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Concurrent use of somatotopic and external reference frames in a tactile mislocalization task

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ABSTRACT

Localizing tactile stimuli on our body requires sensory information to be represented in multiple frames of reference along the sensory pathways. These reference frames include the representation of sensory information in skin coordinates, in which the spatial relationship of skin regions is maintained. The organization of the primary somatosensory cortex matches such somatotopic reference frame. In contrast, higher-order representations are based on external coordinates, in which body posture and gaze direction are taken into account in order to localise touch in other meaningful ways according to task demands. Dominance of one representation or the other, or the use of multiple representations with different weights, is thought to depend on contextual factors of cognitive and/or sensory origins. However, it is unclear under which situations a reference frame takes over another or when different reference frames are jointly used at the same time. The study of tactile mislocalizations at the fingers has shown a key role of the somatotopic frame of reference, both when touches are delivered unilaterally to a single hand, and when they are delivered bilaterally to both hands. Here, we took advantage of a well-established tactile mislocalization paradigm to investigate whether the reference frame used to integrate bilateral tactile stimuli can change as a function of the spatial relationship between the two hands. Specifically, suprathreshold interference stimuli were applied to the index or little fingers of the left hand 200 ms prior to the application of a test stimulus on a finger of the right hand. Crucially, different hands postures were adopted (uncrossed or crossed). Results show that introducing a change in hand-posture triggered the concurrent use of somatotopic and external reference frames when processing bilateral touch at the fingers. This demonstrates that both somatotopic and external reference frames can be concurrently used to localise tactile stimuli on the fingers.

1. Introduction

Localizing tactile stimuli on our body surface, despite its apparent simplicity, is a very complex process that requires the involvement of multiple representations of the tactile event using different coordinate systems (Azañón & Soto-Faraco, 2008; Azañón, Stenner, Cardini, & Haggard, 2015; Badde, Röder, & Heed, 2014; Longo, Azañón, & Haggard, 2010). At early stages of somatosensory processing information is represented in a body-centered, somatotopically organized reference frame in which tactile events are referred to distinct locations on the skin. This is reflected by the brain's somatotopic organization in the primary somatosensory cortex (Penfield & Boldrey, 1937; Tamè, Moles, & Holmes, 2014). In further stages of processing, however, the tactile event can be identified with respect to body-side (Farnè, Brozzoli, Làdavas, & Ro, 2007) or with respect to external space using an egocentric/allocentric reference frame (Azañón, Camacho, & Soto-Faraco, 2010). The transition from body-centered to allocentric coordinates is achieved by making use of postural information coming from proprioceptive, visual or vestibular inputs (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011; Holmes & Spence, 2004) and it is likely to be mediated by sensory regions (Hamada & Suzuki, 2005) and associative brain areas in the posterior parietal cortex (Rusconi

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et al., 2014). This processing of tactile localization from one reference frame to another has been named tactile remapping (Driver & Spence, 1998).

The study of incorrect localizations of faint tactile stimuli to different regions of the body (i.e., tactile mislocalization), proved useful when studying the nature of representations underlying tactile processing at the fingers (Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer, Maier, Braun, & Birbaumer, 2000). In a typical tactile mislocalization task, near-threshold tactile stimuli are delivered to one fingertip at a time to evoke mislocalizations to the other (non-stimulated) fingers of the same hand. Incorrectly localized stimuli are predominantly attributed to fingers that are neighboured to the stimulated ones (e.g., the index or ring finger, when the middle finger is stimulated), thus revealing the dominance of a somatotopic representation when solving this tactile task (Schweizer et al., 2000). Tactile mislocalization profiles appear to be highly context dependent, as revealed by experiments employing interfering stimuli in a mislocalization setup. For instance, Braun, Hess, Burkhardt, Wühle, and Preissl (2005) applied supra-thresholds interference stimuli on the left thumb or little finger either 200 or 500 ms (ms) prior to presenting a near-threshold test stimulus on the right hand. Results showed that stimuli applied on the left hand strongly interfere with the mislocalization profile of the right hand in a finger-specific manner, namely as a function of the fingers' anatomical topology. Tactile stimulation of the left thumb increased mislocalizations to the right thumb. Similarly, stimulation of the left little finger caused a shift in localization responses towards the right ring finger. This suggests that bilateral interactions operate primarily on a skin-based representation – which is compatible with the organization of the primary somatosensory cortex. By skin-based coordinates we mean somatotopic representations that are present regardless of body sides (note that this representation has also been termed anatomical or somatotopic).

