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Balancing body ownership: Visual capture of proprioception and affectivity during vestibular stimulation

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ABSTRACT

The experience of our body as our own (i.e. body ownership) involves integrating different sensory signals according to their contextual relevance (i.e. multisensory integration). Until recently, most studies of multisensory integration and body ownership concerned only vision, touch and proprioception; the role of other modalities, such as the vestibular system and interoception, has been neglected and remains poorly understood. In particular, no study to date has directly explored the combined effect of vestibular and interoceptive signals on body ownership. Here, we investigated for the first time how Galvanic Vestibular Stimulation (left, right, sham), tactile affectivity (a reclassified interoceptive modality manipulated by applying touch at C-tactile optimal versus non-optimal velocities), and their combination, influence proprioceptive and subjective measures of body ownership during a rubber hand illusion paradigm with healthy participants (N = 26). Our results show that vestibular stimulation (left GVS) significantly increased proprioceptive drift towards the rubber hand during mere visual exposure to the rubber hand. Moreover, it also enhanced participants' proprioceptive drift towards the rubber hand during manipulations of synchronicity and affective touch. These findings suggest that the vestibular system influences multisensory integration, possibly by re-weighting both the two-way relationship between proprioception and vision, as well as the three-way relationship between proprioception, vision and affective touch. We discuss these findings in relation to current predictive coding models of multisensory integration and body ownership.

1. Introduction

The perception of the external world, and our own body, is based on the integration of sensory information conveyed by different modalities (i.e. multisensory integration), each weighted according to their contextual reliability (Fetsch et al., 2011; Stein et al., 2014). For instance, in order to estimate the size of an out-of-reach object, we typically rely upon vision; however, if we are close enough to touch the object, our estimation will result from the integration of visual and tactile information. If there is incongruence between different sensory modalities (e.g. visuo-tactile, Pavani et al., 2000), vision can be weighted more (the so-called 'visual capture' effect, Rock and Victor, 1964), or vice versa depending on their contextual relevance (Ernst and Banks, 2002). For example, the precision (i.e. the certainty about sensory representations; Friston et al., 2012) of proprioceptive information (i.e. regarding the position of our body) can be lowered in favour of vision during conflictual situations (Folegatti et al., 2009) and according to the reference plan in space (i.e. vision is more dominant in the horizontal versus in-depth plan, van Beers et al., 2002).

Interestingly, multisensory integration has been linked to bodily consciousness and, specifically, body ownership (i.e. the feeling that our physical body is our own; Gallagher, 2000). Paradigms that generate conflicts between different sensations have been used extensively to explore the role of multisensory integration in body ownership (Tsakiris et al., 2007; Blanke et al., 2015). In the Rubber Hand Illusion (RHI; Botvinick and Cohen, 1998) for example, participants watch a realistic fake hand being stroked in synchrony with their own (unseen) hand (Tsakiris, 2010), giving rise to self-reported feelings of rubber hand ownership and a shift in the perceived location of participants' real hand towards the rubber hand (i.e. proprioceptive drift). Initially, these two measures were seen as the subjective and 'objective' measure of the illusion but it is increasingly understood that subjective feelings of ownership and proprioceptive drift dissociate and may reflect different components of the multisensory integration process (Ehrsson et al., 2004, 2005; Makin et al., 2008; Martinaud et al., 2017; Rohde et al., 2011). More generally, there are now hundreds of studies on the

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RHI, and related psychophysical or virtual reality adaptations (see Kilteni et al., 2015 for a review), indicating that body ownership is mediated by both bottom-up processes of multisensory integration and top–down expectations (Tsakiris, 2010; Apps and Tsakiris, 2014). In line with this, recent predictive coding (Zeller et al., 2015) and Bayesian causal inference (Samad et al., 2015) models suggest that the successful establishment of the illusion relies on the causal attribution of sensory experiences to a common source (in this case, 'my body'), according to prior knowledge and the spatio-temporal congruency of these sensations.

Despite this progress, the contribution of certain modalities, such as the vestibular system and interoception to multisensory integration and body ownership have only recently been studied and hence remain poorly understood. First, although the vestibular system's main role is to contribute to the maintenance of balance and posture (Brandt and Dieterich, 1999), there are some indications that vestibular signals play a role in multisensory integration (Bense et al., 2001). The neuroanatomical correlates of the vestibular system remain debated (Fasold et al., 2002; Eulenburg et al., 2012; Lopez et al., 2012b; Lopez, 2016), yet existing evidence suggests an overlap between the cortical areas supporting vestibular sensations (captured by vestibular receptors in the inner ears and conveyed to the central nervous system via the vestibular nerves) and other sensory experiences (such as vision, Brandt et al., 2002; Seemungal et al., 2013; Della-Justina et al., 2015; touch and proprioception, Lackner and DiZio, 2005; Dijkerman and De Haan, 2007), including multimodal areas linked to multisensory integration (e.g. temporoparietal junction, inferior parietal lobule, insula and cingulate cortex, Lopez et al., 2012b; Lopez, 2016). This suggests that vestibular signals may contribute to multisensory integration.

Moreover, recent studies highlight vestibular network contributions to many facets of body representation (Ferrè and Haggard, 2016; Been et al., 2007), from its metric properties (such as shape and size, Lopez et al., 2012c) to body ownership (Lopez, 2015). For example, excitation of the semi-circular canals of the internal ear by insertion of cold or warm water is known to activate contralateral cortical vestibular areas (Caloric vestibular stimulation, CVS) and to modulate spatial cognition (Cappa et al., 1987), bodily awareness (Cappa et al., 1987; Vallar et al., 1993; Bottini et al., 2005) and body ownership (Bisiach et al., 1991) in patients with right hemisphere stroke.

