Thompson, 2009); body dysmorphic disorder, in which patients become fixated on the idea that some part of their body is horribly ugly (Phillips, 2005; Phillips, Didie, Feusner, & Wilhelm, 2008; Veale & Bewley, 2015); and body integrity identity disorder, in which physically intact individuals wish to amputate an apparently healthy part of their body (Brugger, Lenggenhager, & Giummarra, 2013; Brugger, Christen, Jellestad, & Hänggi, 2016; First, 2005; McGeoch et al., 2011).

This is an incredible list, and it is extremely difficult to identify with or imagine these conditions must be like. The apparent gap between these experiences and our ordinary experience of our body can give the impression that distortions of body representation are limited to disease and brain damage. A substantial body of research, however, has suggested that distorted body representations are in fact an ordinary, even ubiquitous, part of healthy cognitive life (Longo, 2017b). For example, studies of body-size estimation tasks developed for measuring distorted body image in eating disorders have also found substantial overestimation of body width in healthy populations, including visual comparison (Gila, Castro, Toro, & Salamero, 2004; Reitman & Cleveland, 1964; Shontz, 1969), the moving caliper method (Dolan, Birtchnell, & Lacey, 1987; Halmi, Goldberg, & Cunningham, 1977; Hundleby & Bourgouin, 1993; Pierloot & Houben, 1978), the adjustable light-beam apparatus (Dolce, Thompson, Register, & Spana, 1987; Pasman & Thompson, 1988; Thompson & Spana, 1988; Thompson & Thompson, 1986), and the image marking procedure (Bizerra & Gama, 2017; Fonseca, Thurm, Vecchi, & Gama, 2014; Gorham & Hundleby, 1988; Meermann, 1983). Similar distortions have also been observed in tasks involving manipulating images of one's own face (D'Amour & Harris, 2017), judging the relative location of body landmarks (Fuentes, Longo, & Haggard, 2013; Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013; Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013), drawings of one's face (Bianchi, Savardi, & Bertamini, 2008; Carbon & Wirth, 2014), judgments of arm length (Linkenauger, Witt, Bakdash, Stefanucci, & Proffitt, 2009), judgments of the relative lengths of body parts (Linkenauger et al., 2015, 2017; Sadibolova, Ferrè, Linkenauger, & Longo, 2019), and judgments of the internal configuration of landmarks within the hand (Longo, 2015c; Margolis & Longo, 2015; Ambroziak, Tamè, & Longo, 2018). Other studies have reported systematic distortions underlying somatosensory processing, for example in tactile localisation (Culver, 1970; Mancini, Longo, Iannetti, & Haggard, 2011; Medina, Tamè, & Longo, 2018; Sadibolova, Tamè, Walsh, & Longo, 2018; Steenbergen et al., 2012; Trojan et al., 2006) and tactile distance perception (e.g., Cholewiak, 1999; Fiori & Longo, 2018; Green, 1982; Longo & Haggard, 2011; Longo, Ghosh, & Yahya, 2015; Longo & Golubova, 2017; Taylor-Clarke, Jacobsen, & Haggard, 2004). While the link between these distortions in healthy populations and those found in clinical disorders remains unknown, this body of research does demonstrate that distorted representations of the body are a ubiquitous part of ordinary mental life.

Another method that has been widely used to investigate the mental representation of body size and shape is the 'psychomorphometric' paradigm developed by Longo and Haggard (2010), shown in Figure 1. Participants sit with their hand resting on a table underneath an occluding board, and use a long baton to indicate the perceived location of the tip and knuckle of each finger. Responses are captured by an overhead camera for offline coding. By comparing the relative location of judgments of each landmark, perceptual maps of hand size and shape can be constructed and compared to actual hand structure. These maps showed large and highly stereotyped distortions, specifically: (1) overall overestimation of hand width, (2) overall underestimation of finger length, and (3) a radial-ulnar gradient with finger length underestimation increasing from the thumb to the little finger. This basic pattern has been found in numerous subsequent studies, both from my lab (e.g., Longo, 2014, 2015a, 2017a, 2018; Longo, Long, & Haggard, 2012; Longo, Mattioni, & Ganea, 2015; Ganea & Longo, 2017; Tamè, Bumpus, Linkenauger, & Longo, 2017) and other labs (e.g., Cocchini, Galligan, Mora, & Kuhn, 2018; Coelho & Gonzalez, 2017; Coelho, Zaninelli, & Gonzalez, 2017; Coelho et al., 2019; Ferrè, Vagnoni, & Haggard, 2013; Lopez, Schreyer, Preuss, & Mast, 2012; Medina & Duckett, 2017; Peviani & Bottini, 2018; Saulton, Dodds, Bülthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016; Saulton, Bülthoff, & de la Rosa, 2017; Stone, Keizer, & Dijkerman, 2018). In contrast, when participants judge whether hand images are fatter or thinner than their own hand, they show no systematic biases (Longo, 2015d; Longo & Haggard, 2010, 2012b). This dissociation suggests that position sense relies on an implicit body representation, which is distinct from the conscious body image (Azañón et al., 2016; Longo & Haggard, 2010; Longo, 2015b).

