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Research Report

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

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Abstract

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 (the Rubber Hand Illusion paradigm - 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.

Keywords

Vestibular system; Bodily Awareness; Somatoparaphrenia; Multisensory Integration.

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.

Highlights

1. Left-anodal galvanic vestibular stimulation decreases the strength of RHI
2. Vestibular system influences multisensory processes underlying bodily awareness
3. Right hemisphere vestibular projections modulate bodily awareness

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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 to 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 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 and other sensory modalities integrate, i.e. vision and touch. 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 influence 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; Ferrè et al., 2012). Specifically, vestibular inputs influence the gain of different stages along the somatosensory afferent pathway to influence self-representation (Ferrè et al., 2011; Ferrè et al., 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; Bottini et al., 2005; Fink et al., 2003), coupled with deactivation of visual areas (Bense et al., 2001; Deutschländer et al., 2002), 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 normal sense of bodily awareness during vestibular 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; Vallar et al., 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 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 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; Lopez et al., 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. 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 been recently 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. These results are consistent with the asymmetrical cortical vestibular representation in the right hemisphere in right-handed subjects (Bense et al., 2001; 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; Tsakiris et al., 2008). This lateralisation should be particularly strong for the left side of the body (Vallar and Ronchi, 2009). 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. 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; Vallar et al., 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 studies confirm that this level of GVS activates the vestibular organs, without effects persisting beyond the period of stimulation (Fitzpatrick and Day, 2004). Further, behavioural changes have been reported with such low intensities GVS (Wilkinson at al. 2010; Kerkhoff et al., 2011; Schmidt et al., 2013a; Schmidt et al., 2013b; Ferrè et al., 2013b; Ferrè et al., 2013c). Carbon rubber electrodes (area 10 cm^2) coated with electrode gel were placed binaurally over the mastoid processes and fixed in place with adhesive tape. The area of application was first cleaned and electrode gel was applied to reduce the impedance. Left anodal and right cathodal configuration is named ‘L-GVS’. The inverse polarity, namely right anodal and left cathodal configuration, is named ‘R-GVS’. We also applied a sham stimulation (Pseudo-GVS) using electrodes placed on the left and right side of the neck, about 5 cm below the GVS electrodes (Lopez et al., 2010; Ferrè et al., 2013a), with left anodal and right cathodal configuration. This Pseudo-GVS stimulation evoked a tingling skin sensation that was similar to GVS, and so functions as a control for non-specific effects.

2.3. Procedure

Verbal and written instructions about the task were given to participants at the beginning of the session. The experimental procedure and timing was controlled by custom-made software. The participant's left hand was placed at a fixed point inside a box located 20 cm to the left of rubber hand (i.e. the distance between participant’ index finger and the index finger of the rubber hand). The box was 50 cm wide, 22 cm high and 36 cm long with a cover attached to its backside. When the cover was open, participants saw the rubber hand through a 20 cm wide and 33 cm long hole on top of the box, but when it was closed, the view of the rubber hand was concealed. The left half of the box was covered with a removable lid, which was closed throughout the experiment in order to conceal participants’ own hands. Two stepper motors with identical paintbrushes used for delivering tactile stimulation were placed in the box to the right of the rubber hand and participant’ real hand. Participants wore black fabric that was attached to the front side of the box so that their arms were out of their view. Participants were listening to white noise delivered through headphones, which masked the noise of the motors during the task.

