

The influence of vision, touch, and proprioception on body representation of the lower limbs

Kayla D. Stone*, Anouk Keizer, H. Chris Dijkerman

Utrecht University, Experimental Psychology, Helmholtz Institute, Utrecht, The Netherlands

ARTICLE INFO

Keywords:

Legs
Body perception
Body representation
Sensory-guided
Body metrics

ABSTRACT

Numerous studies have shown that the representation of the hand is distorted. When participants are asked to localize unseen points on the hand (e.g. the knuckle), it is perceived to be wider and shorter than its physical dimensions. Similar distortions occur when people are asked to judge the distance between two tactile points on the hand; estimates made in the longitudinal direction are perceived as significantly shorter than those made in the transverse direction. Yet, when asked to visually compare the shape and size of one's own hand to a template hand, individuals are accurate at estimating the size of their own hands. Thus, it seems that body representations are, at least in part, a function of the most prominent underlying sensory modality used to perceive the body part. Yet, it remains unknown if the representations of other body parts are similarly distorted. The lower limbs, for example, are structurally and functionally very different from the hands, yet their representation(s) are seldom studied. What does the body representation for the leg look like? And is leg representation dependent on which sense is probed when making judgments about its shape and size? In the current study, we investigated what the representation of the leg looks like in visually-, tactually-, and proprioceptively-guided tasks. Results revealed that the leg, like the hand, is distorted in a highly systematic manner. Distortions seem to rely, at least partly, on sensory input. This is the first study, to our knowledge, to systematically investigate leg representation in healthy individuals.

1. Introduction

Numerous investigations have revealed that the way in which we perceive the size and shape of our bodies is highly distorted. The magnitude and direction of these distortions are dependent (at least partly) on the most reliable and dominant source of sensory information available when making judgments about that body part. For example, in a task where individuals must rely mainly on proprioception (i.e. the position of the body in space) to localize unseen landmarks (e.g. tip of the finger) on the hand, the hand is perceived to be wider (~20–80%) and the fingers to be shorter (~20–40%) than they actually are (Coelho, Zaninelli, & Gonzalez, 2016; Longo & Haggard, 2010; Longo, Long, & Haggard, 2012; Longo, Mattioni, & Ganea, 2015; Saulton, Dodds, Bulthoff, & de la Rosa, 2015; Saulton, Longo, Wong, Bulthoff, & de la Rosa, 2016). Similar distortions are found when participants are asked to rely mainly on tactile information, and make judgments about the distance between two unseen tactile points applied to the hand: distance estimates made in the transverse (width) direction are overestimated compared to estimates made in the longitudinal (length) direction (Longo & Haggard, 2011). This is consistent with the size and

shape of tactile receptive fields on this part of the skin. However, when asked to rely mainly on vision, and compare images of a template hand to the size and shape of their own hand, participants show near veridical performance (Longo & Haggard, 2012; Saulton et al., 2015, 2016). These results suggest that the representation of our bodies arise from multimodal sources of information and that these representations are shaped differently depending on the sense that is probed and/or most dominant when perceiving that part (see Longo et al., 2016 for an insightful review on this matter). Further support for this comes from studies that have shown that manipulating (the presence of) one aspect of sensory input to a body part (e.g. vision) can alter other aspects of perceived sensory information about that body part (e.g. touch). That is, vision directed a body part (even if it is noninformative) can enhance spatial tactile acuity on that part when external stimuli is applied (a phenomenon known as visual enhancements of touch, Kennett, Taylor-Clarke, & Haggard, 2011; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Taylor-Clarke, Kennett, & Haggard, 2002). Also, depriving a body part of tactile and proprioceptive input (e.g. via anesthesia) influences one's (visually-guided) estimates of the body part's size (Gandevia & Phegan, 1999). Gandevia and Phegan (1999) showed that following

* Corresponding author at: Experimental Psychology, Helmholtz Institute, Utrecht University, Heidelberglaan 1, 3584 CS Utrecht, The Netherlands.
E-mail address: k.d.stone@uu.nl (K.D. Stone).

thumb anesthetization, participants consistently matched the perceived size of their thumbs to images of thumbs that were significantly larger than their own (though this was not the case for controls). So ultimately, body representations are not fixed, and sensory input plays a critical role in shaping the way in which a body part is represented.

In daily life, our hands play a crucial role in the way that we experience the environment. We regularly see the hands in our field of view, we use them for communication (e.g. gesturing), for reaching and grasping, and for touching/manipulating objects. Consequently, the majority of investigations that have systematically looked at how vision, touch, and proprioception influence body representations have focused mainly on the upper limbs (primarily, the hands). Yet, are the representations of all body parts distorted? And if so, do they show similar stereotypical distortions as the hands do? Remarkably, little attention has been given to, for instance, the lower body when examining body representations. The lower limbs are structurally and functionally very different from the upper limbs (and particularly, from the hands), and their body representations might be reflective of these differences (Pozeg, Galli, & Blanke, 2015; Van Elk, Forget, & Blanke, 2013). When compared to the hands, for example, the legs are larger, have reduced tactile sensitivity (Weinstein, 1968), have fewer degrees of freedom for movement, and they play different roles in action production and execution (e.g. walk versus grasp). Some investigations have focused on how the immediate space surrounding the legs (i.e. peripersonal space) is represented (Pozeg et al., 2015; Scandola, Aglioti, Bonente, Avesani, & Moro, 2016; Schicke, Bauer, & Röder, 2009; Schicke & Röder, 2006; Van Elk et al., 2013). For instance, Van Elk et al. (2013) showed that the integration of visual information presented near the hands with tactile stimulation on the hands is more readily facilitated than for the feet. The authors suggest that this may be partly due to differences in the way we integrate sensory information for these body parts on a daily basis. That is, generally we spend more time visually observing our hands than we do our legs or feet (Van Elk et al., 2013). If the space around the legs is represented differently from the upper body, then it is likely that the representation of the legs themselves are also represented differently. Certainly, some investigations that have assessed *full* body representation have also included leg perception (albeit it was not the main focus of the investigations). For example, in visually-guided tasks, such as localizing points with respect to one's own body (e.g. left hip) relative to the outline of a head on a computer screen (the Body Image Task; Fuentes, Longo, & Haggard, 2013) or quantifying one's own leg length using a wooden dowel (Linkenauger et al., 2015), individuals perceive their legs to be shorter than their actual lengths (perceived leg width was not measured). In these studies, however, tactile or proprioceptive perception of the lower limbs was not assessed.

No study, to our knowledge, has systematically investigated how vision, touch, and proprioception differentially contribute to a representation of the size and shape of the lower limbs. Understanding how the legs are represented might provide insight into populations that have an altered experience of their lower bodies (e.g. individuals with Body Integrity Identity Disorder, individuals with lower-limb amputations, individuals with paraplegia). Thus we ask the question: What does the body representation for the leg look like? And is leg representation dependent on how it is probed (e.g. visually, tactually, proprioceptively)? In the current study, participants completed three tasks wherein leg representation (perception of width and length) was measured under different sensory-guided conditions. In the template matching task (visual body perception), participants were asked to indicate whether distorted images shown of their *own* legs were more slender or wider than the actual size of their legs. In the tactile estimation task (tactile body perception), participants were asked to judge the distance between two tactile points applied to the thigh and shin, while blindfolded. In the localization task (proprioceptive body perception; Longo & Haggard, 2010) participants were asked to localize unseen landmarks on their own leg (relying on the position of the leg in

space). As previous studies have shown that stereotypical distortions also emerge when judging hand-shaped objects (e.g. a rubber hand, a rake) and even partly for non-corporeal based objects (e.g. a box or post-it note), we wanted to include similar conditions in our investigations. Thus, participants *also* localized unseen landmarks of 1) their own body but without proprioceptive information, 2) a corporeal-related object (i.e. mannequin leg) and 3) a non-corporeal object (i.e. a wooden board).

2. Methods

2.1. Participants

Twenty-four individuals (15 female) between the ages of 18 and 42 years (mean = 25.0 \pm 4.9 SD) participated in the current study. All participants were right-handed by self-report, and had normal or corrected-to-normal vision. Mean height of participants was 174.6 (\pm 9.5 SD, range 159–193) cm. All participants gave written informed consent in accordance with the Declaration of Helsinki and the approval of the local ethics committee before participating in the study. Participants were naïve to the purposes of the study.

2.2. Materials and procedures

2.2.1. Footedness questionnaire

Participants completed the Waterloo Footedness Questionnaire – Revised (WFQ – R; Elias, Bryden, & Bulman-Fleming, 1998) after signing the informed consent form. The questionnaire included 13 questions which assessed foot preference for different scenarios (e.g. when kicking a ball, hopping on one foot, etc.). Participants were asked to indicate which foot they preferred for each task, with responses of – 2 (left always), – 1 (left usually), 0 (equal), + 1 (right usually), or + 2 (right always). Responses for all questions were summed, and total scores could range from a minimum of – 20 (indicating an exclusive left foot preference) to a maximum of + 20 (indicating an exclusive right foot preference).