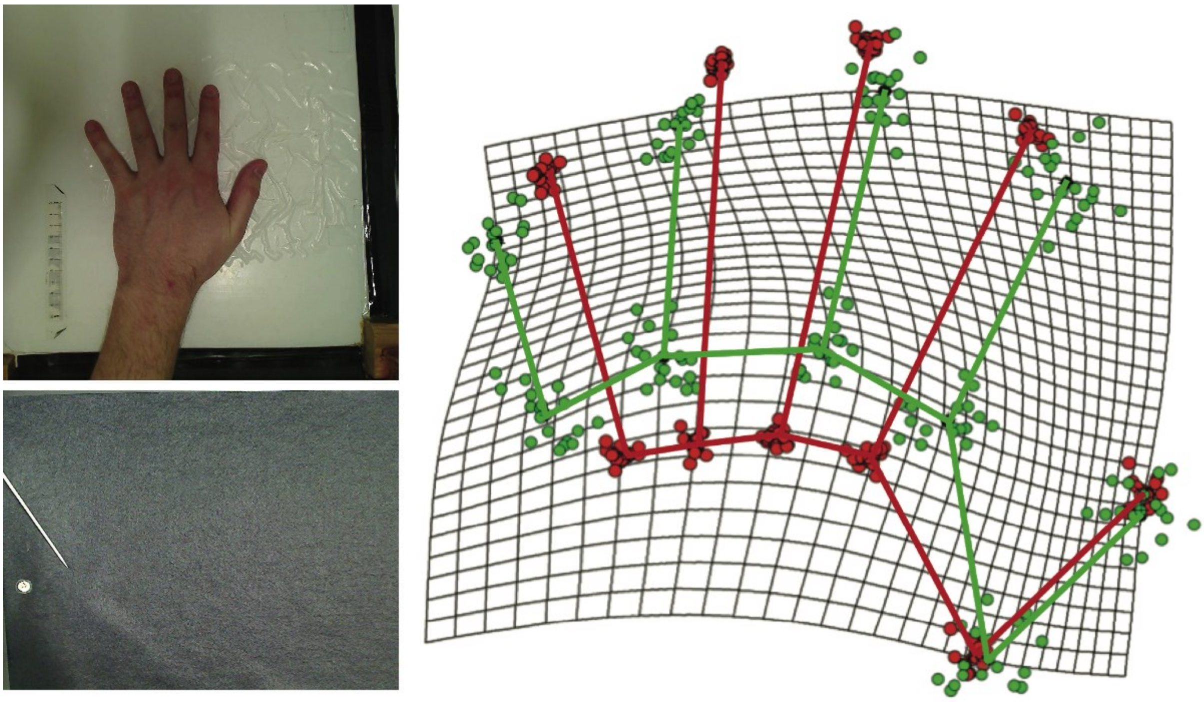

Figure 1: The 'psychomorphometic' paradigm for measuring perceptual hand maps (Longo & Haggard, 2010). The participant rests their hand on a table (top left). Their hand is occluded and they use a long baton to indicate the perceived location of the tip and knuckle of each finger (bottom left). By comparing the relative locations of judgments, implicit maps of hand structure can be constructed and compared with actual hand size and shape. The right panel shows perceptual maps (green) from 18 participants in Experiment 1 of Longo and Haggard (2010), placed into best-fitting alignment with actual hand shape (red), using Procrustes alignment which translates, scales, and rotates the maps to superimpose the shapes as closely as possible (Bookstein, 1991). The green and red lines connect the tip and knuckle of each finger and the knuckles of adjacent fingers, in order to give an overall sense of hand shape. The warped grid shows how a perfectly square grid superimposed on actual hand shape would have to be stretched to transform actual hand shape in the shape of perceptual maps.

Recently, Coelho and Gonzalez (in press) reported sex differences in these implicit hand maps. Women in their study showed greater overestimation of hand width than did men, but less underestimation of finger length. While clear underestimation of finger length was apparent for both men and women, only women showed significant overestimation of hand width. These results suggest that there may be interesting sex differences in implicit body representations. It is noteworthy, however, that the nature of the sex difference observed cannot be interpreted as one sex having more distorted maps than the other. Rather, women show larger distortions of hand width, while men show larger distortions of finger length. In both cases, men show perceptual maps that are *smaller* (as a proportion of actual hand size) than women.

Despite having run numerous experiments using the psychomorphometric paradigm to measure perceptual hand maps, my colleagues and I had never investigated sex differences. Given the report of Coelho and Gonzalez (in press), I therefore decided to conduct a meta-analysis of studies from my own research. As Coelho and Gonzalez note, most studies using this paradigm have had substantially more women than men as participants. However, across studies, a substantial number of people of both sexes have been tested. The current meta-analysis therefore compares women and men across all studies my colleagues and I have conducted investigating perceptual hand maps.

Methods

Included studies

Studies from my own research were included in the analysis if they met the following criteria: (1) they measured perceptual maps of the hand dorsum using the psychomorphometric method of Longo and Haggard (2010), (2) they included judgments of the tip and knuckle of each finger based on verbal instructions, and (3) both women and men were tested. A total of 19 experiments fit these criteria, listed in Table 1. Together, the 19 studies included a total of 216 woman and 129 men. The maps of the palm obtained by Longo and Haggard (2012a) were excluded as not meeting criterion 1. Conditions in which responses were cued by tactile or visual cues (e.g., Longo, Mancini, & Haggard, 2015; Longo & Morcom, 2016; Mattioni & Longo, 2014) were excluded as not meeting criterion 2. No experiments were excluded based on criterion 3.

Table 1: Studies included in the meta-analysis.