At the beginning of each block, both the participant's left hand and the rubber hand were out of sight. A baseline estimate of finger position was obtained prior to visuo-tactile stimulation. Participants wore a cap on which was mounted a computer-controlled laser pointer. They were asked to judge the location of their unseen left index finger tip, by pointing to the location vertically above it on the lid of the box with the laser. During the judgments, there was no tactile stimulation, and the box was closed to make the rubber hand invisible. A digital camera suspended above the box captured images of the laser beam location. After the judgment, the box lid was removed to make the rubber hand appear, and after 500 ms visuo-tactile stimulation begun. To precisely synchronise the timing of the trial sequence, auditory cues signalled to the experimenter when to open/close the lid of the box. The experimenter manually opened/closed the box lid. An initial 120 s period of visuo-tactile stimulation was delivered (Figure 1a). Visuo-tactile stimulation to the rubber hand and the participant’s hand was delivered by two paintbrushes attached to stepper motors under computer control. Stroking was performed either synchronously (with the two brushes moving in a perfect synchronised fashion) or asynchronously (brushes moving in a completely uncorrelated fashion). Importantly, the overall amount of visuo-tactile stimulation was precisely matched across conditions, but the brush movements were spatially and temporally uncorrelated in the asynchronous condition. In synchronous blocks, this induction period was used to establish the illusion. After that, the box was closed and participants again judged finger location. Immediately prior to each judgement, participants were asked to point with the laser to one of several targets on the wall to their left, to prevent responding based on memory for perceived finger position in the previous trial and execution of stereotyped head movements. Next, the box was opened and a block of nine trials started. In each trial, L-GVS, R-GVS or Pseudo-GVS was applied for 4.5 s. After 1 s, visuo-tactile stimulation began, and continued until the end of GVS (Figure 1a). This delay was used to ensure that vestibular cortical projections would be activated when visuo-tactile stimulation was present: Fitzpatrick and Day (2004) reported that 1 s of 1mA GVS produced clear postural adjustments in standing participants, implying successful vestibular stimulation. Each trial ended with a proprioceptive judgement as before. Importantly, the proprioceptive judgement was not recorded *during* vestibular stimulation to avoid the presence of any possible GVS-related postural biases in the responses, but only immediately after. L-

GVS, R-GVS and Pseudo-GVS were administered three times per block in random order. Thus, nine repetitions of our dependent variable measure were recorded for each experimental condition (L-GVS, R-GVS and Pseudo-GVS).

Our design is based on the procedure developed by Tsakiris et al. (2008). That study used ongoing multisensory stimulation, topped-up every few seconds with a new stimulation event. The authors showed that this stimulation schedule induces a strong and progressive illusion, suggesting that accumulation of multisensory evidence during the run leads to the illusory experience. The whole experiment consisted of six blocks. To avoid transfer, we counterbalanced synchronous and asynchronous conditions across participants: half the participants received three blocks with asynchronous stroking followed by three synchronous blocks, while the others received the reversed order. Both at the beginning and end of each block, the camera took a picture of participant's actual hand position to ensure that participants did not move their hands.

