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Vestibular contributions to a right-hemisphere network for bodily awareness: Combining galvanic vestibular stimulation and the "Rubber Hand Illusion"

Elisa Raffaella Ferrè*, Eva Berlot, Patrick Haggard

Institute of Cognitive Neuroscience, University College London, Alexandra House, 17 Queen Square, London WC1N 3AR, UK

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A B S T R A C T

An altered sense of one's own body is a common consequence of vestibular damage, and also of damage to vestibular networks in the right hemisphere. However, few experimental studies have investigated whether vestibular signals contribute to bodily awareness. We addressed this issue by combining an established experimental model of bodily awareness (Rubber Hand Illusion -RHI) with galvanic vestibular stimulation (GVS) in healthy participants. Brief left anodal and right cathodal GVS (which predominantly activates vestibular networks in the right hemisphere), or right anodal and left cathodal GVS, or sham stimulation were delivered at random, while participants experienced either synchronous or asynchronous visuo-tactile stimulation of a rubber hand and their own hand. The drift in the perceived position of the participant's hand towards the rubber hand was used as a proxy measure of the resulting multisensory illusion of body ownership. GVS induced strong polarity-dependent effects on this measure of RHI: left anodal and right cathodal GVS produced significantly lower proprioceptive drift than right anodal and left cathodal GVS. We suggest that vestibular inputs influence the multisensory weighting functions that underlie bodily awareness: the right hemisphere vestibular projections activated by the left anodal and right cathodal GVS increased the weight of intrinsic proprioceptive signals about hand position, and decreased the weight of visual information responsible for visual capture during the RHI.

1. Introduction

The sense of bodily awareness is often described as a feeling of "*mineness*": that one's body belongs to oneself (Metzinger, 2003), over and above any particular bodily sensation. Perhaps the most convincing evidence for such a concept comes from disordered bodily awareness in neuropsychological patients. For example, right brain-damaged patients with *somatoparaphrenia* lack the normal sense of the body as a coherent entity, as well as the feeling that one's body belongs to oneself (Gallagher, 2000). For example, they may have delusional beliefs that their own limbs belong to someone else (see for a review Vallar and Ronchi, 2009).

Studies of individual cases described temporary remissions of somatoparaphrenia following right-hemisphere damage during artificial vestibular stimulation (Bisiach et al., 1991; Rode et al., 1992). These reports suggest a vestibular contribution to bodily awareness that forms the basis for the present study. The vestibular system signals linear and angular acceleration and provides an absolute gravitational reference for control of body posture in space. Information from the vestibular peripheral organs in the inner ear is integrated with several other classes of signals, including visual, tactile and proprioceptive information for purposes of motor control (Lackner and DiZio, 2005). Multimodal convergence has been described in almost all vestibular relays, including the vestibular nuclei, the thalamus and several areas in the cerebral cortex (Zu Eulenburg et al., 2012; Lopez et al., 2012a). Electrophysiological studies have identified a widespread vestibular network whose core area is the parieto-insular vestibular cortex (PIVC) (Guldin and Grüsser, 1998). This area lies in the posterior parietal operculum extending into the posterior insular lobe (Guldin and Grüsser, 1998). The human homologue of the primate PIVC may not be a single area, so much as a distributed multimodal set of regions including the posterior and anterior insula, temporoparietal junction, superior temporal gyrus, inferior parietal lobule, and somatosensory cortices (Lopez et al., 2012a; zu Eulenberg et al., 2012). This anatomical feature leads to the

Abbreviations: RHI, Rubber Hand Illusion; GVS, galvanic vestibular stimulation; L-GVS, left anodal and right cathodal GVS; R-GVS, right anodal and left cathodal GVS; PIVC, parieto insular vestibular cortex.

* Corresponding author.
E-mail address: e.ferre@ucl.ac.uk (E.R. Ferrè).

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suggestion that the vestibular system may provide a basic frame of reference underpinning other sensory modalities (Angelaki and Cullen, 2008).

Several studies have focussed on how vestibular signals and signals from other sensory modalities integrate. For instance, vestibular and visual signals are integrated for perception of self-motion. It has been suggested that this interaction is essential to update a vestibular world-centered frame of reference that continuously influences visual responses in the parietal cortex whenever the head moves (Snyder et al. 1998; Fetsch et al., 2009). Multisensory convergence of visual and vestibular signals happens rapidly, at the subsecond timescale of visual motion. There is also growing evidence for interaction between vestibular and somatosensory signals (Ferrè et al., 2011, 2013a). Specifically, vestibular inputs influence the gain of different stages along the somatosensory afferent pathway (Ferrè et al., 2011, 2013a).

Vestibular input may play a key role in producing the normal experience of a coherent body, linked to the self. However, it remains unclear *how* vestibular inputs contribute to bodily awareness (see for review Pfeiffer et al., 2014). Because vestibular inputs produce activation of extensive right-hemisphere cortical multisensory network (Bottini et al., 1995, 2005), coupled with deactivation of visual areas (Bense et al., 2001), we hypothesised that vestibular input might contribute to bodily awareness by balancing intrinsic somatosensory and proprioceptive information against extrinsic visual information. Adjustments in the relative strengths of these projections might be responsible for restoration of the normal sense of bodily awareness during vestibular-induced remission of somatoparaphrenia. On the other hand, because vestibular stimulation is a highly salient stimulus, and quite different from normal vestibular inputs, we also considered an alternative hypothesis of non-specific effects on bodily awareness. For example, vestibular stimulation is known to have non-specific effects on general attention and arousal (Vallar et al., 1990, 1993).