2.2.2. Template matching task

Visual perception of leg size was assessed using a Template Matching Task (Longo & Haggard, 2012; Saulton et al., 2015). Prior to task initiation, the participant stood in front of a large sheet of green paper board (140 L \times 50 W cm) wherein a photograph of the participant's right leg was taken using a Samsung DV150F HD camera. The camera was positioned approximately 70 cm vertically from the floor and 150 cm horizontally from the participant. Participants wore a pair of shorts during the experiment so that bare skin from the mid-thigh to ankle was visible in the photograph. The photograph was then loaded into a custom MATLAB script which stretched or compressed the image of the leg horizontally by \pm 5–35% (step size of 5%), generating an array of 15 images. Each image had a value between 0.65 (i.e. 65% of actual leg width) to 1.35 (135%), wherein images with a value of 1 (100%) were the participant's actual leg size. Participants sat in front of a computer monitor (approximately 42 cm from the screen, screen dimensions: 27 L \times 34 W; resolution: 1280 \times 1024) and were asked to click-to-indicate whether the image of the leg shown onscreen was wider or more slender than he/she felt the shape of his/her own leg was. See Fig. 1A. The program used two staircase procedures; one in which the starting image shown was 125% of the width of the photographed leg, and one in which it was 75% (using a one-up-one-down procedure, see Saulton et al., 2015 and Levitt, 1971). Initial step size was 5 (i.e. 25%), and decreased after each reversal (to 3, to 2, and 1). The program stopped after 13 reversals. Participants completed the task twice; once for the 125% staircase, and once for the 75% staircase. The average of the last 5 reversals (across both staircases) was taken as the perceived leg-width threshold. Possible averages could range from 0.65 to 1.35, where 1 is veridical. Therefore, a value $>$ 1 indicated an

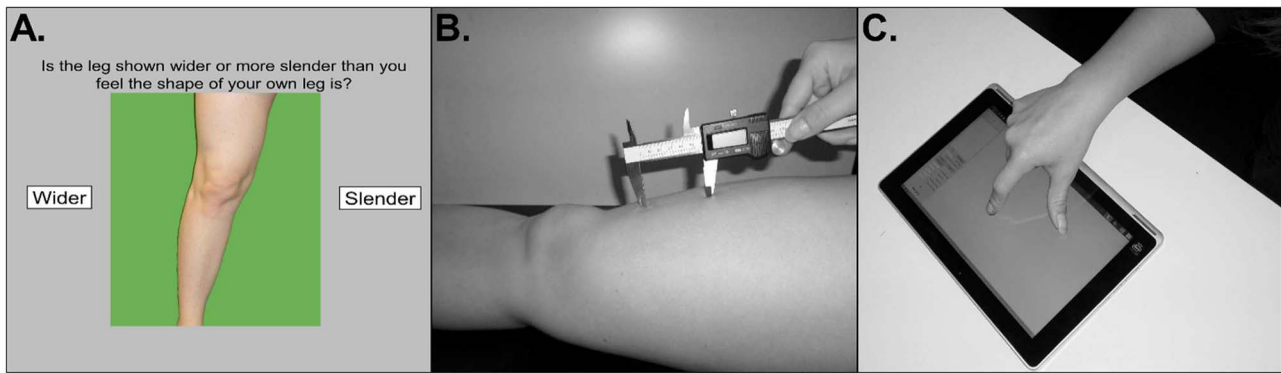


Fig. 1. A) Image showing an example trial from the Template Matching Task. Participants must click “wider” or “slender” as a response to the leg photograph B) Image showing an example trial from the Tactile Estimation Task; in this case, the stimulus is applied to the thigh in the longitudinal direction C) Image showing an example response during the Tactile Estimation Task. Participants estimated the distance applied to the leg using their thumb and index fingers and touching the screen of a tablet.

overestimation of leg width, and a value < 1 indicated an underestimation of leg width. The number of trials ranged from thirteen to eighty. Starting condition (75% or 125% staircase) was counterbalanced between participants.

2.2.3. Tactile estimation task

Tactile perception of leg size was assessed using a tactile distance estimation task (Keizer, Smeets, Dijkerman, van Elburg, & Postma, 2012). The experimenter applied two simultaneous tactile stimuli (i.e. the points on a digital caliper, approximately 1 s duration) to the thigh (approximately 10 cm above the knee) or to the shin (approximately 15 cm below the knee, on the right side in order to prevent undue pressure on the shin bone) of the blindfolded participant. The possible distances between the two points on the caliper were 50, 60, and 70 mm, which were applied in both transverse and longitudinal directions. Participants estimated the distance between the two applied points by using the thumb and index finger of the right hand. They placed their fingers on the screen of an ACER Aspire 10-inch tablet, which measured the distance between the two fingers in a custom-made program called TouchTest (programmed in MATLAB). Each distance was applied 3 times per location (shin, thigh) and per direction (transverse, longitudinal). The average of these 3 trials was taken as a measure of perceived distance estimation. We used a blocked design, wherein participants completed four blocks (i.e. Thigh Transverse, Thigh Longitudinal, Shin Transverse, Shin Longitudinal). Trial order of each applied distance was randomized within each block. Starting block was counterbalanced between participants. See Fig. 1B–C for task set-up.

2.2.4. Localization task

Proprioceptive and visual memory perception of leg size and shape were measured using a modified version of the Localization Task (Longo & Haggard, 2010; Saulton et al., 2015). Prior to task initiation, measurements of the participant's right leg were taken by the experimenter using a tape measure and an MIB Vernier caliper (300 mm). The following measurements were taken: width of knee, width of ankle, width of mid-thigh (mid-thigh was classified as the mid-point between the inner groin and knee), length of upper leg (from mid-thigh to knee), length of lower leg (from knee to ankle). Thus, the landmarks that participants were asked to indicate during the task were: inner mid-thigh, outer mid-thigh, inner knee, outer knee, inner ankle, outer ankle. Small stickers (1 cm in diameter) were placed on each landmark (e.g. inner knee) to facilitate the measuring process, and to familiarize the participant with the location of each landmark before starting the task. These stickers remained on the participants' legs for the duration of the experiment.

In a dark room, participants were seated in front of a 55-inch SONY KDL-55W805C television (screen dimensions: 68.5 cm W (short

edge) \times 121.5 cm L (long edge); resolution: 1920×1080) which lay horizontally on top of a table (120 L \times 80 W \times 70 H cm). Specifically, participants sat with their torso centrally aligned with the short edge of the television screen, with a computer mouse in the right hand (which was positioned on top of a platform 23 L \times 21 W \times 65 H cm). There were four conditions in which participants were asked to click-to-indicate the location of specific landmarks (e.g. inner ankle). At the start of each trial, the cursor was presented at a random y-axis location on the right long edge of the screen (similar to Saulton et al., 2015, 2016). No feedback was given at the end of each trial. The conditions were as follows: a) *Real*: participants placed their right leg on top of a tabletop (100 L \times 60 W \times 44.5 H cm) located 30 cm below the television. The heel of the foot rested on a small foam pad (30 L \times 25 W \times 3 H cm) to prevent movement of the leg during the experiment. During each trial, white text appeared opposite to the participant, at the top and center of the other short edge of the television screen. Each set of text indicated a landmark (e.g. inner knee) and participants were asked to indicate the *felt* position of that landmark by left-clicking directly above where they perceived that part of their leg to be. The program was presented and data was recorded using a custom made MATLAB program. A practice block (12 trials) was completed prior to task initiation. Performance on the practice block was not included in the analysis. For the experimental block, participants completed 60 trials (10 trials per landmark), which were randomized between participants. See Fig. 2 for an example of the set-up and condition. b) *Imagine*: procedures were the same as the Real condition, except participants did not place their legs underneath of the TV screen. Instead they sat with their legs comfortably bent in front of them, and were asked to “imagine as though your leg was extended under the table (as in the Real condition).” Here, participants could not rely on their position sense to complete the task but instead needed to rely on an internal mental representation of their leg. The same landmarks were used as in the Real condition. Participants completed 60 trials (10 trials per landmark), which were randomized between participants. c) *Mannequin*: a mannequin leg was placed on the tabletop below the television (in a similar orientation and position to the way participants placed their legs in the Real condition). The tabletop was slid out from underneath the television screen, and participants were given 30 s to memorize the mannequin leg's size and shape. The tabletop (with the mannequin leg positioned centrally on top) was then slid back underneath of the television. As in the Imagine condition, participants sat comfortably at the chair with their legs bent in front of them. The same landmarks were used as in the Real condition. The mannequin's dimensions were as follows: width of mid-thigh (10.5 cm), width of knee (9.3 cm), width of ankle (4 cm), length of upper leg (mid-thigh to knee: 16 cm), length of lower leg (42.5 cm). Participants completed 60 trials (10 trials per landmark), which were randomized between participants. d) *Object*: similar to the Mannequin condition, the tabletop was slid out from under the television but in this

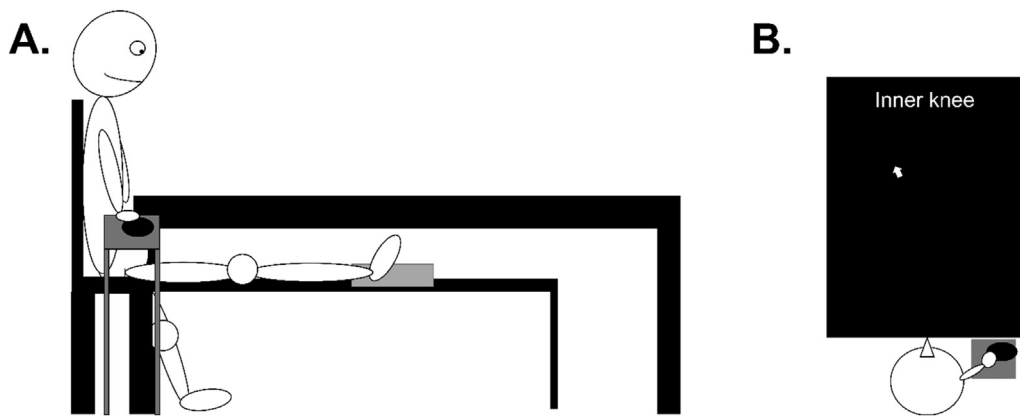


Fig. 2. A) Image showing set-up for the localization task. In this case, the participant is completing the Real condition. Note that the leg is placed under the table top. B) Bird's eye view during the Localization task.

case, participants were given 30 s to memorize the size and shape of a wooden rectangular board (which was positioned in the center of the lower tabletop). Subsequently, the tabletop was slid back underneath the television and participants were asked to click-to-indicate the location of the following landmarks: upper left corner, upper right corner, lower left corner, lower right corner. The object's dimensions were 15 W × 40 L × 2 H cm. Participants completed 40 trials (10 × per landmark), which were randomized between participants.

