Brain and Cognition 86 (2014) 32–41

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Weber's law in tactile grasping and manual estimation: Feedback-dependent evidence for functionally distinct processing streams

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ARTICLE INFO

Article history:
Accepted 27 January 2014
Available online 18 February 2014

Keywords:
Allocentric
Egocentric
Grasping
Perception
Tactile
Weber's law

ABSTRACT

The goal of the present investigation was to test the somatosensory processing model's (SPM) assertion that tactile actions and perceptions are mediated via egocentric and allocentric frames of reference, respectively (Dijkerman & de Haan's 2007: *Behavioral and Brain Sciences*). To accomplish that objective, Experiment 1 required that participants use their right hand to grasp and manually estimate differently sized objects placed on the forearm and palm of their left hand. Following each manual estimation trial, participants grasped the target object to equate tasks (i.e., grasping vs. manual estimation) for terminal tactile feedback. Notably, the different object locations (i.e., forearm and palm) were used to examine whether location-specific differences in mechanoreceptor density impacts the percept of object size (i.e., Weber's illusion). In addition, we computed just-noticeable-difference (JND) scores to determine whether grasping and manual estimations adhere to, or violate, the allocentric principles of Weber's law. Results for the grasping task elicited a null expression of Weber's illusion and JNDs for this task violated Weber's law. Results for the manual estimation task similarly exhibited a null expression of Weber's illusion; however, JNDs for the palm but not the forearm condition adhered to Weber's law. Experiment 2 showed that withdrawing terminal tactile feedback during forearm condition manual estimations resulted in responses that adhered to Weber's law. Thus, results provide some support for the SPM's contention that grasping and manual estimations are mediated via ego- and allocentric frames of reference, respectively. However, results further indicate that the dissociation is not complete and is, in part, influenced by the sensory consequences (i.e., terminal tactile feedback) associated with the response.

1. Introduction

Although vision plays a predominant role in our day-to-day activities, tactile cues from cutaneous mechanoreceptors support a range of perceptual and motor responses. Indeed, consider the scenario in which a friend places a Loonie (i.e., Canadian one-dollar coin) in the palm of your left hand in preparation for your purchase from a vending machine. Given previous experience with Loonies, the tactile cues arising from the current experience (e.g., size) would allow you to perceive that you have been provided the appropriate coinage (i.e., a perceptual task). As well, tactile cues would provide metrical information guiding your right limb to grasp the Loonie (i.e., an action task) so that it could be inserted into the vending machine. Interestingly, Dijkerman and de Haan's (2007) somatosensory processing model (SPM) asserts that tactile perceptions and actions are mediated via functionally and anatomically distinct cortical pathways. In particular, the SPM states that a ventral pathway extending from the anterior parietal cortex (APC) and the secondary somatosensory cortex (SII) to the posterior insular mediates tactile perceptions, whereas a dorsal pathway extending from the APC via SII to the posterior parietal cortex (PPC) supports actions. Moreover, the SPM contends that the ventral pathway supports perceptual judgments by comparing the *relative* properties of a target object with other objects and/or by accessing stored representations from previous tactile experiences (i.e., allocentric frame of reference). In contrast, the dorsal pathway is thought to mediate actions independent of top-down knowledge via *absolute* comparisons between the object and the body (i.e., egocentric frame of reference; for review see Lederman & Klatzky,

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http://dx.doi.org/10.1016/j.bandc.2014.01.014
0278-2626/

2009). For example, the ventral stream is thought to qualify the size of an object as being bigger or smaller (i.e., relative information) than other objects (i.e., allocentric frame of reference), whereas the dorsal stream is thought to access metrical information (i.e., absolute) computed in body-centered coordinates (i.e., egocentric frame of reference).

In support of the SPM, Paillard, Michel, and Stelmach's (1983) seminal work described an individual with a putative ventral pathway lesion that was unable to report (via oral response) whether static pressure had been applied to her affected (i.e., contralesional) limb; however, she was able to use her unaffected (i.e., ipsilesional) limb to accurately point to the stimulus' veridical location (i.e., on the affected limb). Thus, Paillard et al. show that obligatory awareness of tactile stimulation is independent of the use of egocentric information for action control. Moreover, Anema et al. (2009) evaluated two brain-injured individuals (JO and KE) in tasks requiring the localization of tactile stimuli applied to the dorsal surface of the affected hand. In one task, participants used their unaffected limb to point to the location of stimulation as represented on a picture of the hand (i.e., perceptual task), and in a second task used their unaffected limb to point to the stimulus' veridical location (i.e., action task). Results showed that JO accurately localized tactile cues in the action task but not in the perceptual task, whereas KE demonstrated the converse pattern. Notably, although Anema et al.'s neuroimaging data do not provide a clear localization for JO or KE's lesions they do support the SPM's contention that dissociable pathways mediate actions and perceptions.