Study	Exp	N_w	N_m	Conditions
Longo & Haggard (2010)	1	15	3	Single condition
Longo & Haggard (2010)	2	8	4	'Normal' and 'rotated' postures averaged.
Longo & Haggard (2010)	3	8	5	Left hand and right hand conditions averaged.
Longo & Haggard (2010)	4	50	17	Single condition
Longo & Haggard (2012a)	1	9	3	Only dorsum condition used, palm condition excluded.
Longo & Haggard (2012b)	1	6	8	Only 'localisation' task used.
Longo (2014)	1	8	4	'Sighted' and 'blindfolded' conditions averaged.
Mattioni & Longo (2014)	1	11	9	Only 'verbal' condition used, 'tactile' condition excluded.
Longo (2015a)	1	9	9	'Together' and 'apart' postures averaged.
Longo, Mancini, & Haggard (2015)	1	8	4	Only 'verbal' task used, 'tactile' task excluded.
Longo, Mattioni, & Ganea (2015)	1	11	9	Only 'pointing' task used.
Longo, Mattioni, & Ganea (2015)	2	11	9	Only 'own hand' condition used, 'rubber hand' condition excluded.
Tamè et al. (2017)	1	17	9	'Apparent' and 'objective' conditions averaged.
Longo (2017a)	1	8	4	Only 'verbal' task used, 'tactile' task excluded.
Ganea & Longo (2017)	1	5	8	Only 'real' condition used, 'imagined' conditions excluded.
Ganea & Longo (2017)	2	10	5	Only 'real' condition used, 'imagined' conditions excluded.
Longo (2018)	1	4	8	Only 'pointing' condition used, 'verbal' condition excluded.

Longo & Holmes (submitted)	1	10	9	Only 'hand' condition used, 'face' condition excluded.
Longo (unpublished)	1	8	2	Single condition.

Data Extraction

For each experiment I coded the number of female and male participants, as well as the mean and standard deviation for each sex for the three characteristic distortions described above. All of these variables were calculated in the same way as in the original papers, only separately for each sex and in some cases collapsed across conditions, as summarised in Table 1. First, I calculated overestimation of knuckle width (i.e., the distance between the knuckles of the index and little fingers) as a percentage of actual distance. Second, I calculated overestimation of finger length (i.e., the distance between the knuckle and fingertip) as a percentage of actual length, calculated separately for each finger and then averaged. Note that because finger length is in fact underestimated, rather than overestimated, these values are on average negative. Finally, I calculated the gradient in judgments of finger length across the hand by using least-squares linear regression to model the change in percentage overestimation of finger length. In addition, since I had access to the raw data of all these studies, I also organised the data at an individual participant level, including actual hand width and the length of each finger.

Analysis

Separate analyses were conducted on overestimation of hand width (i.e., the distance between the knuckles of the index and little fingers), underestimation of finger length (averaged across the five fingers), and gradient of this underestimation across the hand (i.e., the slope of a regression line fit to underestimation of length across the five fingers). For each measure, I conducted random-effects meta-analyses (Borenstein, Hedges, Higgins, & Rothstein, 2009) using the *metafor* package (Viechtbauer, 2010) for R version 3.4.3. Separate analyses were conducted on each sex separately as well as on the difference between women and men. Because the dependent measure and units were identical across studies, analyses were conducted on raw mean values, rather than on standardised means (e.g., Cohen's d, Hedges g) as used in previous meta-analyses of body perception which have used a range of different tasks (e.g., Cash & Deagle, 1997; Mölbert et al., 2017; Sepúlveda, Botella, & León, 2002; Smeets, Smit, Panhuysen, & Ingleby, 1997).

I also investigated sex differences using individual-level data using linear mixed-effects models (Baayen, Davidson, & Bates, 2008), using the *lme4* toolbox for R (Bates, Maechler, Bolker, & Walker, 2015). Each of the three dependent variables was modelled using sex as a fixed factor and study as a random factor, including random intercepts for studies and by-study random slopes for the effect of sex. The significance of sex was assessed using model comparison (Barr, Levy, Scheepers, & Tily, 2013).

Results

Overestimation of Hand Width

Figure 2 shows forest plots of overestimation of hand width for women (left panel), men (centre panel), and for the difference between women and men (right panel). There was clear overestimation of knuckle width for both women (M: 66.3% overestimation, 95% CI: [59.0 – 73.6%]), z = 17.83, p < 0.0001, and for men (M: 54.8% overestimation, 95% CI: [47.3 – 62.3%]), z = 14.28, p < 0.0001. There was evidence for heterogeneity across studies, both for women, $Q(18)$ = 60.05, p < 0.0001, and men, $Q(18)$ = 34.50, p < 0.02, with the I^2 statistic indicating that 72.8% and 47.6%, respectively, of the between-experimental variability was due to heterogeneity. Despite this heterogeneity, there was clear evidence for large overestimation of hand width in both sexes.