Starting condition (Real, Imagine, Mannequin, Object) was counterbalanced between participants. On-screen coordinates were compared to the actual dimensions of the leg. Each pixel on screen represented 0.63 mm (mm). For each landmark, we took the average clicked x and y screen coordinates of the ten trials. In order to obtain estimated width or length of part of the leg, the distance between the two points (e.g. inner knee and outer knee) on the television screen were calculated using the equation:

$$d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

The value 'd' was then multiplied by 0.63 in order to convert the distance between the pixels to mm. The following perceived values were obtained: width of knee, width of ankle, width of mid-thigh, length of upper leg (average from mid-thigh to knee), length of lower leg (average from knee to ankle).

In line with previous studies (Longo & Haggard, 2010, 2012; Saulton et al., 2015), the output of the localization task offered two outcomes of perceived body representation. The first outcome was the perceived size of the leg (as measured by the %mis-estimation of the width and length of the various parts of the leg). Specifically, the clicked coordinate values from the MATLAB program were compared to the actual dimensions of the participants' legs and percentage of perceived mis-estimation was calculated using the following equation:

$$\% \text{mis-estimation} = \left(\frac{\text{perceived distance} - \text{actual distance}}{\text{actual distance}} \right) * 100.$$

The second outcome was the perceived shape of the leg (as measured by the Shape Index). The shape index is a measure of the overall aspect ratio of an object (Longo & Haggard, 2010; Napier, 1980). We calculated the Shape Index (SI) for the upper (thigh) and lower (shin) parts of the leg using the following equation:

$$SI = 100 * \frac{\text{width}}{\text{length}}$$

where width was calculated as the average of the width of the mid-thigh and knee (for upper leg SI) and average of the width of the ankle and knee (for lower leg SI), and length was calculated as the length of the upper leg (knee to mid-thigh for the upper leg SI) and the length of the lower leg (ankle to knee for the lower leg SI). We calculated the SI separately for the upper and lower parts of the leg so that we could

more reliably compare shapes between the corporeal conditions and the object condition, as participants had to estimate only 4 points for the upper/lower legs, respectively, and 4 points on the object. The upper and lower SIs were calculated for both the actual and perceived measurements for the Real, Imagine, Mannequin, and Object conditions. In order to compare the corporeal objects to the non-corporeal object, we calculated a normalized shape index (NSI) by dividing the perceived SI by the actual SI (i.e. NSI = perceived SI/actual SI; mimicking Saulton et al., 2015). A value of 1 indicates veridical shape perception, whereas a value > 1 indicates that the participant perceived the object to be wider than it is long, and a value < 1 indicates that the participant perceived the object to be more slender than it is wide. Also, the NSI was used in order to compare estimates for the wooden rectangular board to the participant's own leg estimates and the mannequin leg estimates (as the Object had different landmarks than the legs).

The third outcome was the Tapering Index (TI), motivated by an insightful request from one of the reviewers. The SI (above) takes into account the overall shape of the object, but the leg is a 'special' shape that naturally tapers in width from thigh to ankle. To take this into consideration, we calculated a Tapering Index using the following equation:

$$TI = 100 * \frac{\text{width of bottom}}{\text{width of top}}$$

where width of bottom refers to the width of the ankle (corporeal-based condition) or width of the bottom of the object (non-corporeal based condition), and width of top refers to the width of the thigh (corporeal-based conditions) and width of top of the object (non-corporeal-based condition). TIs were calculated for both the actual and perceived measurements for all conditions. It is critical to note the rectangular board did not actually taper. In order to compare across conditions, we calculated a normalized tapering index (NTI) by dividing the perceived TI by the actual TI (i.e. NTI = perceived TI/actual TI). A value of 1 indicates veridical shape perception, whereas a value > 1 indicates that the participant perceived less taper from mid-thigh (or top) to ankle (bottom) than the leg (or object's) actual taper (i.e. they underestimated the taper), and a value < 1 indicates that the participant perceived more taper from mid-thigh (or top) to ankle (bottom) than the leg (or object's) actual taper (i.e. they overestimated the taper).

2.2.5. Statistical analyses

Data were analyzed using IBM SPSS Statistics 23.0 for Windows (IBM Corp., Armonk, N.Y., USA). Normality of the data was assessed using Shapiro-Wilk tests and by calculating the z-scores of the skewness and kurtosis of each data set. In the event that data showed deviation from normality, non-parametric tests were conducted. Partial Eta Squared values were used to show effect size (η^2). All pairwise comparisons were Bonferroni corrected. For the localization task, values > 2 standard deviations from the mean of the tested landmark

were removed prior to analysis. On average, 6.3% of all localization task trials were removed from the analysis. Only two trials were removed from the entire tactile estimation dataset (1 trial from 2 participants, respectively, due to technical issues) and no trials were removed from the template matching task dataset.

3. Results

3.1. Footedness questionnaire

The mean score was +10.8 (± 1.1 SE; range -4 to $+20$) out of a total possible score of $-22/+22$. All participants were right-footed, save for one participant who had a score of -4 (left-footed).

3.2. Template matching task

As noted above, the width of legs in the images shown to the participants ranged from 65% (0.65) to 135% (1.35) of the actual leg width (100%; 1). Thus the average value (i.e. the average across the 125% and 75% staircases) obtained for each participant on this task could range from 0.65 to 1.35. A one-sample t -test comparing the average scores ($M = 1.10 \pm 0.03$ SE) to a value of 1 (i.e. veridical performance) revealed a significant difference ($t(23) = 3.22, p = .004$). Thus, performance on this task was not veridical. Specifically participants showed overestimation of leg width on this task.

3.3. Tactile estimation task

Estimated values were converted to percent mis-estimation for each distance (using the equation described in the *Localization Task* description). A 3 (distance) \times 2 (location) \times 2 (direction) repeated measures ANOVA on the percent mis-estimation values revealed a main effect of distance, indicating that participants estimated larger widths (i.e. opened their hands wider) for estimating 70 mm vs. 60 mm vs. 50 mm distances ($F(2,46) = 8.646; p < .001, \eta^2 = 0.27$). However, there was no main effect of Location ($F(1,23) = 0.08; p = .77, \eta^2 = 0.004$), indicating that estimates made on the thigh and shin were similar. There was also a main effect of Direction ($F(1,23) = 27.1; p < .0001, \eta^2 = 0.54$), indicating that participants estimated smaller distances for stimuli applied in the longitudinal direction when compared to the transverse direction. The interaction between Distance and Location was not significant ($F(2,46) = 0.001; p = .99, \eta^2 < 0.0001$), nor was the interaction between Distance and Direction ($F(2,46) = 1.0; p = .34, \eta^2 = 0.04$). There was, however, an interaction between Location and Direction ($F(1,23) = 6.6; p = .01, \eta^2 = 0.22$). Follow up Bonferroni-corrected paired-samples t -tests revealed that the distances applied to the shin in the longitudinal direction were estimated to be smaller than those applied in the transverse direction ($t(23) = -6.8; p < .0001$). See Fig. 3. However, there was no difference between transverse and longitudinal estimates for the thigh ($t(23) = -1.5; p = .13$). Moreover, there was no difference between legs parts for estimates made in neither the transverse nor the longitudinal directions ($p \geq .07$ for both comparisons). The interaction between Distance, Location, and Direction was not significant ($F(2,46) = 0.7; p = .49, \eta^2 = 0.03$).

3.3.1. Comparison to actual applied distances

Bonferroni-corrected one-sample t -tests for each leg part and direction were conducted to examine if participants misestimated the distances applied per direction and per location.

3.3.1.1. Thigh (upper leg). Estimates made in the transverse direction did not differ from baseline (i.e. 0, $t(23) = -1.1, p = .28$). That is, participants accurately estimated the distance between two points applied to the thigh in the transverse direction. In contrast, estimates made in the longitudinal direction were significantly different from

baseline ($t(23) = -3.7, p = .001$). That is, participants significantly underestimated the distance between two points when they were applied to the thigh in the longitudinal direction. See Fig. 3.

3.3.1.2. Shin (lower leg). Estimates made in the transverse direction did not differ from baseline (i.e. 0, $t(23) = 0.1, p = .89$). That is, participants accurately estimated the distance between two points applied to the shin in the transverse direction. In contrast, estimates made in the longitudinal direction were significantly different from baseline ($t(23) = -5.8, p < .0001$). That is, participants significantly underestimated the distance between two points when they were applied to the shin in the longitudinal direction. See Fig. 3.