Weber's illusion is thought to provide a proxy for tactile dissociation in non-clinical populations. In particular, Weber observed that the two points of a drafting compass moved continuously along a body region with a low density of cutaneous mechanoreceptors (e.g., the forearm) to a region with an increased density (e.g., the palm) induced the precept of divergence, whereas movement in the opposite direction resulted in the percept of convergence. In accounting for this phenomenon, Weber proposed that the illusion is conditioned upon the density (and hence spatial resolution) of receptors in different bodily regions (as cited in Goudge, 1918). More recently, Anema, Wolswijk, Ruis, and Dijkerman's (2008) employed a variant of Weber's methodology wherein participants used their right hand to manually estimate (i.e., perceptual task) and grasp (i.e., action task) differently sized objects (widths of 50, 60, 70 and 80 mm) placed on the supinated palm or forearm of their left hand. Results for the manual estimation task showed that participants perceived objects placed on their palm as being larger than objects placed on their forearm, whereas results for the grasping condition showed that peak grip apertures (PGAs) for objects placed on the forearm were larger than the palm. Concerning the perceptual task, Anema et al. interpreted their findings as reflecting the expression of Weber's illusion. More specifically, the authors proposed that the illusion manifests due to asymmetrical receptor density imparting a non-veridical and allocentrically based rescaling of tactile cues to maintain size-constancy (see also Taylor-Clarke, Jacobsen, & Haggard, 2004). Concerning the motor task, the authors proposed that the reduced density of receptors on the forearm increases uncertainty of object size and results in larger PGAs to avoid the possibility of colliding with the object (see also Jakobson & Goodale, 1991 for visuomotor findings). Most notably, Anema et al. concluded that the selective expression of Weber's illusion in the manual estimation task supports the SPM's contention that perceptions and actions are mediated via functionally distinct frames of reference.

It is important to recognize that results for Anema et al., 2008 manual estimation task offers an interpretation other than the expression of Weber's illusion. Indeed, Anema et al. reported that their 60, 70 and 80 mm objects produced larger manual estimations in the palm as compared to the forearm condition; however, their smallest object (i.e., 50 mm) did not differ between conditions. Moreover, the slope relating manual estimations to object size were shallower in the forearm as compared to the palm. Thus, it is possible that smaller objects (i.e., <50 mm) may produce larger manual estimations in the forearm as compared to the palm condition. Certainly such a finding would counter the expression of Weber's illusion, and also suggest that obligatory judgments related to the size of a *static* object do not represent a direct framework for inducing illusory percepts of size. Instead, the shallower slope for the forearm condition observed in Anema et al.'s study may reflect a perceptual averaging wherein participants report a target object as being the average size of a given set (Albrecht & Scholl, 2010; Albrecht, Scholl, & Chun, 2012; Ariely, 2001; see also Pepper & Herman, 1970; Spencer, 1961). To address this issue, the present investigation employed the same general methodology of Anema et al. and instructed participants to manually estimate or grasp (with their right hand) differently sized objects placed on the forearm and palm of their left hand. In doing so, we employed the object width (i.e., 50 mm) that Anema et al. showed to produce equivalent palm and forearm manual estimations and also employed a smaller set of objects (i.e., 20, 30 and 40 mm). In terms of predictions, if a receptor density asymmetry leads to the expression of Weber's illusion then manual estimations for the palm should be larger than matched-objects on the forearm regardless of object size (i.e., Anema et al., 2008). In contrast, if a receptor density asymmetry engenders a strategy of perceptual averaging then the magnitude and direction of the difference between palm and forearm condition manual estimations should be object-size specific. Indeed, the perceptual averaging hypothesis predicts that manual estimations for small objects (i.e., 20 and 30 mm) will be larger for the forearm as compared to the palm condition, whereas the converse pattern will be observed for larger objects (i.e., 40 and 50 mm). Moreover, evidence favouring perceptual averaging would indicate that size judgments related to a *static* object do not provide a proxy for Weber's illusion. Regarding the grasping task, in line with Anema et al. it is proposed that increased uncertainty of object size in the forearm condition will result in larger PGAs than the palm condition.

In addition to examining whether manual estimations and goal-directed grasping are differentially 'tricked' by Weber's illusion, we examined the extent to which such tasks adhere to, or violate, the psychophysical principle of *Weber's law*. In particular, Weber's law states that changes in a stimulus that will be 'just noticeable' are a constant ratio of the original stimulus magnitude and that the sensitivity of detecting a change in any physical continuum is *relative* as opposed to *absolute*. Thus, the just noticeable difference (JND) for weaker stimuli is smaller and the resolution is greater than more robust stimuli in the same sensory continuum. As such, a comparison of the JNDs associated with manual estimations and grasping provides a direct framework for examining whether such tasks are mediated via distinct metrics (i.e., relative vs. absolute) and their associated frames of reference (i.e., allocentric vs. egocentric). Previous work by our group has computed the within-participant standard deviations of grip aperture (i.e., the JNDs) to determine participants' sensitivity to detecting changes in the visual size of objects (Heath, Holmes, Mulla, & Binsted, 2012; Heath, Mulla, Holmes, & Smuskowitz, 2011; Holmes & Heath, 2013; Holmes, Lohmus, McKinnon, Mulla, & Heath, 2013; Holmes, Marriott, Mackenzie, Sin, & Heath, 2012; see also Ganel, Chajut, & Algom, 2008). Fig. 1 provides exemplar data from a previous study (i.e., Holmes & Heath, 2013) and shows that JNDs for visually based manual estimations (i.e., the comparator stimulus) increased as a function of increasing stimulus intensity (i.e., the target object/original stimulus), whereas JNDs for the grasping task (computed at the time of PGA) were refractory to changes in object size. Thus, manual estimation but not grasping adhered to Weber's law: a finding that has been taken as direct evidence that visually based