In all previous mislocalization studies conducted by Braun and co-workers (Braun et al., 2005; Schweizer et al., 2000; Schweizer et al., 2001) the hands were always kept in their respective hemispace – the left hand on the left side, the right hand on the right side (Braun et al., 2005). As yet it is unclear whether and to what extent representations of bilateral tactile interactions based on skin coordinates dominate also when postural changes require the adoption of external reference frame coordinates. A first possibility is that the sensory representations are updated by posture changes (e.g., Azañón & Soto-Faraco, 2008; Gallace & Spence, 2005; Heed & Röder, 2010; Longo, 2015; Shore, Gray, Spry, & Spence, 2005; Zampini, Harris, & Spence, 2005). An alternative possibility, however, is that the fingers of the two hands are more strongly constrained into a somatotopic representation and much less sensitive to posture changes (e.g., Longo & Haggard, 2010; Longo & Haggard, 2011; Mancini, Longo, Iannetti, & Haggard, 2011; Tamè, Farnè, & Pavani, 2011).

In the present study, we tested this question directly by examining the effect of posture changes (crossed vs. uncrossed hand posture) on the mislocalization profile at the right hand, while the left hand is concurrently stimulated or not stimulated. If the skin-based coordinate representation underlying finger interactions between the two body-sides is preserved regardless of hands posture in external space, the same finger-specific mislocalization profile should emerge regardless of posture. By contrast, if changing hands' posture triggers a representation remapping also for bilateral tactile interactions a different mislocalization profile should emerge when the hands are crossed compared to when they are uncrossed. Finally, if skin-based and external-based coordinates can be concurrently used, the mislocalization profile should be modulated by changes in hands' posture while keeping trace of the finger-specific interactions.

2. Materials and methods

2.1. Participants

Twenty participants (mean ± SD = 23.0 ± 4.2 years; range 19–37 years; 11 females) took part in the study. Participants gave their informed consent prior to participation and reported normal or corrected to normal vision and normal somatosensation. The study was approved by the local ethics panel. Only participants that were right handed by self-report were enrolled in the study. A formal assessment of their handedness was done by the Edinburgh Handedness Inventory on 15 out of 20 participants (Oldfield, 1971; M = 94, range 61–100). Data of five participants were lost due to flawed data storage.

2.2. Stimulation

During the experiment participants placed both hands palms down onto the hand supports of the stimulation apparatus (Fig. 1). Piezoelectrical stimulators were placed on four fingers of the right hand and two fingers of the left hand. Tactile stimulators were modified Braille elements of computer keyboards for the blinds (QuaeroSys Medical Devices UG, Schotten, Germany). Stimulation units were placed beneath four fingers of the right

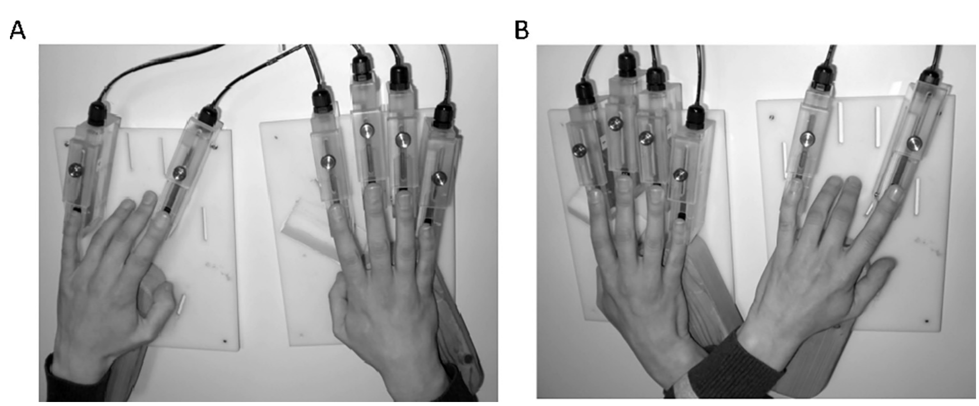

Fig. 1. Illustration of the stimulation devices and the hand's posture across conditions. The blanket covering the hands during the experiment, and the numbers assigned to each finger for the response are not shown. (A) Hands uncrossed. (B) Hands crossed. Note that the spatial relationship between the fingers receiving the prime stimuli on the left hand and fingers receiving the near-threshold targets on the right hand change as a function of posture. Index fingers are close to one another in the uncrossed posture, but farther apart in the crossed posture; whereas little fingers are farther apart in the uncrossed posture but close to one another in the crossed posture.