



Electrophysiological correlates of tactile remapping



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ARTICLE INFO

Article history:

Received 25 September 2012

Received in revised form

3 April 2013

Accepted 23 April 2013

Available online 30 April 2013

Keywords:

Tactile processing

Somatosensory evoked potentials

Spatial reference frames

Hemispheric lateralization

Temporal order judgments

ABSTRACT

Orienting our gaze or attention to the location of tactile events in the skin feels natural and effortless. However, this process requires combining somatosensory and proprioceptive information in a non-trivial, time consuming, fashion. Here we address the time course of tactile remapping, from somatotopically-based representations, to a spatiotopic reference frame. We compared electrical responses at the scalp evoked by touch at one finger as participants held their arms straight or else, crossed about the body midline. This postural manipulation creates a conflict between frames of reference, which can be used to reveal the consequences of spatial remapping. Behavioural performance was gauged online for crossed and uncrossed postures using bimanual temporal order judgment (TOJ) trials occurring occasionally during the recording session. The first electrophysiological signs of tactile remapping were observed around 70 ms after the tactile event, overlapping in time with the somatosensory component N80. This electrophysiological effect was strongly lateralized to the left scalp and independent of the hand being stimulated. Moreover, participants who manifested a stronger behavioural conflict between frames of reference in the TOJ task displayed a larger electrophysiological effect. Based on these findings, and the known properties of the somatosensory network, we argue that remapping of tactile space depends on fast feedback projections from association areas of the parietal cortex, and encompasses a left-lateralized fronto-parietal network supporting the selection of guided actions.

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1. Introduction

Representing the spatial origin of sensory stimulation is of the essence in many of the motor and cognitive behaviours displayed by most animals, including humans. However, the coordination between the various spatial reference frames in which information is encoded represents a fundamental challenge. For example, visual stimuli are initially represented in retinotopic coordinates, but oculomotor behaviour unfolds in a head/trunk-centred coordinate system (Duhamel, Bremmer, BenHamed, & Graf, 1997; Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). Similarly, in touch, sensations on the skin are initially projected to somatotopically-organised maps in somatosensory cortex, and then quickly referred to an external frame of reference that represents information relative to some body part, thus providing an adequate read-out for effector systems (Pouget & Sejnowski, 1997; Cohen & Andersen, 2004). Here we address the time course

of this tactile remapping process, and in particular, we track down its earlier stages. Our aim is to infer some of the functional properties of the brain circuit that supports this relatively unknown aspect of human spatial processing.

Evidence for the dominance of an external reference frame in the execution of tactile tasks comes from deficits in brain damaged patients (e.g., Aglioti, Smania, & Peru, 1999; Moscovitch & Behrmann, 1994) and posture-related studies in healthy humans, often with crossed-hands (Soto-Faraco, Ronald, & Spence, 2004; Spence, Pavani, & Driver, 2004). Crossing the hands over about the body midline induces a misalignment between the anatomical location in body space and the external origin of tactile events, thus offering a chance to dissociate the dominance of one or the other type of representation. Several prior studies show that cross-modal interactions (Spence et al., 2004) and attention orienting (Kennett, Eimer, Spence, & Driver, 2001) tested with crossed hands often abide to an external frame of reference. Thus, in cross-modal cueing, a touch at one hand facilitates detection of upcoming visual targets near that hand (presented 200–350 ms later), regardless of where the hand is placed in space (Kennett et al., 2001; Kennett, Spence, & Driver, 2002). Interestingly, however, Azañón and Soto-Faraco (2008a) found that at shorter cue-target intervals (30–60 ms), this spatial validity effect depends instead on the anatomical side of the stimulated hand, reflecting the initial

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somatotopic reference frame for touch (see also Azañón & Soto-Faraco, 2008b; Azañón, Camacho & Soto-Faraco 2010). According to these results, tactile representations undergo a transition between an anatomical and an externally-based reference frame (between 60 and 360 ms). Similar conclusions regarding the timing of remapping have been inferred from studying saccades to tactile targets at the hands. In particular, when the arms are crossed, quick saccades to tactile events are often executed to the wrong direction and then corrected online about 190 ms after initiation, suggesting that body posture is already encoded by this time (Groh & Sparks, 1996; Overvliet, Azañón, & Soto-Faraco, 2011). In line with this idea, the perceived temporal order of two successive tactile events applied to both hands is often reversed at intervals shorter than 300 ms when the hands are crossed (e.g., Yamamoto & Kitazawa, 2001; Shore, Spry, & Spence, 2002; Wada, Yamamoto, & Kitazawa, 2004; Kóbor, Furedi, Kovacs, Spence, & Vidnyanszky, 2006). This has been proposed to reflect the time it takes to refer a tactile event in external space, with the second touch interfering with the remapping process of the first touch (see also Kitazawa, 2002).