Recently, a less invasive method than CVS (Lopez et al., 2010; Ferrè et al., 2013a, 2013b), namely Galvanic Vestibular Stimulation (GVS), has been used to examine the role of vestibular stimulation on multisensory integration and body ownership. GVS involves a small electrical current applied using two electrodes (one anode and one cathode) positioned on the mastoids (Utz et al., 2011a, 2011b). The change in electrical excitability of the vestibular nerves stimulates the vestibular network of the right hemisphere when the anode is on the left mastoid and the cathode on the right (known as LGVS), while the reverse electrode positioning (RGVS) leads to a bilateral activation (Fink et al., 2003; Utz et al., 2010). Most studies on body ownership have focused on the role of LGVS given the assumed right lateralised activation it causes (in right-handed subjects; Dieterich et al., 2003; Eulenburg et al., 2012) and the link of the latter with body representation disorders (Baier and Karnath, 2008; Bisiach et al., 1991; Moro et al., 2016; Zeller et al., 2011). Specifically, Lopez and colleagues (2010) found that LGVS enhances body ownership during the RHI, and influences multisensory integration by promoting visual dominance over proprioception; however, Ferrè et al. (2015), observed a decrease in proprioceptive drift following LGVS, suggesting that LGVS enhances proprioception over vision. Thus, both studies found that stimulation of the right vestibular network influences the balance between proprioceptive and visual information in a hemispheric-specific fashion (Dieterich et al., 2003), but in opposite directions. These conflicting results may be caused by various methodological differences between the two studies (see Discussion for full details); however, taken together, they provide preliminary indications for the role of vestibular signals to the weighting of different sensations during multisensory integration and, hence, to body ownership. The present study aimed to further specify Lopez and colleagues' findings against those of Ferrè and colleagues by testing two further hypotheses regarding visual capture of proprioception and ownership (VOC; Martinaud et al., 2017), as well as interoception, as explained below.

We administered galvanic vestibular stimulation during a rubber hand illusion task with the hypothesis that LGVS would enhance the RHI, by increasing the weighting of visual signals whilst lowering the precision of proprioceptive ones. During the RHI, the conflict between vision, touch and proprioception is typically solved via a dominance of visual information over proprioceptive one (e.g. see Zeller et al., 2011 and Zeller et al., 2015 for electrophysiological evidence), i.e. what we see can be processed as more reliable than what we feel, resulting in the embodiment of the rubber hand (Folegatti et al., 2009). Hence, when visual information is present and reduces the ambiguity of a conflictual situation, the stimulation of the vestibular system may shift the balance in favour of vision (as in Lopez et al., 2010) rather than proprioception (Ferrè et al., 2015). In order to specifically test this possibility, we included a mere visual capture condition, during which subjects did not receive any touch on either their hand or the rubber hand but were only required to look at the rubber hand (see Crucianelli et al., 2017). However, even though the current study takes into consideration differences in variance at the group level, we could not directly test whether precision is lowered in favour of vision within each of the different trials in each of our subjects (i.e. at the individual level). In order to do so, we would need multiple trials, or some additional signal strength measure (e.g. see Zeller et al., 2015), which were not possible within the current design; hence, we can only speculate, based on previous literature and the current data, that sensory re-weighting of visual and proprioceptive information, with an increase of the former and a concomitant reduction of the latter, may be the mechanism at play should our predictions be confirmed at the group level (see Discussion section for further details on this point).

Furthermore, we wanted to investigate how the combined effects of vestibular stimulation and vision influence body ownership during the RHI when touch is affective rather than neutral. In order to do so, we administered CT-optimal, affective touch and non CT-optimal, neutral touch during both synchronous and asynchronous conditions of the RHI. C-Tactile (CT) afferents are a specialised, unmyelinated class of fibres innervating the hairy skin of the body (McGlone and Reilly, 2010). They are optimally activated by slow, caress-like tactile stimulation at velocities between 1 and 10 cm/s (McGlone et al., 2014). CT-optimal touch is associated with heightened pleasantness (Löken et al., 2009; Shaikh et al., 2015; Pawling et al., 2017) and has been identified as a type of affective touch (McGlone et al., 2014). CT-optimal touch activates multimodal areas of converging sensory and affective information regarding the state of the body (including posterior insula, Craig, 2002, 2003; Olausson et al., 2002; McGlone et al., 2012 and cingulate cortex, Case et al., 2017). Moreover, the pleasantness associated with CT-optimal touch is not affected by inhibition of the primary and secondary sensory cortices (Case et al., 2016, 2017), thus supporting the notion that the CT-system might play a unique role in conveying affective rather than discriminative aspects of touch. CT-afferents are considered as sharing more characteristics with interoceptive (i.e. related to the sense of the physiological condition of one's own body; Ceunen et al., 2016), rather than exteroceptive, modalities (Björnsdotter et al., 2010), in light of their contribution to the maintenance of our sense of self (Crucianelli et al., 2017).

CT-optimal touch has been found to increase embodiment during the RHI (Crucianelli et al., 2013, 2017; Lloyd et al., 2013; van Stralen et al., 2014). For example, Crucianelli and colleagues (2013) found an increase in subjective measures of embodiment during the RHI using synchronous, CT-optimal touch. Nevertheless, the mechanisms behind such enhancement remain unknown. One possibility is that the pleasantness elicited by CT-optimal touch enhances embodiment because