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Mental body representations retain homuncular shape distortions: Evidence from Weber's illusion

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ABSTRACT

Mental body representations underlying tactile perception do not accurately reflect the body's true morphology. For example, perceived tactile distance is dependent on both the body part being touched and the stimulus orientation, a phenomenon called Weber's illusion. These findings suggest the presence of size and shape distortions, respectively. However, whereas each morphological feature is typically measured in isolation, a complete morphological characterization requires the concurrent measurement of both size and shape. We did so in three experiments, manipulating both the stimulated body parts (hand; forearm) and stimulus orientation while requiring participants to make tactile distance judgments. We found that the forearm was significantly more distorted than the hand lengthwise but not widthwise. Effects of stimulus orientation are thought to reflect receptive field anisotropies in primary somatosensory cortex. The results of the present study therefore suggest that mental body representations retain homuncular shape distortions that characterize early stages of somatosensory processing.

1. Introduction

It has been known since the classic investigations of Weber in the 19th century (Weber, 1834/1978) that the perceived distance between distinct points of touch is dependent upon the skin surface being touched. Two tactile points are perceived as farther apart on body parts with higher tactile sensitivity than those with lower sensitivity (e.g., fingers vs. thigh), a phenomenon known as *Weber's illusion*. Several studies with varying methods have since verified and expanded upon this classic finding (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; de Vignemont, Majid, Jola, & Haggard, 2009; Goudge, 1918; Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Marks et al., 1982; Taylor-Clarke, Jacobsen, & Haggard, 2004).

The neural mechanisms underlying Weber's illusion are at present poorly understood. Differences in tactile distance perception are often attributed to cortical magnification factors in primary somatosensory cortex (SI) (Cholewiak, 1999; Green, 1982). However, several recent studies have found that tactile distance perception is modulated by altered multisensory input (Miller, Longo, & Saygin, 2014; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004). Further, quantifications of the magnitude of Weber's illusion (Taylor-Clarke et al., 2004) found it to only be about 10% of what would be expected from cortical magnification factors in SI (Penfield & Boldrey, 1937). These findings suggest that Weber's illusion is also dependent

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upon later stages of somatosensory processing involved in the construction of higher-level mental body representations (Serino & Haggard, 2010). These representations are likely located in the posterior parietal cortex (Bolognini & Maravita, 2007; Duhamel, Colby, & Goldberg, 1998) and arise from reciprocal interactions with SI (Cooke et al., 2014; Goldring et al., 2014).

Weber's illusion is commonly used to investigate the morphology of these higher-level mental body representations. In one popular version of a tactile distance judgment task (TDJ), participants compare the perceived distance of two temporally distinct presentations of touch. Touch is typically administered to two distinct body parts, in order to quantify differences in the represented *size* of body parts (de Vignemont, Ehrsson, & Haggard, 2005; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004). It is inferred that the body part with the greatest perceived tactile distance is represented as larger than the other. Recently, the TDJ has been administered within the same body part, in order to investigate its represented *shape* (Longo & Haggard, 2011). Participants made distance judgments about touch administered in two different orientations (transverse and longitudinal). Longo and Haggard found that tactile distance perception on the hand was greater in the transverse orientation, suggesting that the representation is short and squat. This finding converges with other methods for mapping perceived body shape (Longo & Haggard, 2010), a continuity suggesting that Weber's illusion reflects distortions in body representation. However, this task is limited to measuring the aspect ratio *within* body parts and not shape differences *between* them. A full morphological characterization of mental body representations would require both size *and* shape to be measured *concurrently*. The present study takes the first steps toward this goal.

Here, we present a detailed investigation into the morphological properties of hand and forearm representations. We report three psychophysics experiments that investigated the effect of stimulus orientation on Weber's illusion *between* body parts. In all experiments, touch was presented in two orientations—transverse and longitudinal—to each body part. In Experiment 1, tactile points presented to the hand were compared against tactile points presented to the arm. In Experiments 2 and 3, we isolated tactile distance perception on the hand and arm individually; tactile points presented to a target body part (Experiment 2: hand; Experiment 3: arm) were compared to a shared reference body part, the forehead, which is commonly used when measuring tactile distance perception on the hand and arm (e.g., Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015; Canzoneri et al., 2013; de Vignemont et al., 2005; Miller et al., 2014).

The results of these experiments have important implications for our understanding of the mechanisms underlying tactile distance perception generally, and Weber's illusion specifically. First, by manipulating orientation, we can concurrently measure differences in the represented size and shape of these body parts. This allows us to overcome the limitations of previous methods discussed earlier. Second, by measuring tactile distance perception on the arm and hand separately, we can investigate whether shape distortions measured in Experiment 1 are task-independent characteristics of mental body representations. Third, and most important, our finding would shed light on the neural mechanisms underlying Weber's illusion. Effects of stimulus orientation are thought to reflect anisotropies in receptive field (RF) geometry of SI neurons (Cody, Garside, Lloyd, & Poliakoff, 2008; Fuchs & Brown, 1984; Gibson & Craig, 2005; Wheat & Goodwin, 2000). Therefore, orientation-specific differences in Weber's illusion would suggest an intimate relationship between body representations at early and late stages of somatosensory processing (Serino & Haggard, 2010).

Based on known differences in the size of the homuncular representations of the arm and hand (Penfield & Boldrey, 1937), we hypothesized that we would find a significant Weber's illusion between the two body parts. We further hypothesized that the presence of a Weber's illusion between the arm and hand would reflect differences in RF shape. A model of Weber's illusion that links tactile distance perception to low-level properties of SI—the pixel model (Longo & Haggard, 2011)—motivated these hypotheses.

2. Methods

2.1. Participants

Twenty right-handed adults (13 females) between 19 and 29 years of age (mean: 21.1; SD: 2.2) participated in Experiment 1; Twenty-five right-handed adults (14 females) between 19 and 34 (mean: 21.7; SD: 3.1) participated in Experiment 2; Twenty-five right-handed adults (20 females) between 18 and 34 (mean: 21.3; SD: 3.3) participated in Experiment 3. Each participant took part in only one experiment. The institutional review board at the University of California, San Diego approved each experiment, and all participants gave written informed consent before participating.

2.2. Tactile distance judgment task

The methods used in each experiment were almost identical. We measured Weber's illusion with the TDJ (Fig. 1). On each trial, two pairs of tactile stimuli (two wooden posts, each tapered to a 1 mm flat point) were applied sequentially, one pair to a *target* body part and the other to a *reference* body part. Tactile stimuli were applied for approximately one second, with approximately two seconds in between the administration of each stimulus pair. The combination of body sites was the only factor that differed between experiments (target vs. reference); Experiment 1: hand dorsum vs. forearm dorsum; Experiment 2: hand dorsum vs. forehead; Experiment 3: forearm dorsum vs. forehead. Tactile stimuli were always delivered to the middle of the body part, and the dominant arm/hand (i.e., right). Participants sat blindfolded with their arms rested flat on a table and their fingers splayed. Their task on each trial was to judge whether the distance between the two posts felt farther