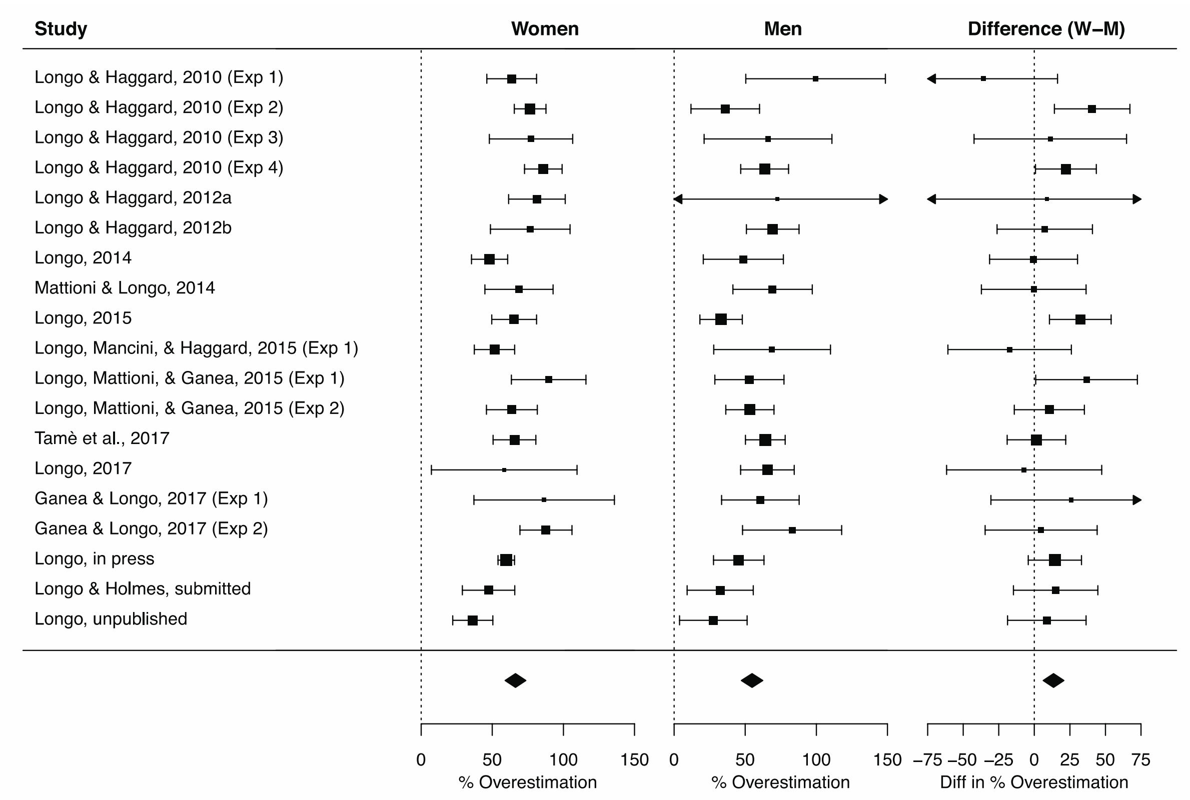

Figure 2: Forest plot showing the results for overestimation of hand width for women (left), men (centre), and the difference between women and men (right). Across studies, clear overestimation of hand width was apparent in both sexes, but was significantly larger in women than in men.

The right panel of Figure 2 shows a forest plot of the difference in overestimation of hand width between woman and men across studies. The magnitude of overestimation was significantly larger for women than for men (*M*: 13.5%, 95% CI: [6.3 – 20.8%]), $z = 3.65$, $p < 0.0005$. There was no evidence for heterogeneity, $Q(18) = 18.44$, $p = 0.43$. I also investigated the effect of sex using individual subject-level data using a linear mixed-effect model, treating sex as a fixed effect and study as a random effect. Consistent with the previous analysis, overestimation was larger for women than for men ($\beta = 12.0\%$, SE $\beta = 4.3\%$), $\chi^2(1) = 6.72$, $p < 0.01$. This result replicates the sex difference in perceived hand width reported by Coelho and Gonzalez (in press).

Underestimation of Finger Length

Figure 3 shows forest plots of estimation of finger length for women (left panel), men (centre panel), and for the difference between women and men (right panel). There was clear underestimation of finger length for both women (M: 26.7% underestimation, 95% CI: [-31.0 – 22.3%]), z = -12.03, p < 0.0001, and men (M: 30.9% underestimation, 95% CI: [-35.0 – 26.9%]), z = -14.91, p < 0.0001. There was evidence for heterogeneity across studies, both for women, $Q(18)$ = 79.68, p < 0.0001, and men, $Q(18)$ = 80.44, p < 0.0001, with the I^2 statistic indicating that 80.0% and 77.1%, respectively, of the between-experimental variability was due to heterogeneity. As with overestimation of hand width, despite study-to-study variability, there was clear evidence for overall underestimation of finger length in both sexes.

