CORTEX 73 (2015) 289–297

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research Report

Dissociable routes for personal and interpersonal visual enhancement of touch

Brianna Beck [a,b,c,*], *Caterina Bertini* [a,b], *Patrick Haggard* [c] *and*
Elisabetta Làdavas [a,b]

[a] *Centre for Studies and Research in Cognitive Neuroscience, University of Bologna, Viale Europa 980, Cesena, 47023, Italy*
[b] *Department of Psychology, University of Bologna, Viale Berti Pichat 5, Bologna, 40127, Italy*
[c] *Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London, WC1N 3AZ, United Kingdom*

ARTICLE INFO

Article history:
Received 18 February 2015
Reviewed 28 March 2015
Revised 26 May 2015
Accepted 14 September 2015
Action editor H. Branch Coslett
Published online 28 September 2015

Keywords:
Body
Multisensory
Proprioception
Self
Somatosensory

ABSTRACT

Seeing a hand can enhance tactile acuity on the hand, even when tactile stimulation is not visible. This visual enhancement of touch (VET) occurs both when participants see their own hand (personal VET), and when they see another person's hand (interpersonal VET). Interpersonal VET occurs irrespective of where the viewed hand appears, while personal VET is eliminated when visual and proprioceptive signals about the location of *one's own* hand are incongruent. This suggests that the neural mechanisms for VET may differ according to ownership of the seen hand. We used continuous theta-burst transcranial magnetic stimulation (TMS) to disrupt either the human ventral intraparietal area (hVIP), which integrates tactile, proprioceptive, and visual information about one's own body, or the extrastriate body area (EBA), which processes visual body information irrespective of ownership. Participants then judged the orientation of tactile gratings applied to their hand while viewing images of their own hand, another person's hand, or a non-body object on a screen placed over their actual hand. Disrupting the hVIP attenuated personal VET but did not affect interpersonal VET, suggesting the hVIP is only involved in VET when one's own hand is seen. Disrupting the EBA reduced both personal and interpersonal VET, suggesting it is common to both routes.

1. Introduction

Vision of the body enhances spatial tactile acuity on the seen body part, even if the tactile stimulation itself is invisible, or vision is non-informative about the stimulus (Cardini, Haggard, & Làdavas, 2013; Cardini, Longo, Driver, & Haggard, 2012; Cardini, Longo, & Haggard, 2011; Fiorio & Haggard, 2005; Haggard, 2006; Haggard, Christakou, & Serino, 2007;

---

[*] *Corresponding author*. Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London, WC1N 3AZ, United Kingdom.

E-mail address: brianna.beck@ucl.ac.uk (B. Beck).

http://dx.doi.org/10.1016/j.cortex.2015.09.008

Harris, Arabzadeh, Moore, & Clifford, 2007; Kennett, Taylor-Clarke, & Haggard, 2001; Konen & Haggard, 2014; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007; Serino, Padiglioni, Haggard, & Làdavas, 2009; Taylor-Clarke, Kennett, & Haggard, 2002, 2004). This visual enhancement of touch (VET) is unlikely to be simply an effect of directing visuo-spatial attention because looking at a non-body object appearing in the same location as the body part does not improve tactile acuity relative to a control condition of complete darkness (Kennett et al., 2001; Serino et al., 2009). Rather, seeing a body part may activate a multisensory representation of the body that is able to modulate the activity of unimodal, somatotopically organized somatosensory cortex (Fiorio & Haggard, 2005; Konen & Haggard, 2014; Serino et al., 2009; Taylor-Clarke et al., 2002).