Here we aimed to clarify the mechanism and specificity of vestibular contributions to bodily awareness in healthy volunteers. The Rubber Hand Illusion (RHI; Botvinick and Cohen, 1998) is an established experimental manipulation of bodily awareness. A rubber hand viewed in peripersonal space is experienced as part of one's body if it is touched in synchrony with the participant's own unseen hand. Psychological (Longo et al., 2008) and physiological (Moseley et al., 2008; Barnsley et al., 2011) evidence suggests that the RHI involves a transposition of the sense of body from one object to another, rather than addition of a new body part. That is, *dis-ownership* of one's own hand accompanies the increased sense of ownership over the rubber hand. Consistent with this account, participants then mislocate their own hand as closer to the fake hand than it actually is. This *proprioceptive drift* increases with the increasing strength of the illusion (Botvinick and Cohen, 1998), and provides a quantitative proxy for assessing bodily awareness (Longo et al., 2008). Some studies have reported that the proprioceptive drift can dissociate from the subjective responses used in illusion questionnaires (Rohde et al., 2011), but this may simply reflect the fact that one measure is fully implicit, while the other is explicit (cf Aglioti et al., 1995). Two previous studies have combined vestibular stimulation and RHI (Lopez et al., 2010, 2012b). In particular, Lopez et al. (2010) found that vestibular stimulation increased RHI as measured by questionnaires, but did not have reliable effects on proprioceptive drift (Lopez et al., 2010). However, in a non-visual variant of the rubber hand illusion, the same group found no influence of vestibular stimulation on either bodily awareness or proprioceptive drift, suggesting that vestibular signals do not interfere with ownership for body parts when visual information about the body is absent (Lopez et al., 2012b).

We used bilateral bipolar galvanic vestibular stimulation (GVS) to non-invasively stimulate the vestibular receptors (Fitzpatrick and Day, 2004). An anode and cathode are placed on the left and right mastoid, or vice versa. Perilymphatic cathodal currents depolarize the trigger site and lead to excitation, whereas anodal currents hyperpolarize it resulting in inhibition (Goldberg et al., 1984). GVS polarity-dependent differences in postural, sensorimotor and cognitive functions have been demonstrated both in healthy volunteers and in brain damaged patients (Utz et al., 2010). For instance, studies using artificial vestibular stimulation have reported that hemisphere-selective left anodal and right cathodal polarity of GVS significantly enhanced sensitivity to mild shocks on either hand, while no such effect was found with either right anodal and left cathodal GVS or sham stimulation (Ferrè et al., 2013a). Importantly, these behavioural effects can be systematically explained by the specific hemispheric cortical projections activated by GVS, as demonstrated by neuroimaging evidence. Fink et al. (2003) found that left anodal and right cathodal GVS caused unilateral activation of the right hemisphere vestibular projections, while the reverse polarity activated both left and right hemispheres (Fink et al., 2003). These results are consistent with the asymmetrical cortical vestibular representation in the right hemisphere in right-handed subjects (Suzuki et al., 2001; Dieterich et al., 2003; Janzen et al., 2008).

We hypothesized that bodily awareness relies on integrating sensory signals in the right hemisphere (Blanke and Arzy, 2005; Tsakiris et al., 2007, 2008). This lateralisation should be particularly strong for the left side of the body. Accordingly, somatoparaphrenia, which provides the most striking neurological evidence for a specific psychological entity of bodily awareness, is characteristically observed for left-side body parts following right-hemisphere lesions (Vallar and Ronchi, 2009). In this case, any effects of vestibular stimulation on bodily awareness should be specific to activation of the right hemisphere vestibular network. Conversely, GVS might also cause non-specific effects, such as changes in arousal. These changes might also influence bodily awareness indirectly (Vallar et al., 1990, 1993). However, such non-specific effects should be independent of GVS polarity. For this reason, we planned to directly compare the effects of GVS polarities to provide the strongest possible test of a right-hemisphere hypothesis regarding bodily awareness. We also planned to compare GVS stimulation of both hemispheres against sham stimulation to test a non-hemisphere-specific hypothesis regarding indirect effects of vestibular stimulation on bodily awareness, such as those mediated by arousal.

2. Material and methods

2.1. Participants

Twenty-six healthy participants were recruited from an online subject pool (15 females, mean age ± SD: 21.1 ± 4.4 years). All participants were right-handed as assessed using the Edinburgh handedness inventory (Oldfield, 1971). Participants with a history of neurological or psychiatric disorders were excluded. Informed consent was obtained prior to participation in the experiment. The experimental protocol was approved by the research ethics committee of University College London. The study adhered to the ethical standards of the Declaration of Helsinki.

2.2. Galvanic vestibular stimulation (GVS)

Bipolar GVS was applied to deliver a boxcar pulse of 1 mA with 4.5 s duration using a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada). This low intensity was used to minimise non-specific cueing effects such as arousal from cutaneous sensations, or vertigo. Importantly, postural