3.4. Localization task

To investigate if the perceived size (width and length) of different parts of the leg are distorted (under different conditions), we first report the comparisons to the actual leg width and length (i.e. a value of 0) for all corporeal-related conditions (Real, Imagine, Mannequin). Second, and in line with previous reports (Longo & Haggard, 2010; Saulton et al., 2015), separate repeated-measures ANOVAs were conducted for the width estimates and for the length estimates in the corporeal-based conditions (Real, Imagine, Mannequin). Negative values indicate an underestimation of width/length and positive values indicate an overestimation of width/length of the specified leg part.

3.4.1. Leg width

3.4.1.1. Comparisons to actual leg width. Bonferroni-corrected (critical $p = .005$) one-sample t -tests revealed that the conditions/leg parts that did not differ from zero (i.e. veridical estimate) were the Mannequin thigh ($t(23) = 1.5, p = .13$), Mannequin knee ($t(23) = -2.4, p = .02$), and Real thigh ($t(23) = -2.6, p = .01$) conditions, suggesting accurate perception of the width of these parts. All other width estimates were different from zero ($p < .0005$).

3.4.1.2. Differences in width perception as a function of condition and leg part. A 3 (condition) \times 3 (leg part) repeated measures ANOVA was conducted on the percentage of mis-estimation for width. Condition (Real, Imagine, Mannequin) and Leg part (thigh, knee, ankle) were within subject factors. There was a main effect of condition ($F(2, 46) = 14.0; p < .0001, \eta^2 = 0.38$), indicating that participants overestimated the width of the leg more in the Mannequin condition ($M = 24.7\% \pm 6.7$ SE) compared to both the Real ($p < .0001; M = 3.9\% \pm 4.4$ SE) and the Imagine ($p = .001; M = 3.2\% \pm 5.0$ SE) conditions. Intriguingly, estimates made in the Real and Imagine conditions did not differ ($p = 1.0$). There was also a main effect of leg part ($F(2, 46) = 81.7; p < .0001, \eta^2 = 0.78$), indicating that the knee ($M = -13.6\% \pm 3.5$ SE) was underestimated significantly more than both the thigh ($M = -4.7\% \pm 3.7$ SE) and the ankle ($M = 50.3\% \pm 8.5$ SE). Estimates for the thigh and ankle were also significantly different ($p < .0001$). Comparisons to baseline (one-sample t -test) revealed that the ankle was significantly overestimated ($t(23) = 5.9, p < .0001$), the knee was significantly underestimated ($t(23) = -3.8, p < .001$), while the thigh was perceived as veridical ($t(23) = -1.2, p = .22$). Moreover, the interaction between condition and leg part was significant ($F(4, 92) = 12.3; p < .0001, \eta^2 = 0.34$). Follow-up Bonferroni-corrected paired-samples t -tests revealed that thigh estimates for the Mannequin leg were significantly overestimated compared to the Real ($t(23) = -4.5, p < .0001$) and Imagine ($t(23) = 5.8, p < .0001$) conditions. Real and Imagine conditions showed no difference in estimates for thigh width ($t(23) = 1.0, p = .3$). Ankle estimations for the Mannequin leg were also significantly overestimated compared to the Real ($t(23) = -4.5, p < .0001$) and Imagine ($t(23) = 4.3, p < .0001$) conditions. Once again, Real and Imagine did not differ for ankle estimations ($t(23) = -0.03, p = .97$). There were no differences in estimates for

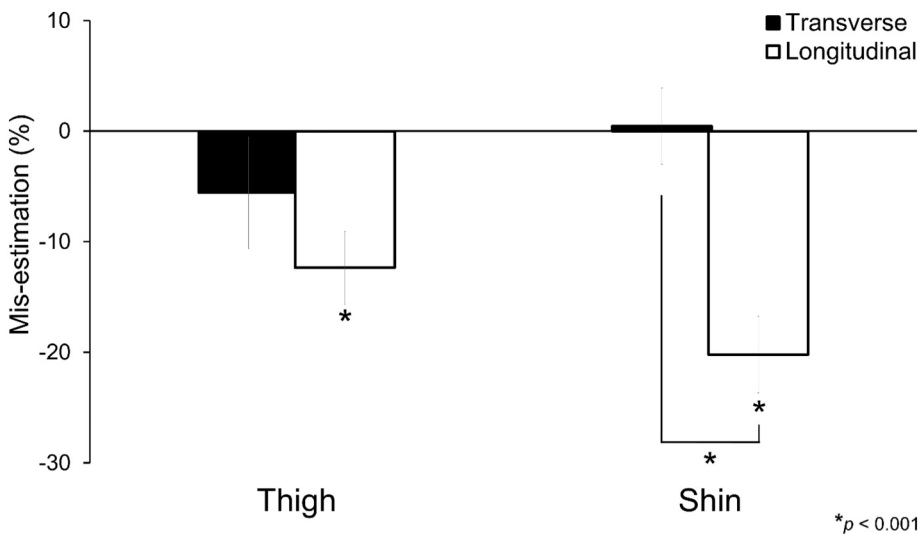


Fig. 3. Bar graph showing percent mis-estimation of transverse and longitudinal stimuli applied to the thigh and shin during the tactile estimation task. The black bars represent percent mis-estimation in the transverse directions and the white bars represent percent mis-estimation in the longitudinal direction. The single asterisk above the longitudinal bars denotes a significant difference from actual applied measurements (i.e. 0%). Note the significant difference between transverse and longitudinal estimates for the shin. Error bars represent standard error of the mean.

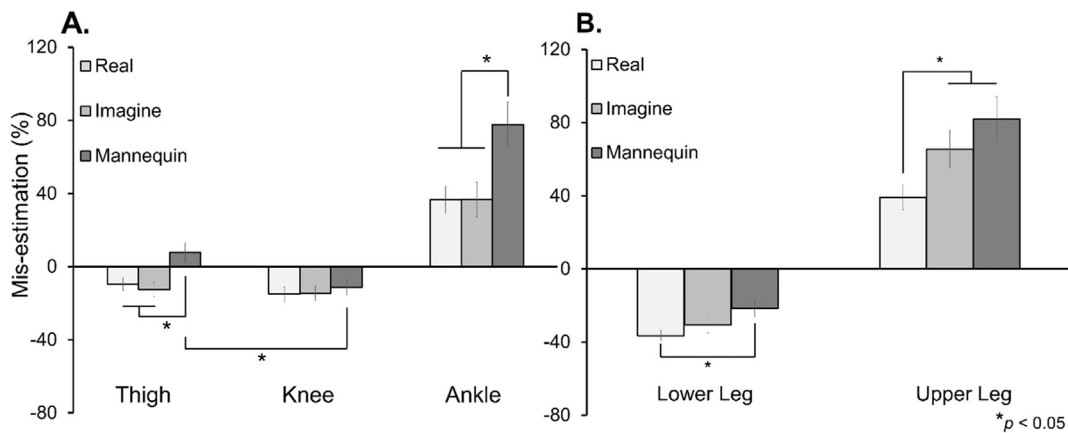


Fig. 4. A) Bar graph demonstrating percent mis-estimation for width estimates of thigh, knee, and ankle. Light grey bars represent the Real condition, medium grey bars represent the Imagine condition, and dark grey bars represent the Mannequin condition. Values > 0 denote overestimation of the width of the body part, while values < 0 denote underestimation of the width of the leg part. Note the significant differences within the thigh and ankle conditions. Also note the significant difference between the Mannequin knee and thigh. Error bars represent standard error of the mean. B) Bar graph demonstrating percent mis-estimation for length estimates of lower leg and upper leg. Note that the Real condition differs significantly from at least one other condition for both parts of the leg. Error bars represent standard error of the mean.

knee width between the Real and Imagine ($t(23) = -0.1, p = .88$), the Real and Mannequin ($t(23) = -1.2, p = .22$), nor between the Imagine and Mannequin ($t(23) = 0.7, p = .44$) conditions. However, when considering within condition, there was a significant difference between the knee and thigh estimates in the Mannequin condition ($t(23) = 5.5, p < .0001$), while differences did not emerge between the knee and thigh estimates for the Real ($t(23) = 1.9, p = .07$) nor for the Imagine ($t(23) = 0.6, p = .54$) conditions. The knee estimates differed from the ankle estimates, however, within all three conditions ($p < .0001$ for each comparison). Similarly, the thigh estimates differed from the ankle estimates within all three conditions as well ($p < .0001$ for each comparison). See Fig. 4A.

3.4.2. Leg length

3.4.2.1. Comparisons to actual leg lengths. Bonferroni-corrected (critical $p = .008$) one-sample t -tests revealed that all length estimates differed significantly from zero ($p < .0001$ for all comparisons), suggesting a distorted representation of leg length, regardless of condition.