Prior research suggests that VET involves changes in the activity of the primary somatosensory cortex (SI) (Fiorio & Haggard, 2005; Serino et al., 2009; Taylor-Clarke et al., 2002). However, the sources of this modulation are not well understood. According to one view, posterior parietal cortex may receive inputs from body-specific areas in the occipito-temporal visual cortex and then send feedback to SI that influences the corresponding part of the somatotopic map (Fiorio & Haggard, 2005; Kennett et al., 2001; Taylor-Clarke et al., 2002). This view is consistent with primate studies that identified multisensory body-centered response patterns from single-cell recordings in the monkey ventral intraparietal area (VIP). Neurons in this posterior parietal area responded to visual, tactile, vestibular, and auditory information pertaining to self-motion (Avillac, Ben Hamed, & Duhamel, 2007; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Duhamel, Colby, & Goldberg, 1998; Schlack, Hoffmann, & Bremmer, 2002; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). Functional magnetic resonance imaging (fMRI) studies support the existence of a similar multisensory body-centered representation in the human intraparietal sulcus (IPS) (Bremmer et al., 2001; Gentile, Petkova, & Ehrsson, 2011; Makin, Holmes, & Zohary, 2007). Importantly, Makin et al. (2007) found a hand-centered representation in the anterior IPS where visual, tactile, and proprioceptive inputs converge. Disrupting this area by delivering transcranial magnetic stimulation (TMS) during a brief interval between viewing one's own hand and receiving tactile stimulation eliminates VET (Konen & Haggard, 2014). The anatomical and temporal specificity of the disruptive effect suggests that the human ventral intraparietal area (hVIP) of the anterior IPS contributes to VET by providing a relay between visual and tactile cortices.

The studies described above examined the effect of seeing *one's own* body on tactile acuity. Seeing the body of another person can also enhance spatial tactile acuity on the corresponding body part of the observer (Cardini et al., 2013; Haggard, 2006). Nevertheless, the mechanisms mediating VET in these two situations may be different, because they are differentially sensitive to spatial incongruence. VET was abolished when one's own hand was seen in a location incongruent with the hand's true location, suggesting that proprioceptive signals regarding spatial location contribute to personal (own-body) VET. However, when the viewed hand clearly belonged to another person, VET was found irrespective of whether the hand appeared at the proprioceptively sensed location of the participant's own hand or elsewhere (Cardini et al., 2013). Thus, personal VET relies on congruent proprioceptive information, and is therefore *inherently* self-referential (O'Shaughnessy, 1995). In contrast, the integration of congruent proprioceptive information is not required for interpersonal VET, when the seen hand belongs to another person.

This behavioral dissociation raises the possibility of two dissociable routes linking visual and somatosensory areas to produce VET. A self-specific route would pass through multisensory regions that also process proprioceptive signals, while the second, interpersonal route would pass through a set of intermediate relays insensitive to proprioceptive processing. Importantly, both routes might originate in a common visual source area; indeed, extrastriate occipital cortex contains visual areas that are specific for viewing bodies and body parts irrespective of whether they belong to oneself or another person (Chan, Peelen, & Downing, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001; Hodzic, Kaas, Muckli, Stirn, & Singer, 2009; Hodzic, Muckli, Singer, & Stirn, 2009; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Urgesi, Berlucchi, & Aglioti, 2004). Equally, both VET routes presumably converge on SI, which contains the key cortical circuitry underlying tactile acuity (Roland, 1987). Nevertheless, the neural mechanisms that *mediate* personal (own-body) and interpersonal (other-body) VET may be at least partially distinct, relying upon different sources of SI modulation.

We have tested the hypothesis of dissociated routes for personal and interpersonal VET by using TMS to disrupt the intermediate relay specific to the personal route, the hVIP (Konen & Haggard, 2014). Changes to personal but not interpersonal VET from such disruption would support the dual route hypothesis. We further sought to confirm that both routes have a common visual source in body-specific areas of the occipital cortex. We tested tactile acuity while participants viewed high-quality visual images of their own hand, another person's hand, and a non-body object. Prior to the tactile acuity task, participants underwent continuous theta-burst stimulation (cTBS) to modulate the left hVIP, a multisensory area implicated as a source of SI modulation in personal VET (Konen & Haggard, 2014) but untested as of yet in interpersonal VET. We hypothesized that temporarily disrupting the hVIP would reduce enhancement of tactile acuity at the sight of one's own hand but leave enhancement at the sight of another's hand intact. In a further session, cTBS was applied over the extrastriate body area (EBA), a region in the lateral occipito-temporal cortex involved in the visual processing of human bodies (Downing et al., 2001; Pitcher et al., 2009; Urgesi et al., 2004). The EBA appears either insensitive (Chan et al., 2004; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009) or only minimally sensitive (Vocks et al., 2010) to whether one's own body or another's body is viewed. We predicted that disrupting the EBA would affect both personal and interpersonal VET because it provides a common visual source for VET, before the personal and interpersonal routes divide.