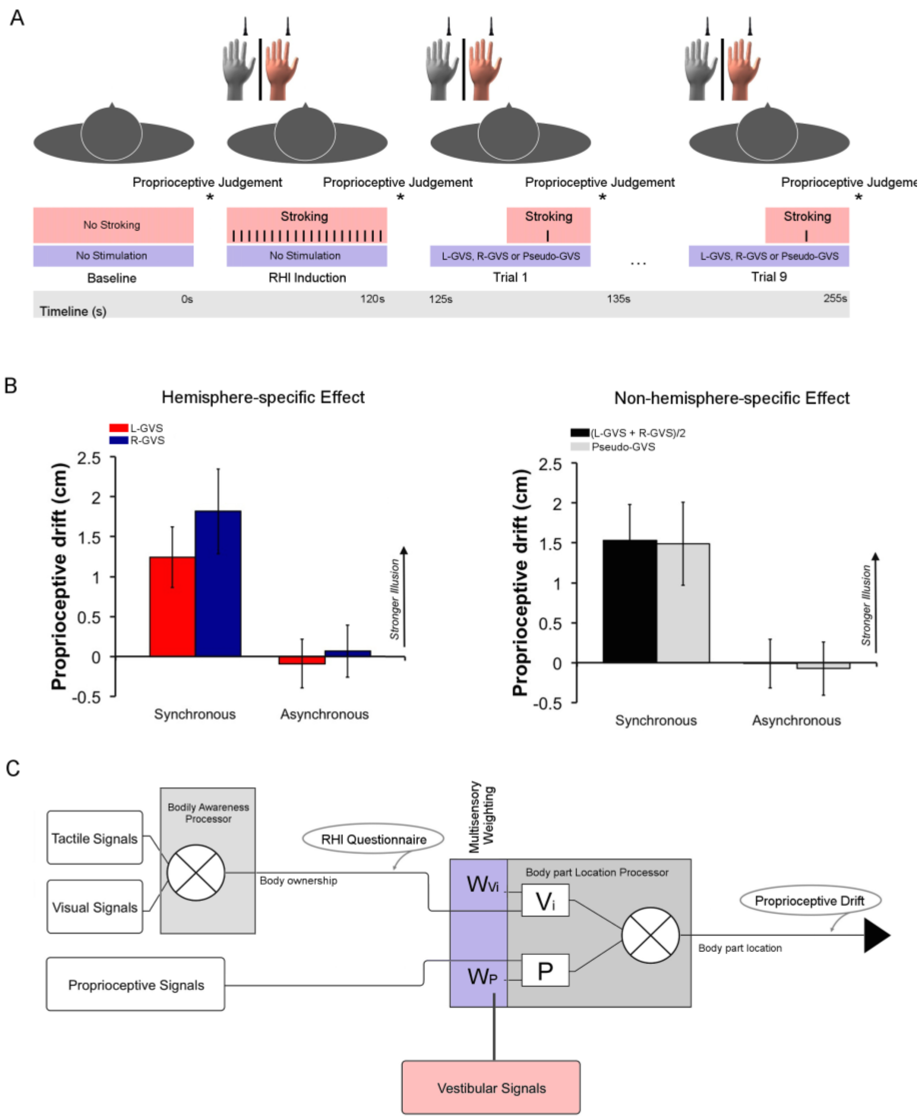

Figure 1. Experimental paradigm and results.

(A) Timeline of the experimental block. An initial proprioceptive judgement was followed by a two minutes of visuo-tactile stimulation to induce the illusion. This was followed by 9 shorter periods of visuo-tactile stimulation with concurrent GVS or Pseudo-GVS. Each period of visuo-tactile stimulation was followed by proprioceptive pointing judgement.

(B-left panel) Mean of proprioceptive drifts in L-GVS and R-GVS conditions. Drifts were larger in synchronous blocks than in asynchronous blocks for both L-GVS and R-GVS. Drifts after synchronous stroking were significantly larger after trials where R-GVS was applied than when L-GVS was used. (B-right panel) Mean of proprioceptive drifts in Pseudo-GVS and non-hemisphere-specific GVS conditions. Proprioceptive drifts were not affected by the non-hemipshere-specific vestibular effect. Error bars indicate SEM.

(C) A schematic representation of the vestibular reweighting hypothesis. Concurrent tactile and visual signals are combined, which influences the experience of one's own body (Bodily Awareness Processor). Tactile and visual interaction induces bodily awareness with respect to the rubber hand ("the rubber hand feels like my hand"). Next, visual (Vi, i.e. rubber hand) and proprioceptive (P, i.e. real hand) signals are integrated to construct a representation of the hand location in space ("where is my hand?"). The perceived self-location is captured by the proprioceptive drift in the RHI paradigm. Vestibular signals influence the weighting function between proprioceptive and visual inputs by increasing the weight of proprioceptive signals (Wp) and decreasing the reliance on extrinsic visual signals (Wvi), thus reducing visual capture. Note that the vestibular system acts on the weighting function, rather than directly influencing the precision of raw proprioceptive signals.

3. Results

The pixel coordinates of each laser beam were measured on each image using ImageJ software (http://rsbweb.nih.gov/ij/) to estimate the proprioceptive drift in each experimental condition. The measures of proprioceptive drift were transformed from pixels to centimetres. The proprioceptive drift refers to the change in the perceived position of the hand relative to baseline (Botvinick and Cohen, 1998; Longo et al. 2008; Tsakiris et al., 2006). Positive proprioceptive drifts represent a mislocalisation towards the rubber hand. Baseline subtraction is important and standard in RHI studies (Botvinick and Cohen, 1998). The main purpose is to adjust for the substantial drifts in proprioception that occur over time, independent of any specific experimental stimulation. Proprioceptive drift was measured for each combination of GVS and visuo-tactile stimulation. These values were compared across different stimulation conditions using planned contrasts, to isolate hemispheric-specific and non-hemisphere-specific effects of GVS on bodily awareness (see above). No outlier rejection has been applied in our analysis. Data were analysed using the Statistical Package for Social Sciences (SPSS) 21.0 (Illinois).