It is important to understand the sequence of neural events leading from anatomically- to externally-based representations, and to help infer its underlying brain network. Although some studies report modulation of somatosensory-evoked activity by online finger movement (Huttunen et al., 1996), evidence for the influence of an external reference frame on neural activity is mostly confined to *spatial attention* paradigms. In particular, spatial attention effects on the somatosensory evoked potentials (SEPs), typically expressed in mid-latency components (from N80; Eimer & Forster, 2003), are enhanced by increasing hand separation (Eimer, Forster, Fieger, & Harbich, 2004; Gillmeister, Adler, & Forster, 2010) and abolished by hand crossing (Eimer, Cockburn, Smedley, & Driver, 2001; Eimer, Forster, & Van Velzen, 2003). These results suggest that external space is already taken into account when spatial attention is deployed, though the influence of an anatomical reference frame remains evident at latencies up to 100–140 ms (Heed & Röder, 2010). Two recent fMRI studies have addressed tactile temporal order tasks across different arm postures (Takahashi et al., 2012; Wada et al., 2012). Despite the many differences between these studies in methodology and focus, their results reveal surprising coincidences. First, both studies highlighted the relevance of posterior parietal areas for the spatial updating of tactile representations across postures (in line with Azañón, Longo, Soto-Faraco & Haggard, 2010; Bolognini & Maravita, 2007). In addition, Takahashi et al. reported the activation of frontal areas, thus suggesting the importance of a coordinated fronto-parietal network (see also Lloyd, Shore, Spence, & Calvert, 2003). Second, in both studies, the comparison between crossed and uncrossed postures resulted in stronger/more extended BOLD responses in the left hemisphere.

Here, and in contrast to these previous fMRI studies, we used SEPs to concentrate on the temporal course of remapping. In addition, contrary to most electrophysiological research to date, we addressed tactile remapping outside the context of *spatial attention*. That is, we did not study the effects of attended vs. unattended events. We instead focused on the moment at which the spatial representation of the tactile event starts to be encoded in external coordinates, rather than the timing at which the spatial allocation of *attention* is expressed in such terms. To this aim, we compared SEPs to single, predictable, finger stimulation with hands uncrossed (i.e., when anatomical and external frames of reference are better aligned) and with hands crossed (i.e., when anatomical and external frames of reference are placed in conflict). Under these conditions of focused, constant, spatial attention we aimed at inferring the functional significance of SEP modulations by way of their timing, scalp distribution, and correlation with behavioural measures of remapping.

In the present study, a single tactile tap was presented to the left hand in one group of subjects and to the right hand in a second group of participants. Interleaved within the stream of frequent single taps, we included infrequent trials requiring a bimanual temporal order judgment task, so we could index the cost of remapping between reference frames behaviourally. As mentioned above, we ran two separate sets of participants, each receiving the stimulus stream at a different hand, to pinpoint any possible lateralization effects regarding tactile remapping (Lloyd et al., 2003; Takahashi et al., 2012; Wada et al., 2012).

2. Materials and methods

2.1. Participants

Forty-seven healthy adult volunteers participated in the study, of whom twenty-five were tested with the left hand (LH experiment) and twenty-two with the right hand (RH experiment). Seven volunteers from the LH experiment and eight from the RH experiment were excluded from the final analyses according to the following criteria: (1) unacceptable number of EEG artefacts (affecting > 60% of the SEP data; LH:3, RH:4) and (2) poor performance on the behavioural task (based on outlier rejection analysis, Rosner, 1975, on the following parameters: σ , P_{\max} , P_{\min} and r^2 ; see Eq. (1); LH:4, RH:4). Thus, the LH experiment was based on 18 participants (12 female) with mean age of 25 years (20–36 years), right handed and normal tactile sensitivity. The RH experiment included 14 (10 female) participants with 24 years average age (also right handed). All were naïve as to the purpose of the experiment and gave written informed consent prior to the study, which was approved by the local ethics committee.

2.2. Materials and procedure

Participants sat at a comfortable chair, wearing the EEG recording cap and a solenoid tapper (rounded tip 0.2 mm diameter; M&E Solve, Kent, UK) strapped to the middle finger of each hand (dorsal aspect of the middle phalange) at a constant, comfortable, pressure. They placed both hands, crossed or uncrossed depending on the block, on a flat wooden plate placed on their lap, with their middle fingers resting each on a response button, 30 cm apart. An orange LED, in front of the participant, served as fixation. Otherwise, the room was kept dark and the hands were visible only under the dim illumination of the fixation light.

Each participant was presented with 2240 trials. Amongst these, 2000 were single tactile events (9 ms mechanical supra-threshold tap driven by a 12-v square wave) at the middle finger of a single hand (i.e. the *left* or *right* hand for the LH and RH experiments respectively). Participants wore disposable foam ear-plugs and earmuffs to prevent hearing the stimulator noise. The single taps were presented in a continuous stream at a rate of ~ 1.33 Hz (Stimulus Onset Asynchrony -SOA- jittered between 600–900 ms). In order to maintain the participants' alert state and to gauge behavioural performance during the recording session, we included a bimanual temporal order judgment (TOJ) task which allowed us to index the cost of conflict between spatial reference frames (Azañón & Soto-Faraco, 2007; Collignon, Charbonneau, Lassonde, & Lepore 2009; Röder, Rösler, & Spence 2004; Schicke & Röder, 2006; Shore et al., 2002; Yamamoto & Kitazawa, 2001; Heed et al., 2012). Thus, randomly intermingled within the sequence of single taps at one particular hand (left or right, depending on group), an extra $\sim 10\%$ of trials (240 total) consisted of a double tap, one at each hand. The SOA and hand order between taps in double-tap trials was sampled equiprobably following a constant stimulus distribution (± 10 , ± 30 , ± 60 ,

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