3.4.2.2. Differences in length perception as a function of condition and leg part. A 3 (condition) \times 2 (leg part) repeated measures ANOVA was conducted on the percentage of mis-estimation for length. Condition (Real, Imagine, Mannequin) and Leg part (upper leg, lower leg) were

within subject factors. There was a main effect of condition ($F(2, 46) = 15.9; p < .0001, \eta^2 = 0.4$), indicating that participants overestimated the average leg lengths significantly more in the Mannequin condition ($M = 30.1\% \pm 6.9$ SE) than in the Imagine ($M = 17.4\% \pm 6.1$ SE) and Real ($M = 1.2\% \pm 3.8$ SE) conditions. The Imagine and Real conditions also differed significantly ($p = .005$). There was also a main effect of leg part ($F(1, 23) = 125.1; p < .0001, \eta^2 = 0.84$), indicating that participants significantly overestimated the length of the upper leg ($M = 62.1\% \pm 8.6$ SE) when compared to the lower leg ($M = -29.5\% \pm 2.9$ SE). The interaction between condition and leg part was also significant ($F(2, 46) = 4.8; p = .01, \eta^2 = 0.17$). Follow-up Bonferroni-corrected (critical $p = .008$) paired-samples t -tests revealed that this interaction was driven by the finding that estimates in the Imagine condition differed significantly from the Real condition for length estimates made for the upper leg ($t(23) = 3.6, p = .001$) but not for estimates made for the lower leg ($t(23) = 1.7, p = .09$). There were no differences between the Imagine and Mannequin conditions for either upper ($t(23) = 1.9, p = .06$) or lower ($t(23) = 2.2, p = .03$) leg estimates. Estimates made in the Real condition differed from the Mannequin condition for both upper ($t(23) = -3.9, p = .001$) and lower leg ($t(23) = -3.2, p = .003$). See Fig. 4B.

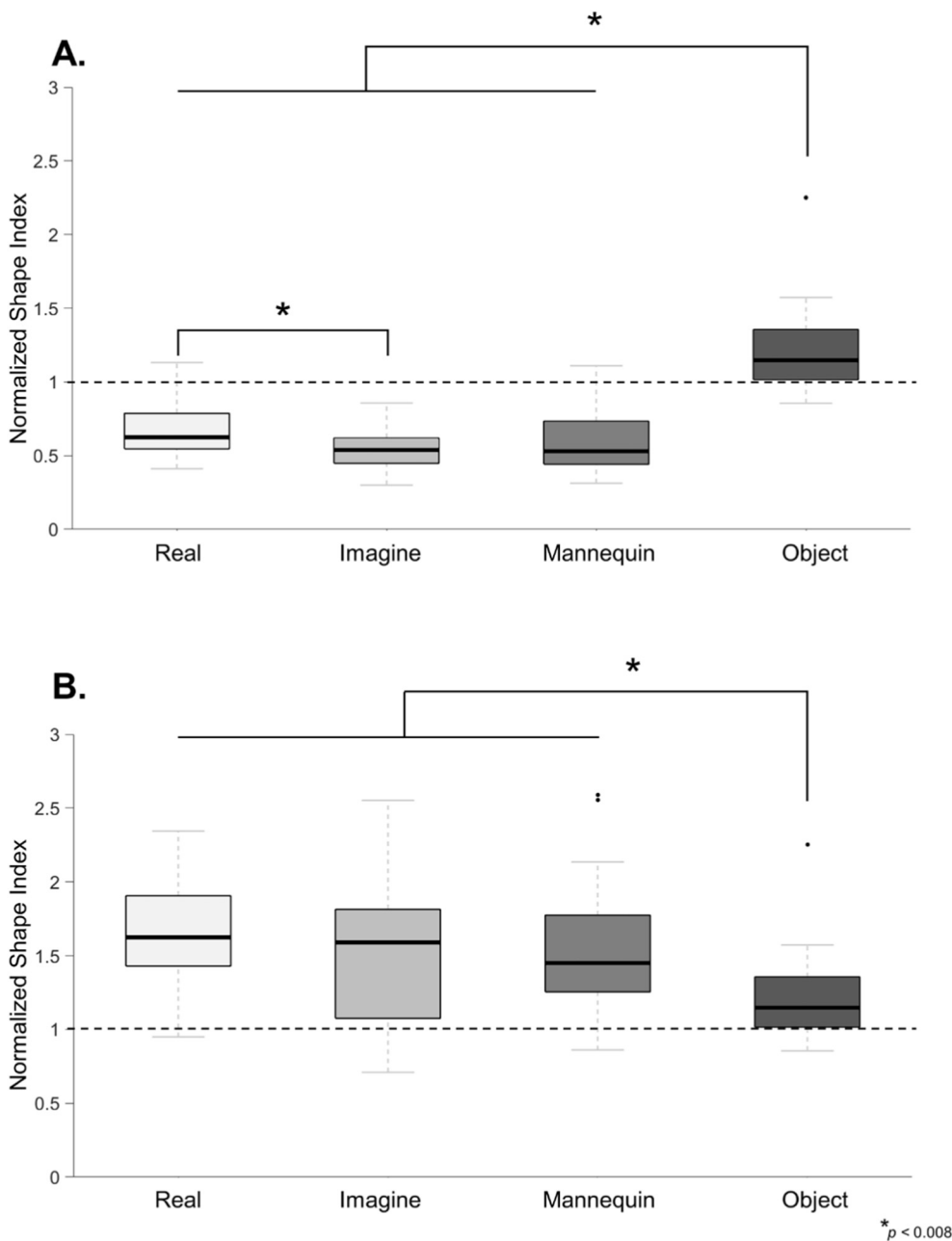


Fig. 5. A) Box plots demonstrating upper leg shape indices for all conditions. The medians are represented as the centered thick lines. Above the medians represent the third quartiles, and below the medians represent the first quartile. The whiskers represent maximum (above box) and minimum (below box) values. The opaque circles above Mannequin and Object conditions represent the outliers. The dotted horizontal line adjacent to x-value '1' represents veridical shape perception. All conditions significantly differed from 1. Asterisks denote significant differences at $p < .008$. Note the significant difference between the Real and Imagine condition. Also note the significant difference between the Object conditions and all other conditions. B) Box plots demonstrating lower leg shape indices for all conditions. Again, note the significant difference between the Object conditions and all other conditions.

3.4.3. Normalized shape indices

Shapiro Wilk tests (and examination of the skewness and kurtosis) revealed that the Object condition was not normally distributed ($p = .001$). Therefore, the appropriate non-parametric tests were conducted for each set of comparisons. Thus the median is reported and variability is expressed as the interquartile range (IQR).

3.4.3.1. Upper leg shape indices

3.4.3.1.1. *Comparisons to actual shape.* Bonferroni corrected (critical $p = .012$) Wilcoxin Signed Rank Tests revealed that the NSIs for all conditions differed from 1 (i.e. veridical perception; $p < .001$ for all comparisons). For the corporeal-based conditions, participants perceived the upper legs to be, on average, longer and/or thinner than the actual shape of the upper leg(s). For the non-corporeal condition, participants perceived the object to wider and/or shorter than the actual shape of the object. See Fig. 5A.

3.4.3.1.2. *Comparisons between conditions.* Friedman's test was conducted to examine differences between the perceived upper leg

NSIs across all conditions. The Friedman test was significant ($\chi^2(3) = 51.0, p < .0001$). Follow-up Bonferroni-corrected (critical $p = .008$) Wilcoxin-Signed Ranked tests revealed that the Real (Med = 0.62, IQR = 0.54–0.80), Imagine (Med = 0.54, IQR = 0.44–0.62), and Mannequin (Med = 0.53, IQR = 0.43–0.73) conditions differed from the Object (Med = 1.14, IQR = 1.0–1.36) condition ($p < .0001$ for each comparison). The Real condition differed from the Imagine condition ($Z = -3.3, p = .001$), but not from the Mannequin condition ($Z = -2.1, p = .03$). The Imagine and Mannequin conditions did not differ ($Z = -0.9, p = .33$). See Fig. 5A.

3.4.3.2. Lower leg shape indices

3.4.3.2.1. *Comparisons to actual shape.* Bonferroni corrected (critical $p = .012$) Wilcoxin Signed Rank Tests revealed that the NSIs for all conditions differed from 1 (i.e. veridical perception; $p < .001$ for all comparisons). For the corporeal-based conditions, participants perceived their lower legs to be, on average, shorter and/or wider than the actual shape of the lower legs. To reiterate, for the non-corporeal

condition, participants perceived the object to wider and/or shorter than the actual shape of the object. See Fig. 5B.

3.4.3.2.2. Comparisons between conditions. Friedman's test was conducted to examine differences between the perceived lower leg NSIs across all conditions. The Friedman test was significant ($\chi^2(3) = 19.0$, $p < .0001$). Follow-up Bonferroni-corrected (critical $p = .008$) Wilcoxon-Signed Ranked tests revealed that the Real (Med = 1.62, IQR = 1.41–1.92), Imagine (Med = 1.59, IQR = 1.06–1.83), and Mannequin (Med = 1.45, IQR = 1.24–1.83) conditions differed from the Object (Med = 1.14, IQR = 1.0–1.36) condition ($p \leq .005$ for each comparison). The Real condition did not differ from the Imagine ($Z = -1.4$, $p = .14$) condition nor from the Mannequin condition ($Z = -1.5$, $p = .11$). Also, the Imagine and Mannequin conditions did not differ ($Z = -0.17$, $p = .86$). See Fig. 5B.

3.4.4. Normalized tapering indices

3.4.4.1. Comparisons to actual taper. Bonferroni-corrected (critical $p = .012$) one-sample t -tests revealed that TIs for the Real, Imagine, and Mannequin conditions were significantly different from 1 (i.e. baseline; $p < .0001$ for all comparisons). Participants significantly underestimated the taper from the thigh to the ankle. However, the NTI for the Object condition did not differ from baseline ($t(23) = -0.7$, $p = .44$). Participants accurately estimated the 'taper' of the Object. However, it is critical to emphasize here that the actual shape of the Object did not taper from the top to the bottom (given its rectangular shape). See Fig. 6.