3.1. Proprioceptive drift as a measure of the induced illusion

A proprioceptive judgment was obtained immediately after the illusion induction phase in both synchronous and asynchronous blocks, and prior to any GVS or PSEUDO-GVS pulses. Proprioceptive drift towards the rubber hand was significantly larger in the synchronous blocks (M=1.40 cm, SD=1.76 cm) than in the asynchronous blocks (M=-0.32 cm, SD=1.64 cm) (t(25)=4.648; p<0.001; Cohen's *d* effect size = 1.01). This suggests that synchronous multisensory stimulation successfully induced the RHI: participants localized their own index finger closer to the rubber hand during synchronous visuo-tactile stimulation relative to asynchronous visuo-tactile stimulation.

3.2. Vestibular effects on proprioceptive drift

We hypothesised that vestibular stimulation might influence bodily awareness in two distinct ways (Ferrè et al., 2013b; Ferrè et al., 2013c), which we expressed as planned contrasts between our conditions. In both contrasts, the dependent variable was the proprioceptive drift, which we treated as a quantitative proxy of the RHI.

First, it has been demonstrated that bodily awareness relies on integrating sensory signals in the right hemisphere (Blanke and Arzy, 2005; Tsakiris et al., 2007; Tsakiris et al., 2008). Accordingly the effects of vestibular stimulation could be *specific* to the hemisphere activated, and would therefore differ between L-GVS and R-GVS conditions. Importantly, this contrast precisely controls for the immediate sensory consequences of GVS, since both peripheral vestibular stimulation and concomitant cutaneous stimulation are exactly matched. Second, vestibular stimulation might also cause non-specific effects on bodily awareness (Vallar et al., 1990; Vallar et al., 1993) because of generic effects of arousal. Such effects would, presumably, be driven by the immediate sensations triggered by the stimulation, including afferent input from the vestibular organs, and from the skin under the stimulating electrodes. Crucially, such non-specific effects should be independent of polarity and hemisphere activated. To test this *non-hemipshere-specific* hypothesis, we compared the average of the L-GVS and R-GVS conditions to the Pseudo-GVS condition. This analysis is an established method of describing effects of such interventions (Schmidt et al., 2013a).

Hemisphere-specific effect. We used a planned comparisons approach to directly compare L-GVS and R-GVS conditions, in order to investigate how vestibular projections in each hemisphere might influence the neural processes responsible for bodily awareness. The effect of GVS polarity on proprioceptive judgements was analysed using a 2 (Stimulation: L-GVS, R-GVS) X 2 (Synchrony of stroking: synchronous, asynchronous) ANOVA. We preferred to use ANOVA as statistical approach, rather than the more conventional planned comparison using t-tests, to highlight the possible interaction between hemisphere-specific vestibular effects and synchrony of stroking. The analysis revealed a significant main effect of Synchrony of stroking (F(1,25)=13.799; p=0.001) and a significant main effect of Stimulation (F(1,25)=5.894; p=0.023). A significant interaction between Synchrony of stroking and Stimulation was also found (F(1,25)=4.749; p=0.039). Importantly, the interaction in this ANOVA is formally equivalent to a t-test planned comparison between L-GVS and R-GVS on the difference between synchronous and asynchronous measures that is conventionally used as the index of the strength of the RHI (Tsakiris and Haggard, 2005). Thus, the hypothesis of a hemisphere-specific GVS effect on bodily awareness was supported. Post-hoc t-tests revealed that the proprioceptive drifts were lower after L-GVS than after R-GVS on synchronous blocks (L-GVS: M=1.24 cm, SD=1.86; R-GVS: M=1.81 cm, SD=2.59; t(25)=-2.874; p=0.008; Cohen's *d* effect size=0.25), but there was no significant difference between the drifts in asynchronous blocks (t(25)=-1.019; p=0.318) (Figure 1b). Further inspection of the data indicated that 21 out of 26 participants showed less proprioceptive drift after L-GVS compared to R-GVS in synchronous blocks.

