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On the neural basis of sensory weighting: Alpha, beta and gamma modulations during complex movements



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ABSTRACT

Previous studies have revealed that visual and somatosensory information is processed as a function of its relevance during movement execution. We thus performed spectral decompositions of ongoing neural activities within the somatosensory and visual areas while human participants performed a complex visuomotor task. In this task, participants followed the outline of irregular polygons with a pen-controlled cursor. At unpredictable times, the motion of the cursor deviated 120° with respect to the actual pen position creating an incongruence between visual and somatosensory inputs, thus increasing the importance of visual feedback to control the movement as suggested in previous studies. We found that alpha and beta power significantly decreased in the visual cortex during sensory incongruence when compared to unperturbed conditions. This result is in line with an increased gain of visual inputs during sensory incongruence. In parallel, we also found a simultaneous decrease of gamma and beta power in sensorimotor areas which has not been reported previously. The gamma desynchronization suggests a reduced integration of somatosensory inputs for controlling movements with sensory incongruence while beta ERD could be more specifically linked to sensorimotor adaptation processes.

Introduction

Our capacity to allocate resources to relevant sensory information is a central tenet in establishing proper and safe interactions with our environment. According to prevailing theories of motor control, this would involve increasing feedback gains of pertinent sensory inputs and decreasing the gains of irrelevant sensory inputs (e.g., Ernst and Banks, 2002; Scott, 2004; Todorov and Jordan, 2002). This theoretical assumption has received considerable support from studies in which human participants performed goal-directed movements with incongruent visual and somatosensory feedback (Rossetti et al., 1995; Sarlegna and Sainburg, 2007; Sober and Sabes, 2003). Seeing our hand movements through a mirror or moving a cursor with a computer mouse are examples of experimental contexts where the mapping between these sensory inputs is altered. Consistent with sensory gain control theories, Bernier et al. (2009) found that the amplitude of evoked potentials recorded in the somatosensory cortex following median nerve stimulation (SEP) is substantially smaller when drawing with mirror-reversed vision compared to normal vision. This reduction in SEP amplitude was interpreted as a result of the functional downweighting of proprioceptive inputs to facilitate movement performance during sensory conflict (Balslev et al., 2004; Bernier et al., 2009; Lajoie et al., 1992). Evidence for visual information up-regulation has also been suggested for movements performed with mirror-reversed vision, as participants who had more accurate tracing movements showed greater sensitivity to visual inputs compared to their less accurate counterparts (Lebar et al., 2015).

To date, the neural mechanisms underlying the weighting of afferent inputs when controlling movements with incongruent visual and somatosensory feedback are poorly understood. We set out to shed light on this issue by investigating neural oscillations within the visual and somatosensory cortices in humans. Our approach builds on the current consensus that functional processing of sensory inputs is associated with distinct band-specific neural oscillations within the cerebral cortex. For instance, alpha oscillations (~8-12 Hz) are considered to be a local marker of the level of excitability of the somatosensory and visual cortices, with a smaller alpha power being associated with greater excitability (Anderson and Ding, 2011; Pfurtscheller and Lopes da Silva, 1999). The power of alpha is therefore thought to be lowest when sensory inputs are task-relevant (e.g. Haegens et al., 2011; Zumer et al., 2014). On the other hand, beta oscillations (~15-25 Hz) predominate during unchanged states (or status quo) of the sensorimotor cortex and largely decrease prior to (~1-2 s) and during movements. Therefore, beta desynchronization in the somatosensory cortex is classically associated with the processing, or preparation to process, somatosensory inputs (Cheyne et al., 2003;

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N. Lebar et al. NeuroImage 150 (2017) 200–212

Pfurtscheller and Lopes da Dilva, 1999; van Ede et al., 2011, 2012). From a functional point of view, the power of alpha and beta has been found to be inversely related to sensory detectability and discriminability (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Romei et al., 2010; van Dijk et al., 2008), and also to the speed of visual and motor information processing (Pogosyan et al., 2009; Thut et al., 2006; Zhang et al., 2008). In this light, the co-modulation of alpha and beta power might provide an efficient mechanism to contextually weight visual and somatosensory inputs, according to their relevance, during movement control.

Contrary to alpha and beta oscillations, gamma oscillations (> 30 Hz) increase in the visual and somatosensory cortices during visual and proprioceptive stimulation. Gamma power is therefore frequently reported as being negatively correlated with the alpha and beta power (Pfurtscheller et al., 2003, Tallon-Baudry and Bertrand, 1999). Contributing to a higher level of sensory information processing, gamma oscillations are considered as neural markers of unimodal and multimodal sensory binding (Engel et al., 2012; Ghazanfar et al., 2008; Krebber et al., 2015; Maier et al., 2008; Wang, 2010). For instance, gamma response in the occipital cortex is observed following the presentation of two coherent visual stimuli (Tallon-Baudry et al., 1996; Zarka et al., 2014). This response is absent when a visual stimulus is presented simultaneously with incongruent visual (Tallon-Baudry et al., 1996; Zarka et al., 2014) or non-visual stimuli (Ghazanfar et al., 2008; Krebber et al., 2015; Maier et al., 2008). In the case of incongruent visuo-tactile stimulation, this decrease of gamma power is not only observed over the visual cortex but is also found centrally, over the somatosensory cortex (Krebber et al., 2015). These latter findings are also consistent with the suggestion that gamma oscillations serve to connect neural populations that encode stimuli of different sensory modalities (Fries, 2009; Wang, 2010).