3.4.4.2. Comparisons between conditions. A repeated measures ANOVA with condition (Real, Imagine, Mannequin, Object) as the within-subject factor conducted on the NTIs revealed a main effect of Condition ($F(3, 69) = 24.5$, $p < .0001$). Bonferroni-corrected Pairwise comparisons revealed a significant difference between the Object condition and all other conditions ($p < .0001$). The Real, Imagine, and Mannequin conditions did not differ from one another ($p > .7$ for all comparisons). See Fig. 6.

4. Discussion

The aim of the current study was to reveal what the body representation of the leg looks like. Moreover, we wanted to investigate if body representation of the leg relies on the sensory modality (vision, touch, or proprioception) that is probed when making a judgment about

the size and shape of one's own leg. Participants were asked to make judgments about the length and/or width of their legs in three different tasks. Results showed that the representation of the leg, like the hand (Coelho et al., 2016; Longo & Haggard, 2010; Saulton et al., 2016), is distorted with respect to its physical dimensions. The direction and magnitude of these distortions depend (at least partly) on the sensory demands of the task. This is the first study, to our knowledge, to systematically examine leg representation in healthy participants. As the representation of the lower body is seldom studied, these results might provide insight into populations in which the experience of the body is altered (e.g. individuals with lower-limb amputations, Anorexia, Somatoparaphrenia, Body Integrity Identity Disorder).

Visual perception of the leg was measured using the Template Matching Task (TMT). Participants were shown distorted images of their own legs, and were asked to indicate whether the leg shown was wider or more slender than their actual leg. Results showed that participants overestimated the widths of their legs by approximately 10%. This is interesting, as previous studies have reported veridical performance on such a task (Longo, 2015a; Longo & Haggard, 2010, 2012; Saulton et al., 2015, 2016). There are at least two possible reasons for the discrepancy between the current and previous studies. Most of the previous reports using the TMT have focused on the representation of the hand. And in these reports, participants were asked to compare the shapes of their hands to template (or average-looking) hands, rather than to a distorted image of their own hand. Also, hand width and length were simultaneously manipulated. In the current study however, we used photographs of the participants' own legs (and only width was manipulated). Although we were interested in the role that vision plays when making judgments about the body, it is possible that attitudes about one's own body influenced the results as well. Glucksman and Hirsch (1969), for example, conducted a similar experiment with obese and non-obese participants. A photograph was taken of the participant's full body, and it was distorted to be wider or more slender than the participant's actual body (similar to what we employed in the current study with the images of the leg). Interestingly, obese participants tended to overestimate the width of their bodies, whereas non-obese participants tended to (slightly) underestimate the width of their bodies. Noteworthy, obese participants continued to overestimate the width of their bodies to the same extent, even after losing weight. And moreover, when making estimates about someone else's body, the magnitude of the mis-estimations were significantly reduced. These results suggest that visual information about one's body, combined with

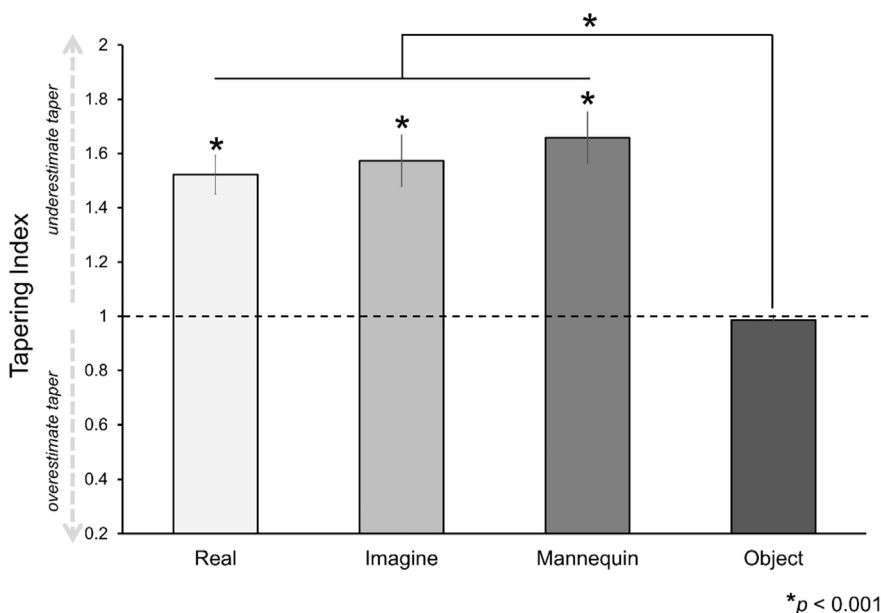


Fig. 6. Bar graph demonstrating normalized tapering indices for all conditions. The single asterisk directly above a bar denotes a significant difference from actual taper (i.e. a value of 1, dotted horizontal line). Also note the significant difference between the Object condition and all other conditions. Values significantly > 1 indicate an underestimation of perceived taper, while values significantly < 1 indicate an overestimation of taper. The dashed arrows on the left side of the figure indicate the direction of mis-estimated taper. The upward-facing arrow indicates that the taper was underestimated more with higher Tapering Index values, and the downward-facing arrow indicates that the taper was overestimated more with lower Tapering Index values. Please also note that the Object did not actually taper from the top to the bottom.

attitudes about the body, can influence one's perception of its width. Although attitudes about body were not explicitly assessed in the current sample, perhaps the overestimation of leg width would be attenuated when making judgments about a template leg instead.

A second possible reason that participants tended to overestimate the width of their legs may be due to the visual information we receive about our legs on a daily basis. For example, we see our hands from many viewpoints, and they are almost always in our field of view. Conversely, we mainly see our legs from a top-down view (i.e. looking down when we are standing or sitting). Focal attention to the upper and lower body is therefore likely to be different (Fuentes et al., 2013). For example, when we sit, our thighs become wider from the pressure against the chair. It is possible that visual experiences like this influence the perception of the body. For example, simply visually perceiving your hand as larger can change tactile perception on that body part (Bruno & Bertamini, 2010). Also, the photographs used in the current paradigm were displayed to the participant from a third person perspective. Normally, one does not see his/her legs from a third person perspective (unless standing before a full-length mirror), which might lead to mis-estimations (as reported here) when making visually-guided judgments about one's own leg width. It would be interesting to investigate if the visual representation of the leg would still be distorted if the photograph were taken from a first-person perspective. In any case, it seems that visual information about the body (or leg, in this case), although informative, does not provide an accurate representation of the leg.

Tactile perception of the leg was measured using a tactile estimation task (TET). Participants underestimated the distance between two unseen points applied to the leg in the longitudinal (length-wise) direction, while they accurately estimated the distance between points applied in the transverse (width-wise) direction, suggesting that the leg is perceived as shorter than it really is when relying on tactile input. Moreover, the length-wise estimates were significantly underestimated compared to width-wise estimates, but only for the lower leg (shin). The few studies that have investigated lower limb tactile distance perception have focused only on the thigh. For instance, Cholewiak (1999) showed no effect of direction when making judgments about two unseen tactile stimuli applied to the thigh (as we show here), whereas Green (1982) showed that participants significantly underestimated distances applied to the thigh in the longitudinal direction compared to the transverse direction. Similar findings have been replicated for estimates made about the hand (Longo & Haggard, 2011) and arms (Le Cornu-Knight et al., 2014; Green, 1982; Wong, Ho, & Ho, 1974) as well. With respect to the shin, investigations on tactile distance perception for the lower leg are lacking in the literature. Our finding that participants significantly underestimated stimuli applied in the longitudinal direction when compared to the transverse direction might relate to one study that investigated tactile *direction* (but not distance) perception on the shin. Ackerley, Carlsson, Wester, Olausson, and Backlund Wasling (2014) showed that participants were significantly worse at judging the direction of moving stimuli on the shin (in the longitudinal direction) than for other body surfaces including the thigh, arm, palm, and forehead. However, more investigations on lower leg tactile distance perception are needed. Noteworthy, the tactile receptors themselves do not provide shape and size information about metrics of the leg (or any body part, for that matter; Longo, 2015b). Thus, in order to make a judgment about the distance between two unseen applied points to the skin, one must refer to a stored representation of the body metrics (i.e. a body model; Longo, 2015b; Longo & Haggard, 2010, 2012). Previous studies have shown that the body model underlying tactile and proprioceptive information about the body is highly distorted; that is, estimates made (on hairy skin) in the longitudinal direction are underestimated more than estimates made in the transverse direction, due to the size and shape of the tactile receptive fields on the hairy skin (i.e. oval-shaped; e.g. see Brown, Fuchs, and Tapper (1975), Treede, Meyer, and Campbell (1990) and

Fig. 4 of Longo and Haggard (2011)). The current findings align with this suggestion (at least for the shin). But regardless of leg part, participants showed a significant underestimation when making judgments in the longitudinal direction. Thus the perception of the leg based on tactile input is also distorted with respect to the leg's physical dimensions.

