



Distinct vestibular effects on early and late somatosensory cortical processing in humans



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ARTICLE INFO

Article history:

Received 4 June 2015

Accepted 1 October 2015

Available online 23 October 2015

Keywords:

EEG

Somatosensory evoked potentials

Vestibular system

Multisensory processing

Electrical neuroimaging

Somatosensory cortex

ABSTRACT

In non-human primates several brain areas contain neurons that respond to both vestibular and somatosensory stimulation. In humans, vestibular stimulation activates several somatosensory brain regions and improves tactile perception. However, less is known about the spatio-temporal dynamics of such vestibular–somatosensory interactions in the human brain. To address this issue, we recorded high-density electroencephalography during left median nerve electrical stimulation to obtain Somatosensory Evoked Potentials (SEPs). We analyzed SEPs during vestibular activation following sudden decelerations from constant-velocity (90°/s and 60°/s) earth-vertical axis yaw rotations and SEPs during a non-vestibular control period. SEP analysis revealed two distinct temporal effects of vestibular activation: An early effect (28–32 ms post-stimulus) characterized by vestibular suppression of SEP response strength that depended on rotation velocity and a later effect (97–112 ms post-stimulus) characterized by vestibular modulation of SEP topographical pattern that was rotation velocity-independent. Source estimation localized these vestibular effects, during both time periods, to activation differences in a distributed cortical network including the right postcentral gyrus, right insula, left precuneus, and bilateral secondary somatosensory cortex. These results suggest that vestibular–somatosensory interactions in humans depend on processing in specific time periods in somatosensory and vestibular cortical regions.

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Introduction

The vestibular system contributes to numerous adaptive functions including gaze control (Bertolini et al., 2008), balance (Johansson and Magnusson, 1991; Lacour et al., 1997), self-motion perception (Fetsch et al., 2007; MacNeilage et al., 2007), spatial cognition (Berthoz, 1991) and bodily self-consciousness (Blanke et al., 2002; Lopez et al., 2010). These functions are based on the integration of vestibular signals with multisensory inputs, including visual and somatosensory signals. Although animal research identified several subcortical and cortical structures that process vestibular and multisensory signals (see Lopez and Blanke, 2011 for a review), little is known about the spatio-temporal dynamics of vestibular and multisensory processing in the human brain.

In non-human primates distinct, distributed, and multisensory cortical regions receive vestibular inputs from the thalamus. These include several somatosensory regions, such as the parieto-insular vestibular cortex (PIVC (Chen et al., 2010; Grüsser et al., 1990a,b)) and the primary

somatosensory cortex (S1, i.e. Brodmann areas 2v (Büttner and Buettner, 1978; Fredrickson et al., 1966) and 3a (Odkvist et al., 1974)). Vestibular information is further relayed to multisensory regions in the ventral intra-parietal area (Bremmer et al., 2002; Schlack et al., 2002), the middle superior temporal area (Duffy, 1998), as well as other regions (see Guldin and Grüsser, 1998; Lopez and Blanke, 2011 for reviews). This prominent anatomical overlap of somatosensory and vestibular processing (i.e. in PIVC, area 2v, area 3a, and ventral intra-parietal area (Akbarian et al., 1993, 1994; Bremmer et al., 2002; Fredrickson et al., 1966; Guldin et al., 1992; Odkvist et al., 1974; Schwarz and Fredrickson, 1971; Vogt and Pandya, 1978) raises the question whether the vestibular and somatosensory systems might interact at the functional level as well.

This hypothesis has been largely supported by neuroimaging evidence for vestibular–somatosensory interactions in animals and humans. For instance, Fredrickson et al. (1966) described responses from monkey area 2v not only to electrical stimulation of the vestibular nerve, but also to electrical stimulation of the median nerve, or simultaneous stimulation of both nerves. Another study found that subdivisions of monkey area 3a respond to vestibular, proprioceptive, and deep muscle (neck, limbs) stimulation (Odkvist et al., 1974). Similarly, in humans undergoing pre-surgical epilepsy evaluation, direct electro-cortical

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stimulation of the posterior insula cortex (Mazzola et al., 2014) (i.e. human correlate of the PIVC, Lopez et al., 2012a,b; zu Eulenburg et al., 2012) or the anterior parietal cortex (i.e. human homologue of area 2v) induced vestibular and somatosensory sensations (Blanke et al., 2000; Penfield and Jasper, 1954).

Overlap of vestibular and somatosensory processing in the human brain has been further demonstrated by functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies using caloric (CVS) or galvanic vestibular stimulation (GVS). In these studies, somatosensory and vestibular stimulation activated both the putamen and the secondary somatosensory cortex (S2; Bottini et al., 2005; Bottini et al., 1995) as well as the temporo-parietal junction including the parietal operculum and the medial and posterior insula (Lopez et al., 2012a,b; Mazzola et al., 2014; zu Eulenburg et al., 2012). In these fMRI and PET studies, GVS and CVS further modulated activity in S1 (Bense et al., 2001; Fasold et al., 2002; Lobel et al., 1998; Suzuki et al., 2001). In turn, somatosensory (i.e. proprioceptive) stimulation by neck-muscle vibration has been shown to activate the posterior insula (i.e. PIVC) and the somatosensory cortex (i.e. area 3a and S2; Fasold et al., 2008).

In addition to neuroimaging evidence for vestibular–somatosensory convergence, psychophysical and behavioral studies in humans suggest functional vestibular–somatosensory interactions. In neurological patients with hemianesthesia or tactile extinction, who showed profound somatosensory perception deficits due to damage to the parietal cortex, CVS or GVS temporarily recovered tactile perception (Bottini et al., 1995, 2005; Kerkhoff et al., 2011; Vallar et al., 1990). A similar improvement of tactile detection thresholds at the hands was found in healthy subjects during passive whole-body rotation, GVS, or CVS (Ferrè et al., 2011, 2013, 2014).