Examination of the spectral content of cortical neural oscillations therefore suggests that multiple flexible mechanisms could intervene to dynamically weight sensory information during movements. However, two important points emerge from the literature that currently precludes drawing firm conclusions regarding these mechanisms. First, current assumptions on the link between neural oscillations and sensory re-weighting primarily derive from studies in which the sensory inputs were task-irrelevant (e.g., Krebber et al., 2015) or relevant for non-motor processes (e.g., visual, tactile or pain perception, see Tallon-Baudry et al., 1996; Bauer et al., 2006). Second, in studies targeting sensorimotor processes, neural oscillations were principally assessed either during the planning phase of the movements or during discrete motor actions of short duration (e.g., <1 s; Chung et al., 2017; Thürer et al., 2016; Torrecillos et al., 2015).

In the present study, we investigated the mechanisms underlying feedback gain modulation by assessing the oscillatory activity of the visual and somatosensory cortices when individuals controlled their movements with either a congruence or incongruence between visual and somatosensory feedback. Importantly, exposure to the sensory incongruence was set to be sufficiently long (i.e., ~6–10 s for each trial) to allow this assessment during the movement itself (rather than before or after movement). Based on the conclusions of previous studies (i.e., Balslev et al., 2004; Bernier et al., 2009; Lajoie et al., 1992; Lebar et al., 2015), we hypothesized that there would be an increased gain of visual feedback and a decreased gain of somatosensory information when the two modalities become incongruent during movement. Specifically, in the visual cortex, we expected that there would be an increase in alpha and beta desynchronization, as well as a synchronization of gamma. In contrast, in the somatosensory cortex, we predicted that there would be a synchronization of alpha and beta frequency bands and a desynchronization of gamma activity.

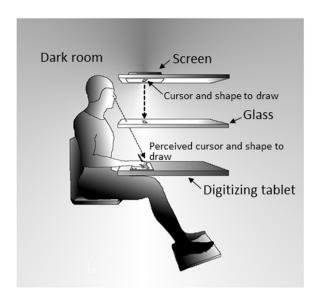


Fig. 1. Experimental set-up. Participants had to follow as precisely as possible the outline of a two-dimensional shape with a cursor controlled by the tip of a digitizing pen held in their right hand. Because of the equal distance between the screen, the glass and the tablet, participants perceived the cursor and the shape at the hand level. The room was dark and the glass prevented the direct vision of the drawing hand.

Materials and methods

Participants

Eighteen right-handed participants, aged between 22 and 38 years old (mean: $26\pm 4{\rm yrs}$ (SD), 10 females, 8 males) participated to the experiment which lasted ~1h45. They all signed informed consent documents prior to the experiment, and were paid for their participation to the study. Prior to participation, the participants underwent the Edinburgh Handedness Inventory 2 test to ensure that they were right-handed. A score of zero to this test indicates no preference for either hand while a score of 100 or –100 reveals a maximal preference for the right or left hand, respectively. The participants' scores ranged between 20 and 100 (mean 79 ± 25 (SD)). All protocols and procedures were in accordance with the 1964 declaration of Helsinki.

Apparatus and stimuli

A schematic representation of the experimental set-up is shown in Fig. 1. The set-up was structured in 3 levels: a top level with a computer screen oriented downward, a mid-level with a semi-reflecting glass and a lower level with a digitizing tablet laid on a table. The glass was positioned at an equal distance between the screen and the digitizing tablet. With this configuration, the images projected by the screen appeared as virtual images on the digitizing table. As a panel prevented direct vision of the screen and because the experimental set-up was located in a dark chamber, these virtual images were the only visual information that the participants could see.

The participants' task was to follow, as precisely as possible, the outline of two-dimensional shapes with a cursor controlled by the tip of a digitizing pen held in their right hand. Visual feedback of the tip of the pen was provided by a 3-mm white dot. The presentation of visual stimuli and the collection of hand trajectories were controlled using custom MATLAB (Mathworks) program and the Psychophysics toolboxes (Brainard, 1997; Pelli, 1997). Six different irregular white polygons were used (Fig. 2A shows one of them). These shapes were displayed on a black background and consisted of 10 thin (1 mm) straight lines (10 angles) whose lengths varied between 31–90 mm. The total perimeter was 186 mm for all shapes.

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