Proprioceptive perception of the leg was measured using the localization task. The goal of the localization task was two-fold: it was used to assess 1) proprioceptive perception of the leg representation, and 2) shape perception of corporeal and non-corporeal objects. In general, participants showed similar mis-estimations (e.g. underestimation of thigh width, underestimation of lower leg length, overestimation of ankle width), regardless of corporeal-based condition (Real, Imagine, Mannequin; see Fig. 4). This suggests that participants used the same internal reference (or body model) to make judgments about the length and width of a leg. Perhaps most surprising is the lack of a difference between the Real and Imagine condition for width estimates. That is, participants judged the width of different parts of the leg to be the same regardless if the participant was relying on proprioception (i.e. Real, leg under TV screen) or simply relying on an internal mental model of the leg (Imagine, leg not under the TV screen). This suggests that proprioception is not playing a critical role when making estimates about the width of the leg, at least using the current paradigm. In line with this, Longo et al. (2012) asked an individual with phantom limb (hand) syndrome to localize points on her (unseen) intact hand and on her phantom hand. Intriguingly, there was no difference between the estimated metrics between the two hands (as shown in the current experiment with the Real vs. Imagine conditions). The authors suggest proprioception is not always necessary to make judgments about the body structure, and in the absence of it, one can rely on other sources of information (such as a “body in the brain”) to make these judgments (Longo et al., 2012). More recently, a study by Ganea and Longo (2017) revealed highly similar distortions for Real and Imagined estimates on the hand in the general population too, reinforcing the previous claim. Therefore how much of a role does proprioceptive actually play when making estimating about the body's metrics? In the current study, proprioception appeared to play a role when making estimates about the overall length (average of upper and lower leg proportion mis-estimates) of the leg. That is, average estimates of overall length proportions were most accurate when the participant was instructed to rely on proprioception to make the estimates (i.e. the leg was laying beneath the screen) compared to simply imagining its presence or making judgments about a fake leg. Particularly, participants overestimated their upper legs to the same proportion as they underestimated their lower legs in the Real condition only. Perhaps proprioceptive feedback about leg length is more informative than feedback about leg width. For example, leg width can change over the life span based on one's weight. Leg length, on the other hand, is usually unchanged once one reaches adulthood. During locomotion, one is constantly confronted with feedback about the length of the leg when the foot sole contacts the ground. What is more, manipulating proprioceptive feedback by applying vibrations to the tendons of a limb can induce a feeling that the limb is becoming longer or shorter (but not necessarily wider or more slender; Kammers, van der Ham, & Dijkerman, 2006; Lackner, 1988). This highlights the important role that proprioception plays in length perception. Future studies should investigate this further by manipulating proprioceptive feedback during the localization task (e.g. moving the position of the leg during the task, changing the pressure on the joints, vibrating the tendons, etc.).

Slight differences emerged when participants made localization estimates about their own leg compared to a fake leg (Mannequin condition). That is, participants overestimated the average width and length of the mannequin leg more than their own legs in the localization task. Specifically, participants overestimated the width of the thigh and ankle more for the Mannequin condition compared to the Real and Imagine conditions. Here it should be noted that the mannequin leg

used in the current study was not matched to the size of each participants' leg, and that participants have inarguably more sensory and learning experience about their own legs. Indeed, participants only viewed the mannequin leg briefly prior to task initiation. However, the direction of these mis-estimations were similar across all three conditions, suggesting that participants were relying (at least partly) on a similar internal model of a 'leg' to make their judgments. Previous studies have investigated how individuals localize points on an unseen hand-like object (e.g. a rubber hand, rake), and have shown similar results (Longo et al., 2015; Saulton et al., 2016). Individuals tend to make judgments about the hand-like objects in the same stereotypical manner as they do for their own hands (i.e. perceive them to be wider and shorter than they really are), albeit the magnitude of the distortions are generally larger for one's own hand. These findings have been attributed to the additional information provided by somatosensation when estimating one's own hand. Yet the hand is much more tactually sensitive than the leg (Weinstein, 1968), and therefore, somatosensory factors might have a lesser influence on estimating points on the leg than on the hand. Future studies could investigate this query by constraining somatosensory feedback during the task, for example, by reducing tactile feedback (through locally numbing or cooling) the body part under investigation.

With respect to the overall width estimations of different leg parts, participants overestimated the width of the ankles significantly more than the knees and the thighs, as made evident from the main effect of leg part. In fact, when compared to actual widths, ankle width was significantly overestimated, knee width was significantly underestimated, and the thigh width was veridical. The finding that participants were significantly distorted (on average) in making judgments about the width of major 'joint' locations (knee, ankle) but not for 'non-joint' locations (mid-thigh) is intriguing. Perhaps it is a reflection of the directional capability of the joint and/or tendon governing movement of the leg part. For example, the joints in the knee easily allow for movement of the lower leg in the vertical (but not much in the horizontal) direction, which might lead to a compressed proprioceptive representation of knee width. Yet, the joints of the ankle allow for movement of the foot in the horizontal and vertical directions (e.g. imagine drawing a circle in the air with your toes), and this type of motor capability might lend to a proprioceptive representation of width that is exaggerated. Indeed, the perceived width of the wrist (which allows for multidirectional movement of the hand) is also over-exaggerated in healthy participants (Longo, 2017). However, as this idea is speculative, an investigation examining perceived locations of joint and non-joint parts of the body would make for an informative study. With respect to perceived *length* of the different leg parts, participants overestimated the length of the upper legs, but underestimated the length of the lower legs. This suggests a perceived distal shift of the knee's position towards the foot. This finding aligns with previous reports (Longo, 2015c; Longo et al., 2015; Margolis & Longo, 2015), which revealed that participants consistently perceive the knuckles to be farther forward on the hand than they are in reality (but Gross, Webb, and Melzack (1974) for the opposite pattern for arms). Although the reason for this mis-estimation of joint location remains unknown, Longo et al. (2015) speculate that it might be due to a conceptual misunderstanding of body part organization.

Analyses of the normalized shape indices revealed that participants also mis-estimated the width and length of the rectangular wooden board (Object condition). Previous studies have shown similar results regarding shape perception of non-corporeal related objects (Glucksman & Hirsch, 1969; Saulton et al., 2015; Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010). For example, Saulton et al. (2015) asked participants to localize points on an unseen rectangular post-it note. Interestingly, the perceived shape of the rectangular post-it note was strikingly similar to the perceived shape of the rectangular board in the current study (i.e. NSI = ~1.2). Thus, individuals also misperceive the metrics of objects that are not related to the body. However, when

comparing the Object conditions to the perceived shapes of the lower and upper parts of the legs respectively, we found that participants' perceptions of legs (be it their own or a mannequin leg) are significantly more distorted than their perceptions of the overall shape of the object. That is, participants perceived their upper legs to be thinner and/or longer than they actually are, while participants perceived their lower legs to be fatter and/or shorter than they are in reality. The finding that participants were significantly more distorted in making judgments about a corporeal-based objects (at least for the lower leg) compared to a non-corporeal based object is in line with the findings of Saulton et al. (2015). Borrowing the same logic as Saulton and colleagues, these distortions might be a product of an underlying distorted somatosensory model of the body (parts). However, the observation that the perception of legs and the object were distorted with respect to their physical dimensions reveal that non-somatosensory factors could also be playing a role (as also noted by Saulton et al., 2015), such as the reliance on a shared representation in the brain for objects and body parts. For instance, similar (and neighboring) regions of the occipito-temporal cortex (OTC) process both body part and shape perception (Bracci, Caramazza, & Peelen, 2015; Bracci & Peelen, 2013). One study showed that areas of the lateral OTC preferentially responds to not only body effectors (including the lower limbs) but also to the presentation of certain types of objects (Bracci & Peelen, 2013), making it plausible that perceived metric distortions with respect to actual shape occur to both categories. After all, our body parts are also shapes; shapes that can utilize sensory input to relay information about their structure.

Finally, we also analyzed the tapering indices for all conditions. As the leg naturally tapers from mid-thigh to knee, another way to investigate its perceived shape is to look at perceived taper. Participants significantly underestimated the taper of the legs, but accurately estimated the taper of the object (which, indeed had 0% taper). This is reflective of the large overestimation of the ankle width found in the localization task (across all conditions). Moreover, it suggests that participants are capable of making accurate metric judgments for (some aspects of) common shapes, and reinforces the possibility that systematic distortions found in the corporeal-based conditions might be a product of an underlying (distorted) body model.

In conclusion, the representation of the leg is distorted. Participants tended to mis-estimate the width and length of the leg differently based on sensory demands. Certainly, it is probable that the judgments were not made in sensory isolation. In reality, our brains rely on the combination and integration of these senses and other forms of multimodal information (e.g. spatial cues) to give rise to body representations (Longo et al., 2016). Nevertheless, the current study does provide insight into the distortions and flexibility in perception of the lower limbs. And although the distortions observed in the current study were not the same as what is reported for the hands, it is possible that each body part elicits its own repertoire of multimodal-based distortions. Similar systematic investigations should be employed for other body parts as well (e.g. foot, arm, torso, face).

Conflict of interest

We have no conflict of interest to declare.

Acknowledgements

This study was supported by a Netherlands Organisation for Scientific Research (NWO) talent grant (406.15.282) and a Natural Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship.