Despite the evidence for vestibular–somatosensory neuroanatomical overlap and functional interactions in humans, little is known about the specific spatio-temporal dynamics by which vestibular inputs affect human somatosensory cortical processing. Perhaps, this is due to the limited temporal resolution of fMRI and PET, the constant vestibular activations induced by the static magnetic field of the MR scanner (Roberts et al., 2011), and somatosensory co-activation induced by artificial vestibular stimulation techniques such as CVS and GVS (Lopez et al., 2012a). To address these issues, the main aim of the present study was to identify the spatio-temporal dynamics by which natural vestibular signals affect somatosensory cortical processing in humans. We combined somatosensory evoked potentials (SEPs) with short sequences of constant-velocity passive whole-body yaw rotations that selectively activated the horizontal semicircular canals of the vestibular system (Bertolini et al., 2011; Prsa et al., 2012; van Elk and Blanke, 2013). Based on an earlier study testing the effects of CVS on SEPs (Ferrè et al., 2012), we here recorded SEPs during the post-rotational period (see below), because this period is marked by prolonged vestibular activation (Bertolini et al., 2011; Goldberg and Fernandez, 1971). Critically, because vestibular activation was ongoing after body rotation had stopped, we avoided effects of somatosensory co-activation that accompany the onset of vestibular yaw rotation (Allison et al., 1989a). In addition, because the vast majority of vestibular neurons in animals encode rotation velocity of the head by modulation of response strength (i.e. gain; Barresi et al., 2013; Goldberg and Fernandez, 1971; Waespe et al., 1980) and because humans can accurately discriminate between different rotation velocities based on vestibular inputs alone (Grabherr et al., 2008; Prsa et al., 2012), we asked here whether different rotation velocities would further modulate vestibular–somatosensory interactions. Thus, SEPs were recorded during vestibular activation immediately following decelerations from fast (90°/s) or slow (60°/s) constant-velocity yaw rotations and during a later control period without any vestibular activation. We predicted that any vestibular modulation of the SEP response strength would further depend on rotation velocity. We performed electrical neuroimaging analysis (Murray et al., 2008) and analyzed whether early (Fredrickson et al., 1966; Odkvist et al.,

1974) and/or late SEP components (Ferrè et al., 2012) were modulated by vestibular activation and rotation velocity.

Materials and methods

Participants

Sixteen students from the Ecole Polytechnique Fédérale de Lausanne participated (4 females; mean age = 23.8 years, SD = 4.2 years, range = 19–32 years). All participants verbally indicated that they were right-handed, had normal balance and somatosensory perception, and no history of psychiatric or neurologic diseases. Before inclusion in the study each participant gave informed consent and after having participated each participant received a 60 Swiss Francs monetary compensation. The experimental protocol was approved by the local ethics committee—La Commission d’Ethique de la Recherche Clinique de la Faculté et de Médecine de l’Université de Lausanne—and was conducted in accordance with the Declaration of Helsinki.

Experimental setup

Fig. 1A shows a top view of the experimental setup modified from a similar experimental setup used by us in Prsa et al. (2012) and van Elk and Blanke (2013). Inside of a faraday cage (Industrial Acoustics Company, Niederkrüchten, Germany), used to shield the experimental setup from external electromagnetic, visual, and auditory signals, a motion platform was installed. A racing car seat was firmly mounted at the axial center of a beam platform (2 m diameter) that was fixated on an electrical engine (PCI-7352 servo control). Platform rotations were controlled with 0.1 angular degree precision at 100 Hz sampling rate using LABVIEW software (version 8.6, National Instruments, Austin, TX, US).

The participant sat comfortably in upright posture with safety belts attached. The racing car seat had a tight anatomical fit, which both stabilized body position and constrained any involuntary trunk or leg movements during rotation. The participant’s head was centered above the trunk and the rotation axis. The participant’s head was tilted by 30° forward, which because of the anatomical configuration of the semicircular canals aligned participant’s horizontal canals with the yaw rotation plane (Day and Fitzpatrick, 2005). A chin- and forehead-rest were used to stabilize participant’s head posture during platform rotation. This setup allowed to apply passive whole-body yaw rotations about an earth-vertical axis through the participant’s head center and thus selectively stimulated the horizontal semicircular canals of the vestibular system. Indeed, we cannot exclude inter-subject variability of head position with respect to the rotation axis that may have also led to additional otolith vestibular activation. However, these variations were comparatively small and random between subjects and can, therefore, be considered negligible.

A screen (Samsung Syncmaster 2233RZ, Seoul, Korea) with 120 Hz refresh rate and 22-inch diameter was positioned at eye-level in front of the participant and was firmly attached to the motion platform. The screen had 29 cm eye-to-screen distance giving rise to 56° vertical and 80° horizontal visual angles. A white fixation cross was presented at the center of the screen on a black background. Apart from the fixation cross the experiment was conducted in complete darkness, such that no visual signal informed participants whether the platform rotated or not. Furthermore, the participant wore earphones (Sennheiser CX 400, Hannover, Germany) on which white noise (individually adjusted between 40–70 dB loudness) was presented to mask auditory cues from platform rotations. A computer was laterally mounted on the platform that was used to control the visual display (i.e. presenting instructions and a fixation cross) and for scheduling median nerve stimulations.

An electrical stimulator (Grass S48, Astor-Med Inc., West Warwick, RI, US) was installed laterally on the beam platform and was used to generate electrical currents for median nerve stimulation. The electrical stimulator was connected to an isolation unit (Grass SIU5), a constant

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