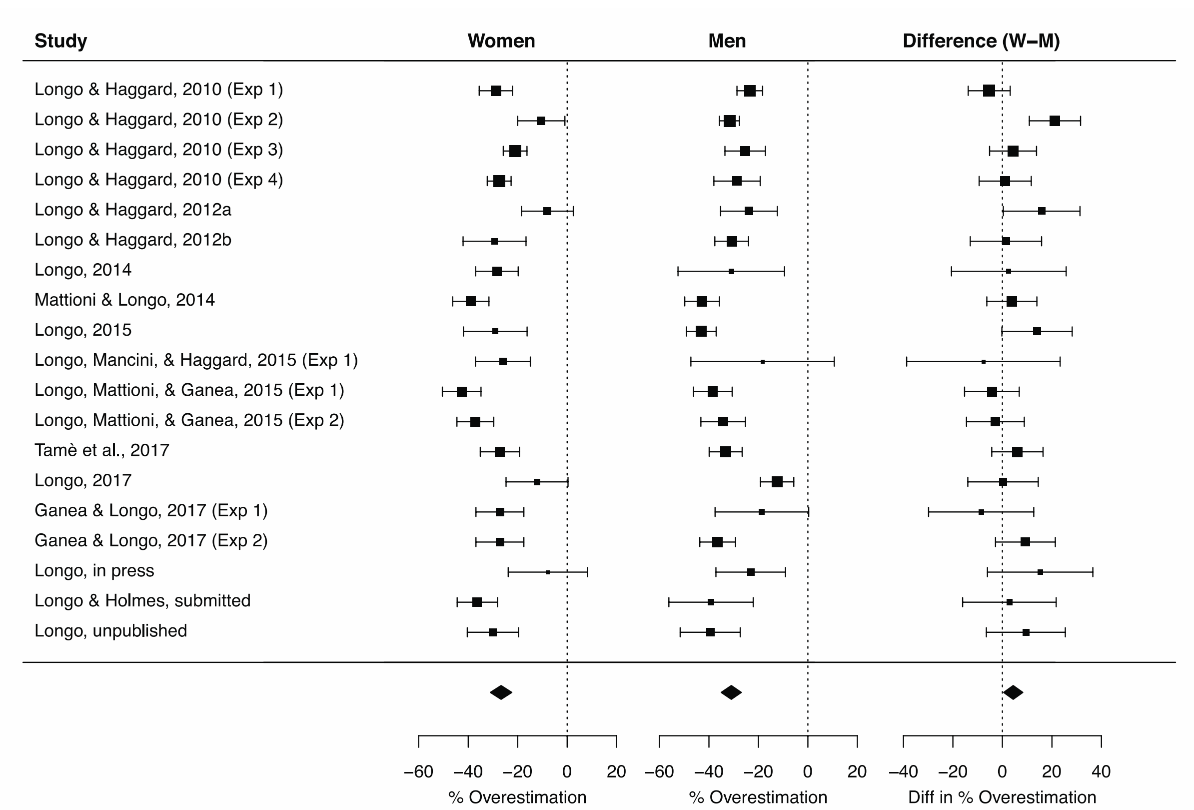

Figure 3: Forest plot showing the results for estimation of finger length for women (left), men (centre), and the difference between women and men (right). Across studies, clear underestimation of finger

length (i.e., negative overestimation) was apparent in both sexes, but was significantly larger in men than in women.

The right panel of Figure 3 shows a forest plot of the difference in estimation of finger length between women and men. The magnitude of underestimation was significantly larger for men than for women (M: 4.4%, 95% CI: [0.5 – 8.3%]), $z = 2.21$, $p < 0.05$. There was marginally significant evidence for heterogeneity, $Q(18) = 27.88$, $p = 0.064$, with the I^2 statistic indicating that 38.6% of between-experiment variability was due to heterogeneity. Similar results were obtained from the individual subject-level data using a linear mixed-effect model (β = 3.8%, SE β = 1.8%), $\chi^2(1) = 4.11$, $p < 0.05$. This result replicates the sex difference in perceive finger length reported by Coelho and Gonzalez (in press).

Radial-Ulnar Gradient Across Fingers

Figure 4 shows forest plots of the gradient of finger length underestimation across the hand for women (left panel), men (centre panel), and the difference between women and men (right panel). There were clear gradients across the hand for both women (M: -5.3% / digit, 95% CI: [-6.1 – -4.6], $z = -14.53$, $p < 0.0001$, and men (M: -3.7% / digit, 95% CI: [-4.6 – -2.8%], $z = -8.14$, $p < 0.0001$. There was evidence for heterogeneity for both women, $Q(18) = 39.26$, $p < 0.005$, and men, $Q(18) = 32.79$, $p < 0.02$, with the I^2 statistic indicating that 54.0% and 49.7%, respectively, of the between-experiment variance was due to heterogeneity.