Non-hemisphere-specific effect. We calculated the non-hemisphere-specific effect of vestibular stimulation, defined as (L-GVS+R-GVS)/2, and compared this to the Pseudo-GVS condition in a 2 (Stimulation: (L-GVS+R-GVS)/2, Pseudo-GVS) X 2 (Synchrony of stroking: synchronous, asynchronous) ANOVA. As expected, this analysis revealed a significant main effect of Synchrony of stroking (F(1,25)=12.208; p=0.002) indicating that only synchronous stroking induces illusory hand-ownership and self-localisation toward the rubber hand. No significant main effect of Stimulation (F(1,25)=0.209; p=0.651) and no interaction between Stimulation and Synchrony of stroking (F(1,25)=0.020; p=0.890) was found (Figure 1b). Again, the interaction of this ANOVA is formally equivalent to a t-test planned comparison of the non-hemisphere-specific effects of GVS against Pseudo-GVS on the RHI. The hypothesis of a non-hemisphere-specific effect of GVS on bodily awareness was not supported. This analysis suggests that GVS inputs per se do not influence proprioceptive judgements in the RHI.

3.3. Vestibular effects on pointing precision

We measured bodily awareness using a quantitative proxy based on proprioceptive information. In principle, any direct effect of GVS on proprioception could be mistaken as an effect on bodily awareness. Any low-level biasing effect of GVS on proprioception should be present in both synchronous and asynchronous conditions, and would already be controlled for by our analyses. However, GVS might also alter the *precision*, and hence the reliability of proprioceptive information.

Thus we performed a control analysis to consider whether vestibular stimulation might directly influence proprioceptive signals, independently of bodily awareness. For example, if L-GVS were to improve the reliability of proprioceptive signals, this would in turn reduce the visual capture of proprioception by the fake hand (Ernst and Banks, 2002), which could result in reduced proprioceptive drifts. To address this issue, we used the standard deviations of repeated proprioceptive drift estimates in each condition as a measure for (inverse) reliability. Means and standard deviations for each experimental condition are reported in Table 1. We applied the same planned analyses to these estimates of proprioceptive reliability as to the main analysis of proprioceptive drift.

For the hemisphere-specific contrast, data were analysed using a 2 (Stimulation: L-GVS, R-GVS) X 2 (Synchrony of stroking: synchronous, asynchronous) ANOVA. We found no evidence for differences in proprioceptive reliability due to either Stimulation (F(1,25)=0.916; p=0.348), or Synchrony of stroking (F(1,25)=1.568; p=0.222), or for the interaction between these factors (F(1,25)=1.385; p=0.250).

A similar analysis was performed for the non-hemisphere-specific contrast. A 2 (Stimulation: (L-GVS+R-GVS)/2, Pseudo-GVS) X 2 (Synchrony of stroking: synchronous, asynchronous) ANOVA showed no differences in proprioceptive reliability due to either Stimulation (F(1,25)=1.102; p=0.304), or Synchrony of stroking (F(1,25)=0.277; p=0.603), or for the interaction between these factors (F(1,25)=0.843; p=0.367). These control analyses suggests that vestibular stimulation did not directly affect reliability of proprioceptive signals.

	Vestibular Stimulation Conditions			
	L-GVS	R-GVS	(L-GVS+R-GVS)/2	Pseudo-GVS
Synchronous RHI	M: 0.77 SD: 0.33	M: 0.99 SD: 1.04	M: 0.88 SD: 0.68	M: 0.90 SD: 1.08
Asynchronous RHI	M: 0.75 SD: 0.42	M: 0.73 SD: 0.40	M: 0.74 SD: 0.41	M: 0.88 SD:0.63

Table 1. Vestibular effects on pointing precision.
Mean (M) and standard deviation (SD) are reported as function of RHI conditions and vestibular stimulation conditions.

3.4. Non-vestibular aspects of the stimulation do not influence RHI

Pseudo-GVS was applied as a control for non-specific vestibular effects. However, the Pseudo-GVS might potentially influence the RHI *per se*, for instance by somato-somatosensory interactions driven by the skin sensations evoked at the GVS electrodes. We thus compared the proprioceptive drift recorded during no stimulation (i.e. immediately after the induction phase) with the drift in the Pseudo-GVS trials. A 2 (Stimulation: Absent, Pseudo-GVS) X 2 (Synchrony of stroking: synchronous, asynchronous) ANOVA showed a significant main effect of Synchrony of stroking ($F(1,25)=16.136$; $p<0.001$). No significant main effect of Stimulation ($F(1,25)=0.928$; $p=0.345$), nor interactions between Stimulation and Synchrony of stroking ($F(1,25)=0.284$; $p=0.599$) were found. This analysis excludes the possibility that non-specific effects, such as arousal or somatosensory stimulation, might influence the RHI.

