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

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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, Bülthoff, & 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

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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 ± 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 (± 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 × 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 ± 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 × 34 W; resolution: 1280 × 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