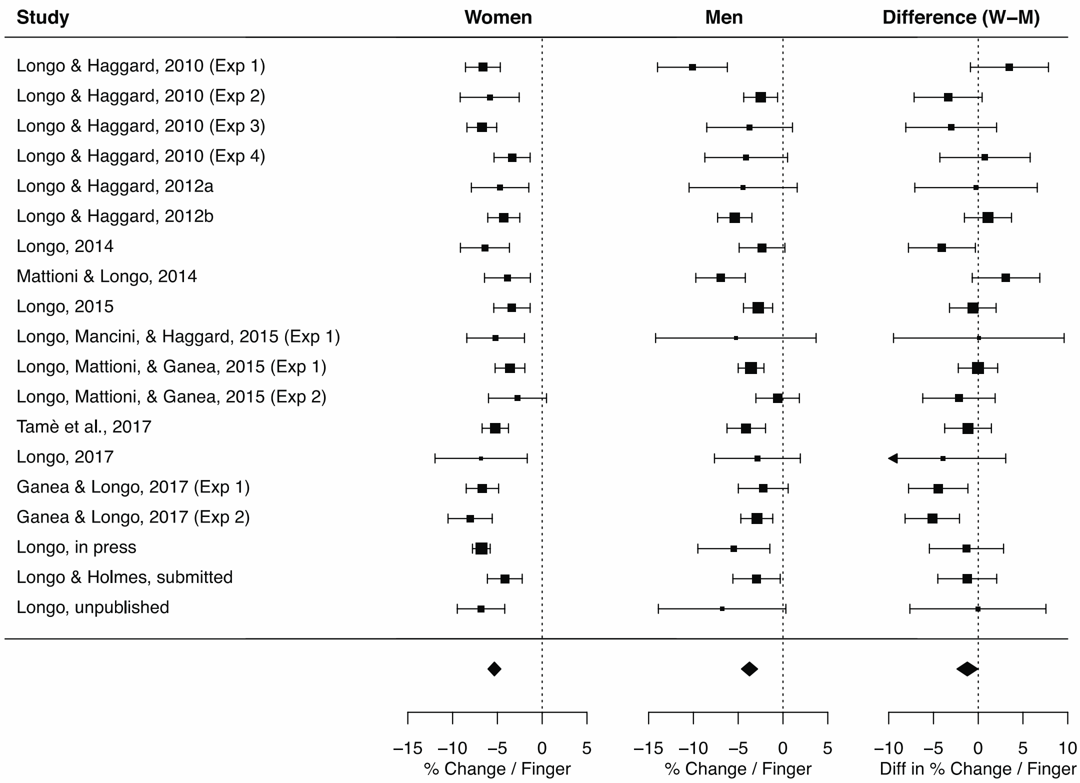

Figure 4: Forest plot showing the results for the gradient in estimated finger length across the hand for women (left), men (centre), and the difference between women and men (right). Across studies, clear gradients were apparent in both sexes. There was no significant difference between women and men.

The right panel of Figure 4 shows a forest plot of the difference in gradient between women and men. The magnitude of this gradient was significantly larger for women than for men (M: -1.22% / digit, 95% CI: [-2.38 – -0.05], z = -2.05, p < 0.05. There was evidence for heterogeneity across studies, $Q(18) = 29.39$, $p < 0.05$, with the I^2 statistic indicating that 43.0% of the between-experiment variability was due to heterogeneity. Similar results were obtained from the individual subject-level data using a linear mixed-effect model (β = -1.1%, SE β = 0.6%), $\chi^2(1) = 5.15$, $p = 0.076$, though did not quite reach statistical significance.

Relation to Actual Hand Size

Men's bodies – including their hands – are, on average, larger than those of women (Tilley, 1993). This obvious fact has potentially interesting connections with the observed sex differences, since it suggests that the differences in distortions between men and women could arise not from differences in the perceptual maps themselves, but in differences in actual hand size. That is, if men and women produced on average identical perceptual maps, this would elicit sex differences for percent overestimation similar to those described by Coelho and Gonzalez (in press) and in the present study, namely men should show reduced overestimation of hand width and increased underestimation of finger length compared to women because the same perceptual judgments would be divided by a larger denominator. As data on actual hand size was available for all participants in the present study, I therefore investigated the relation between distortions and actual hand size.

I first confirmed that there was a sex difference in actual hand size in this data. I ran linear mixed-effects models on actual knuckle spacing and actual finger length (averaged across the five fingers), treating sex as a fixed effect and study as a random effect. For consistency with the above analyses, random intercepts for studies and by-study random slopes for the effect of sex were included. Unsurprisingly, there were large sex differences in hand size, with women having shorter fingers (β = -0.89 cm, SE β = 0.07 cm), $\chi^2(1) = 42.90$, $p < 0.0001$, and smaller hand width (β = -0.65 cm, SE β = 0.05 cm), $\chi^2(1) = 47.51$, $p < 0.0001$, than men.

Next, I re-ran the analyses on distortions reported above, including actual size as a covariate. The key questions were whether people with smaller hands show different distortions than those with larger hands, and whether there is evidence for sex differences controlling for the fact that women have smaller hands on average than men. For percent overestimation of hand width, there was a marginally-significant effect of actual knuckle spacing (β = -7.9 %/cm, SE β = 4.2 %/cm), $\chi^2(1) = 3.31$, p = 0.069. Critically, however, with actual size included as a covariate there was no longer a significant effect of sex (β = -6.8%, SE β = 5.1%), $\chi^2(1) = 1.67$, $p = 0.20$. Similar results were found for finger length, with a clear effect of actual length (β = -5.0 %/cm, SE β = 1.4 %/cm), $\chi^2(1) = 11.77$, $p < 0.001$, and no significant effect of sex (β = -0.6%, SE β = 2.3%), $\chi^2(1) = 0.07$, $p = 0.80$.

Thus, there does not appear to be evidence for sex differences in perceptual hand maps over-and-above differences in actual hand size. This suggests that far from perceptual maps in men and women being dissimilar, they may actually be *more* similar than actual hand shape. Such a "regression to the mean" could produce apparent sex differences due to the normalisation by actual hand size, which clearly does differ between sexes. The suggestion that participants may be producing highly similar maps regardless of differences in actual hand size raises the question of whether there is any evidence for self-specificity in perceptual maps or whether participants produce completely generic maps with no resemblance to their own hand. To address this, I ran another series of analyses on judged hand width and finger length expressed in cm (rather than overestimation as a percentage of actual size), including sex as a fixed effect, study as a random effect, and actual size as a covariate, again including random intercepts for studies and by-study random slopes for the effect of sex. For hand width, there was a clear effect of actual size on judgments (β = 1.18 cm/cm, SE β = 0.26 cm/cm), $\chi^2(1) = 19.66$, $p < 0.0001$; participants with wider hands produced wider hand maps, showing clear evidence for at least some level of self-specificity. There was no effect of sex over-and-above actual hand size, (β = -0.45 cm, SE β = 0.31 cm), $\chi^2(1) = 2.01$, $p = 0.16$. Similar results were found for finger length, with a clear effect of actual size on judgments (β = 0.26 cm/cm, SE β = 0.12 cm/cm), $\chi^2(1) = 4.38$, $p < 0.05$; participants with longer fingers produced maps with longer fingers as well. Again, there was no effect of sex over-and-above the effect of actual finger length (β = 0.08 cm, SE β = 0.19 cm), $\chi^2(1) = 0.18$, $p = 0.67$.