4. Discussion

Neuroanatomical (Bottini et al., 1995) and perceptual (Vallar et al., 1990; Vallar et al., 1993; Ferrè et al., 2011) studies confirmed that vestibular signals are integrated with several somatosensory signals in a wide cortical network, centred on the right hemisphere. Neuropsychological reports further suggested a vestibular contribution to the sense of one's own body, over and above any specific somatosensory signal. For example, artificial vestibular stimulation caused temporary remission of somatoparaphrenia, restoring normal bodily awareness (Bisiach et al., 1991). However, the vestibular contribution to bodily awareness has proved difficult to study experimentally. Here, we demonstrated that vestibular input *per se* did not influence our measure of the RHI. However, we found a clear difference between the two GVS polarities, corresponding to a difference in hemispheric activation: L-GVS, which primarily activates right-hemisphere networks, reduced the illusory experience of ownership over a rubber hand compared to R-GVS, as measured by proprioceptive drift.

Potentially, GVS could have affected proprioceptive drifts indirectly through attentional or arousal mechanisms, rather than through any effects on bodily awareness. L-GVS produces shift in spatial attention toward the left space, whereas R-GVS induces an attentional bias toward the right

(Ferrè et al., 2013d; Utz et al., 2011). In L-GVS trials, the attention of participants might be shifted toward the left hemispace, which would indeed reduce proprioceptive drift. Crucially, such attentional effects would be independent from the synchrony of stroking. However, we found a clear interaction between GVS polarity and synchrony of stroking. This interaction was due to the synchronous condition only: there was no difference in proprioceptive drifts between L-GVS and R-GVS in the asynchronous condition. Thus, an explanation based on shifts of spatial attention cannot readily account for our results.

During the RHI, the brain integrates synchronous visual and tactile signals to produce illusory ownership over the rubber hand. However, this experience induces a conflict between visually-observed and proprioceptively-sensed location of the hand, which the brain must resolve. Multisensory theories suggest that multiple sensory signals need to be combined, and that the nervous system faces a key challenge in selecting the correct weighting for each signal in the combination. As in other cases of visual-proprioceptive conflict (Hay et al., 1965; Van Beers et al., 2002), resolution occurs by weighting each individual sensory signal according to its importance. Visual information about location is usually highly reliable, and the participant's hand location is accordingly perceived as shifted towards the rubber hand. We suggest that right hemisphere vestibular projections increased the weight of intrinsic proprioceptive signals about hand position, and decreased the weight of the extrinsic visual information responsible for visual capture. As a result, proprioceptive information about hand position is less subject to visual capture by the rubber hand after L-GVS, and proprioceptive drifts are reduced. Most studies focus on perception of a single stimulus or event (e.g., judging the size of an object experienced by both vision and touch, Ernst and Blanks, 2002). However, the same remarks apply to the total perceptual landscape at any moment. The content of current perception is the organism in its environment (Gibson, 1966). This percept has exteroceptive, proprioceptive and interoceptive elements, whose relative weightings must be adjusted appropriately for the animal's current action. Our reweighting hypothesis proposes that vestibular signals play a key role in setting these weights.

Critically, the reduction of proprioceptive drifts induced by L-GVS was found only in the synchronous stroking condition, again suggesting that vestibular stimulation influenced the multisensory weightings contributing to bodily awareness, rather than actually altering proprioceptive or visual signals. Importantly, our control analysis showed that raw proprioceptive input was not affected by GVS. Indeed, the precision of proprioception (measured by the variability of pointing) was not significantly influenced by vestibular stimulation, suggesting that GVS did not directly alter proprioceptive uncertainty.