References

- Ackerley, R., Carlsson, I., Wester, H., Olausson, H., & Backlund Wasling, H. (2014). Touch perceptions across skin sites: Differences between sensitivity, direction

- discrimination and pleasantness. *Frontiers in Behavioral Neuroscience*, 8, 54. <http://dx.doi.org/10.3389/fnbeh.2014.00054>.
- Bracci, S., Caramazza, A., & Peelen, X. M. V. (2015). Representational similarity of body parts in human occipitotemporal cortex. *The Journal of Neuroscience*, 35, 12977–12985. <http://dx.doi.org/10.1523/JNEUROSCI.4698-14.2015>.
- Bracci, S., & Peelen, M. V. (2013). Body and object effectors: The organization of object representations in high-level visual cortex reflects body-object interactions. *The Journal of Neuroscience*, 33, 18247–18258. <http://dx.doi.org/10.1523/JNEUROSCI.1322-13.2013>.
- Brown, P. B., Fuchs, J. L., & Tapper, D. N. (1975). Parametric studies of dorsal horn neurons responding to tactile stimulation. *Journal of Neurophysiology*, 38, 19–25.
- Bruno, N., & Bertamini, M. (2010). Haptic perception after a change in hand size. *Neuropsychologia*, 48, 1853–1856. <http://dx.doi.org/10.1016/j.neuropsychologia.2010.01.006>.
- Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception*, 28, 851–876. <http://dx.doi.org/10.1068/p2873>.
- Coelho, L. A., Zaninelli, G., & Gonzalez, C. L. R. (2016). A kinematic examination of hand perception. *Psychological Research*. <http://dx.doi.org/10.1007/s00426-016-0815-9>.
- Elias, L. J., Bryden, M. P., & Bulman-Fleming, M. B. (1998). Footedness is a better predictor than is handedness of emotional lateralization. *Neuropsychologia*, 36, 37–43. [http://dx.doi.org/10.1016/S0028-3932\(97\)00107-3](http://dx.doi.org/10.1016/S0028-3932(97)00107-3).
- Fuentes, C. T., Longo, M. R., & Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica*, 144, 344–351. <http://dx.doi.org/10.1016/j.actpsy.2013.06.012>.
- Gandevia, S. C., & Phegan, C. M. L. (1999). Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *The Journal of Physiology*, 514, 609–616. <http://dx.doi.org/10.1111/j.1469-7793.1999.609ae.x>.
- Ganea, N., & Longo, M. R. (2017). Projecting the self outside the body: Body representations underlying proprioceptive imagery. *Cognition*, 162, 41–47. <http://dx.doi.org/10.1016/j.cognition.2017.01.021>.
- Glucksman, M. L., & Hirsch, J. (1969). The response of obese patients to weight reduction. III. The perception of body size. *Psychosomatic Medicine*, 31, 1–7.
- Green, B. G. (1982). The perception of distance and location for dual tactile pressures. *Perception & Psychophysics*, 31, 315–323. <http://dx.doi.org/10.3758/BF03202654>.
- Gross, Y., Webb, R., & Melzack, R. (1974). Central and peripheral contributions to localization of body parts: Evidence for a central body schema. *Experimental Neurology*, 44, 346–362. [http://dx.doi.org/10.1016/0014-4886\(74\)90201-5](http://dx.doi.org/10.1016/0014-4886(74)90201-5).
- Kammers, M. P. M., van der Ham, I. J. M., & Dijkerman, H. C. (2006). Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia*, 44, 2430–2436. <http://dx.doi.org/10.1016/j.neuropsychologia.2006.04.009>.
- Keizer, A., Smeets, M. A. M., Dijkerman, H. C., van Elburg, A., & Postma, A. (2012). Aberrant somatosensory perception in anorexia nervosa. *Psychiatry Research*, 200, 530–537. <http://dx.doi.org/10.1016/j.psychres.2012.05.001>.
- Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology*, 11, 1188–1191. [http://dx.doi.org/10.1016/S0960-9822\(01\)00327-X](http://dx.doi.org/10.1016/S0960-9822(01)00327-X).
- Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain*, 111, 281–297.
- Le Cornu-Knight, F., Longo, M. R., & Bremner, A. J. (2014). Categorical perception of tactile distance. *Cognition*, 131, 254–262. <http://dx.doi.org/10.1016/j.cognition.2014.01.005>.
- Levitt, H. (1971). *Transformed Up-Down Methods in Psychoacoustics*. 49, 467–477.
- Linkenauger, S. A., Geuss, M., Stefanucci, J. K., McCulloch, K. C., Mohler, B. J., & Proffitt, D. R. (2015). The perceptual homunculus: The perception of the relative proportions of the human body. *Journal of Experimental Psychology: General*, 144, 103–113. <http://dx.doi.org/10.1037/xge0000028>.
- Longo, M. R. (2015a). Three-dimensional coherence of the conscious body image. *The Quarterly Journal of Experimental Psychology*, 68, 1116–1123.
- Longo, M. R. (2015b). Implicit and explicit body representations. *European Psychologist*, 20, 6–15. <http://dx.doi.org/10.1027/1016-9040/a000198>.
- Longo, M. R. (2015c). Intuitive anatomy: Distortions of conceptual knowledge of hand structure. *Cognition*, 142, 230–235. <http://dx.doi.org/10.1016/j.cognition.2015.05.024>.
- Longo, M. R. (2017). *Expansion of Perceptual Body Maps Near – But Not Across – The Wrist*, 11, 1–9. <http://dx.doi.org/10.3389/fnhum.2017.00111>.
- Longo, M. R., Azañón, E., Tamè, L., Ferrè, E. R., Maravita, A., Tajadura-Jiménez, A., & Linkenauger, S. A. (2016). Multimodal contributions to body representation. *Multisensory Research*, 1–27. <http://dx.doi.org/10.1163/22134808-00002531>.
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 11727–11732. <http://dx.doi.org/10.1073/pnas.1003483107>.
- Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance*, 37, 720–726. <http://dx.doi.org/10.1037/a0021921>.
- Longo, M. R., & Haggard, P. (2012). Implicit body representations and the conscious body image. *Acta Psychologica*, 141, 164–168. <http://dx.doi.org/10.1016/j.actpsy.2012.07.015>.
- Longo, M. R., Long, C., & Haggard, P. (2012). Mapping the invisible hand: A body model of a phantom limb. *Psychological Science*, 23, 740–742. <http://dx.doi.org/10.1177/0956797612441219>.
- Longo, M. R., Mattioni, S., & Ganea, N. (2015). Perceptual and conceptual distortions of implicit hand maps. *Frontiers in Human Neuroscience*, 9, 1–12. <http://dx.doi.org/10.3389/fnhum.2015.00656>.
- Margolis, A. N., & Longo, M. R. (2015). Visual detail about the body modulates tactile localisation biases. *Experimental Brain Research*, 233, 351–358. <http://dx.doi.org/10.1007/s00221-014-4118-3>.
- Napier, J. (1980). *Hands*. Princeton, NJ: Princeton University Press.
- Pozeg, P., Galli, G., & Blanke, O. (2015). Those are your legs: The effect of visuo-spatial viewpoint on visuo-tactile integration and body ownership. *Frontiers in Psychology*, 6, 1–14. <http://dx.doi.org/10.3389/fpsyg.2015.01749>.
- Press, C., Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Visual enhancement of touch in spatial body representation. *Experimental Brain Research*, 154, 238–245. <http://dx.doi.org/10.1007/s00221-003-1651-x>.
- Saulton, A., Dodds, T. J., Bulthoff, H. H., & de la Rosa, S. (2015). Objects exhibit body model like shape distortions. *Experimental Brain Research*, 233, 1471–1479. <http://dx.doi.org/10.1007/s00221-015-4221-0>.
- Saulton, A., Longo, M. R., Wong, H. Y., Bulthoff, H. H., & de la Rosa, S. (2016). The role of visual similarity and memory in body model distortions. *Acta Psychologica*, 164, 103–111. <http://dx.doi.org/10.1016/j.actpsy.2015.12.013>.
- Scandola, M., Aglioti, S. M., Bonente, C., Avesani, R., & Moro, V. (2016). Spinal cord lesions shrink peripersonal space around the feet, passive mobilization of paraplegic limbs restores it. *Scientific Reports*, 6, 24126. <http://dx.doi.org/10.1038/srep24126>.
- Schicke, T., Bauer, F., & Röder, B. (2009). Interactions of different body parts in peripersonal space: How vision of the foot influences tactile perception at the hand. *Experimental Brain Research*, 192, 703–715. <http://dx.doi.org/10.1007/s00221-008-1587-2>.
- Schicke, T., & Röder, B. (2006). Spatial remapping of touch: Confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11808–11813. <http://dx.doi.org/10.1073/pnas.0601486103>.
- Sposito, A. V., Bolognini, N., Vallar, G., Posteraro, L., & Maravita, A. (2010). The spatial encoding of body parts in patients with neglect and neurologically unimpaired participants. *Neuropsychologia*, 48, 334–340. <http://dx.doi.org/10.1016/j.neuropsychologia.2009.09.026>.
- Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Current Biology*, 12, 233–236. [http://dx.doi.org/10.1016/S0960-9822\(01\)00681-9](http://dx.doi.org/10.1016/S0960-9822(01)00681-9).
- Treede, R.-D., Meyer, R. A., & Campbell, J. N. (1990). Comparison of heat and mechanical receptive fields of cutaneous C-fiber nociceptors in monkey. *Journal of Neurophysiology*, 64, 1502–1513.
- Van Elk, M., Forget, J., & Blanke, O. (2013). The effect of limb crossing and limb congruency on multisensory integration in peripersonal space for the upper and lower extremities. *Consciousness and Cognition*, 22, 545–555. <http://dx.doi.org/10.1016/j.concog.2013.02.006>.
- Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In D. R. Kenshalo (Ed.). *The skin senses* (pp. 195–222). Springfield, IL: Charles L. Thomas.
- Wong, T. S., Ho, R., & Ho, J. (1974). Influence of shape of receptor organ on the horizontal-vertical illusion in passive touch. *Journal of Experimental Psychology*, 103, 414.