Discussion

These results replicate the sex differences in perceptual hand maps reported by Coelho and Gonzalez (in press). Overestimation of hand width was larger in women than in men, while underestimation of finger length was larger in men than in women. There was also some evidence for a sex difference in the gradient of finger length underestimation from the thumb to little finger, with women showing a more pronounced change than did men. Together with the results of Coelho and Gonzalez (in press), this study thus provides evidence for sex differences in the magnitude of distortions in perceptual hand maps. Notably, however, there was no apparent effect of sex once actual hand size was included as a covariate.

As noted by Coelho and Gonzalez (in press), the sex differences observed in perceptual hand maps show intriguing parallels to the distortions seen in clinical disorders of body image, although the exact relation between these two classes of distortions remains uncertain. On one side, anorexia, which involves overestimation of body size, is substantially more common among women than men (Hoek, 2006; Treasure, Claudino, & Zucker, 2010). On the other side, men are more likely to suffer from muscle dysmorphia, in which individuals believe their body is too small or not muscular enough (Pope et al., 1997; Pope, Phillips, & Olivardia, 2000; Olivardia, 2001), and which has been described as the reverse of anorexia (Pope, Katz, & Hudson, 1993). While the sex differences in perceptual hand maps do not involve a reversal in the direction of distortions between men and women, they do involve a relative decrease in perceived hand size in men compared to women or, equivalently, a relative increase in women compared to men. It is an intriguing possibility that distortions such as those described here in healthy people may have some relation to the emergence of body image distortions in disease (cf. Longo 2015b). Recent results have shown that individuals with anorexia show abnormalities in other implicit, action-based tasks (Guardia et al., 2010, 2012; Keizer et al., 2013), as well as illusions like the rubber hand illusion (Eshkevari et al., 2012, 2014).

The functional reasons for such misperceptions remain unclear. They do bear a striking similarity to aspects of the low-level organisation of the somatosensory system. For example, the receptive fields of tactile neurons in the spinal cord (Brown, Fuchs, & Tapper, 1975) and primary somatosensory cortex (Brooks, Rudomin, & Slayman, 1961; Alloway, Rosenthal, & Burton, 1989) are generally oval-shaped, rather than circular, with the long-axis of the ovals aligned with the proximo-distal axes of the limbs. This is presumably related to the higher spatial sensitivity of touch in the medio-lateral limb axis (e.g., Weber, 1834/1996; Boring, 1930; Schlereth, Magerl, & Treede, 2001; Cody, Garside, Lloyd, & Poliakoff, 2008). Such anisotropies are a basic part of the organisation of somatosensory processing in the nervous system, along with features such as the well-known differences of cortical magnification of body parts in the somatosensory 'homunculus' (Penfield & Boldrey, 1937; Sur, Merzenich, & Kaas, 1980). It is an intriguing possibility that mental body representations emerge through a combination of such distorted somatosensory body maps with more veridical information coming from visual experience of the body (cf. Longo & Haggard, 2012b; Longo, 2015b).

One point of difference between the present results and those of Coelho and Gonzalez (in press) concerns the absolute presence of distortions in men. Coelho and Gonzalez found clear underestimation of finger length in both sexes, but significant overestimation of hand width was apparent only in women, not in men. In contrast, the present meta-analysis provided strong evidence for both distortions in both men and women. The reason for this difference is not clear. One possibility is the way in which actual hand size was assessed. In my studies, I have measured actual hand size by taking photographs of each participant's hand next to a ruler, whereas Coelho and Gonzalez (in press) measured hand size by asking participants to point to landmarks on their on a transparent board above the hand, a procedure which could potentially introduce various biases of its own relating to motor control of pointing or visual biases such as the horizontal-vertical illusion. Presumably, Coelho and Gonzalez adopted this approach exactly because of the possibility of such biases, since they would naturally also influence responses in the main experimental task. Coelho and Gonzalez (in press) further suggest that overestimation of body width may be specific to women, pointing to overestimation of body width in healthy women in more traditional body size estimation tasks (Schneider et al., 2009; Urdapilleta, Cheneau, Masse, & Blanchet, 2007). However, it is important to note that while the majority of studies in the body size estimation literature have tested only women, numerous studies have also reported overestimation of body width in healthy men (e.g., Shontz, 1969; Thompson & Thompson, 1986; Dolan et al., 1987; Pasman & Thompson, 1988; Keeton, Cash, & Brown, 1990; Mizes, 1991). Thus, whether or not it may differ in magnitude between sexes, absolute overestimation of body width appears to be a general characteristic of both healthy men and women.

In the literature on body size estimation in the context of eating disorders, it is common to quantify performance using a measure called the 'body perception index' (BPI), first introduced by Slade and Russell (1973), which quantifies judged size as a percentage of actual size (for discussion see Smeets, Smit, Panhuysen, & Ingleby, 1998). The BPI is logically equivalent to the percentage overestimation measure used in this paper and in my other studies using this paradigm, but defines veridical judgments at a score of 100, rather than 0. The BPI has been criticised by Ben-Tovim and colleagues (e.g., Ben-Tovim, Whitehead, & Crisp, 1979; Ben-Tovim & Crisp, 1984; Ben-Tovim, Walker, Murray, & Chin, 1990) who found no correlation between judgments of body width using the moving caliper method and actual body size. These authors argued that this undermined the basis for using actual body size in the denominator of the BPI. This point is especially acute in the context of anorexia in which patients are much thinner than controls. Apparent overestimation of body width in patients compared to controls, therefore, could reflect their differences in actual body size, rather than differences in judgments. Indeed, there is some evidence that overestimation in body size estimation tasks is systematically related to actual body size (e.g., Smeets et al., 1998; Cornelissen, Johns, & Tovée, 2013; Cornelissen, Bester, Cairns, Tovée, & Cornelissen, 2015; Kuskowska-Wolk & Rössner, 1989). It is therefore important to note that the present results show a clear relation between the size of perceptual hand maps and actual hand size.

Concerns that apparent overestimation of body width in anorexia might be an artefact of patients having a smaller actual body size than controls have an exact parallel in the context of the sex differences in perceptual hand maps reported by Coelho and Gonzalez (in press) and replicated here. Differences between men and women in the magnitude of distortions are in each case for men to show *smaller* perceptual maps than women (i.e., less overestimation of hand width, more underestimation of finger length). But men's hands are also larger, on average, than women's. So the sex difference could result from similar perceptual maps normalised by different denominators. Indeed, I found that when actual hand size was included as a covariate in analyses that there was no longer any significant difference between men and women.

This pattern could indicate that participants show a bias to judge their hand as more similar to an average hand than it actually is, a form of regression to the mean. Analogous combination of actual memory traces with categorical information have been described in a number of domains by Huttenlocher and colleagues (Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Hedges, & Vevea, 2000; Huttenlocher, Hedges, Corrigan, & Crawford, 2004). I recently suggested that the body image might be coded not as an absolute 3-D form, but as a vector deviation from a prototypical body (Longo, 2017c), analogous the idea of prototype-referenced coding in visual face perception (Leopold, O'Toole, Vetter, & Blanz, 2001). The present results do provide evidence for at least some level of self-specificity in perceptual hand maps, but also suggest a general bias for maps to be biased towards an average hand, that is people with bigger hands showed more underestimation of finger length, but less underestimation of hand width, than people with smaller hands. Implicit representation of hand form may therefore involve a weighted combination of actual memory of one's own hand with categorical information about the size and proportions of typical hands. As mentioned earlier, findings that overestimation of body size relates systematically to actual body size is consistent with the idea of such a regression to a mean body type (cf. Cornelissen et al., 2015).

The idea that sex differences might result from differences in actual body size has also been advanced in the context of tactile acuity by Goldreich and colleagues (e.g., Peters & Goldreich, 2013; Peters, Hackeman, & Goldreich, 2009; Wong, Peters, & Goldreich, 2013). For example, Peters and colleagues (2009) measured tactile spatial acuity at the fingertips using a grating orientation task, finding that women on average were able to discriminate smaller spatial frequencies than men. Critically, however, this sex difference was fully explained by differences in the surface area of the finger, which was on average smaller in women than in men. Indeed, in a subsequent study Wong and colleagues (2013) showed that perceptual learning could improve tactile spatial acuity, but only to a limit determined by fingertip area. The current study suggests that physical differences in actual hand size may similarly account for sex differences in the distortions of perceptual hand maps.

The studies included in this meta-analysis showed overwhelming consistency in the direction of the effects. Overestimation of hand width, underestimation of finger length, and a gradient across the five fingers were clearly apparent in essentially every experiment. Nevertheless, the quantitative analysis of the data showed that the heterogeneity of effect size between experiments was greater than would have been predicted based on the within-experiment variability alone. This suggests the presence of un-modelled factors affecting the magnitude (if not the direction) of the results. There may be a number of factors contributing to this heterogeneity. First, three of the experiments included conditions in which differences in the magnitude of distortions were apparent, but which were collapsed for the present analysis (Longo & Haggard, 2010, Exp 2; Longo, 2014; Longo, 2015a). Second, Longo (2015a) found that differences in finger splay affected the magnitude of biases, but these were not systematically controlled in most of the experiments included, potentially contributing to study-to-study differences. Third, many of the experiments included additional conditions which were not included in the analysis (described in Table 1), but which could potentially have resulted in carry-over effects between blocks. Finally, while we have made efforts to keep instructions similar across experiments, a range of experimenters ran these studies, and the composition of the participant pool also varies depending on the time of year the studies were run, all of which may introduce variability in the results.

In conclusion, the present study provides further evidence for sex differences in perceptual hand maps, replicating the main finding of Coelho and Gonzalez (in press). However, the results also suggest that such differences may be related to differences in physical hand size between women and men. These results highlight the importance of investigating how misperceptions of the body may differ across populations and be connected to the true physical properties of the body.

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Data Availability

All data analysed for this study is included in the supplementary files.