Optimal multisensory integration involves higher weighting of more reliable signals (Ernst and Banks, 2002), so stronger weighting of proprioception might in principle be due to vestibular-induced improvement of proprioceptive precision. Again, our control analysis of proprioceptive precision found no evidence for this interpretation. For these reasons, we suggest that the vestibular system acts directly on the multisensory weighting functions that underlie bodily awareness, and not only on the primary contributing signals (Figure 1c). The hemisphere-specific effects of GVS are not simply due to changes in precision of proprioceptive signalling, leading to subsequent optimal adjustments of feedforward multisensory integration. Rather, L-GVS appears to act directly on the multisensory integration *process* itself.

Our result suggests a dynamic, on-line contribution of vestibular inputs to bodily awareness. GVS was delivered in short 4.5 s pulses, with randomised polarities. Nevertheless, the experience of bodily part location, as measured by proprioceptive drift, was modulated between trials. Thus, vestibular modulation of bodily awareness could be changed over intervals as short as few seconds.

Although the parallelism between somatoparaphrenia and RHI is not straightforward, neuropsychological studies have posited a theoretical construct of bodily awareness that may be compared to that manipulated in RHI experiments. Bisiach et al. (1991) explained vestibular modulation of somatoparaphrenia as an enhancement in attentional mechanisms that restored spatial representation of the body. However, it has been recently reported that multisensory stimulation can lead to remission from somatoparaphrenia, without affecting concomitant attentional disorders, suggesting a dissociation between attentional mechanisms and bodily awareness (Bolognini et al., 2014). Our results are coherent with this dissociation between attention and bodily awareness. Somatoparaphrenia might reflect disturbed integration of current body-related signals, making patients disown specific body parts. Vestibular stimulation would increase the weighting of intrinsic somatosensory/proprioceptive representation of the limb, restoring the normal attribution to the self (Figure 1c).

One can wonder whether the effects reported here would also occur for the participant's right hand. We chose to study the left hand only for several reasons. First, there is a strong prediction from previous literature of right-hemisphere specialization for both proprioception and for vestibular representation (Bense et al., 2001; Suzuki et al., 2001; Dieterich et al., 2003; Janzen et al., 2008). Second, the right cerebral hemisphere is generally more involved in body part representation and attribution (Tsakiris et al., 2007; Tsakiris et al., 2008). Clinically, abnormal ownership of the left hand is much common than disownership for the right hand (Vallar and Ronchi, 2009), suggesting a right cerebral dominance for body part ownership. Future research might usefully use similar vestibular stimulation, combined with visuo-tactile stimulation of the right hand.

Lopez et al. (2010) found that vestibular stimulation increased RHI as measured by questionnaires – an effect in the opposite direction from our results. However, there are several differences between the two studies. First, their duration of vestibular stimulation was much longer than ours. Second, they used a blocked design, as opposed to our randomised, event-related design. The interpretations also differ. Lopez et al. (2010) argued that their results are a sign of GVS interfering with the mechanisms of bodily awareness. In contrast, we suggest that GVS functionally activates the cortical vestibular network. Indeed brief low intensity GVS pulse induces vestibular activations similar to those of natural movement (Fitzpatrick and Day, 2004). Our interpretation may be more in line with the view that RHI involves a dis-ownership of the hand, as a result of visual capture by the rubber hand. Vestibular stimulation is known to enhance somatosensory function (Ferrè et al., 2011; Ferrè et al., 2013a). GVS may boost a somatosensory contribution to bodily awareness, thus increasing resistance to visual capture by the rubber hand.

While the RHI is well accepted as an experimental model of embodiment, there has been less consensus on how to measure the phenomenon. Subjective, questionnaire-type reports have either been difficult to quantify, or confined to the mere occurrence of the illusion. They are also quite synthetic, and represent overall interpretations of an experiential episode, thus they are not suited to online, event-driven tasks, like that used here. We therefore used proprioceptive drift as a measure of

RHI. Although participants reported experiencing the illusion during synchronous blocks when questioned informally, we did not systematic elicit verbal reports of their subjective experience. One large study suggested a strong association between proprioceptive drift and psychometric questionnaire measures of “body ownership” (Longo et al., 2008). Others reported drifts without illusions of ownership (Rohde et al., 2011). However, the aim of our study was to investigate the on-line influence of the vestibular signals on bodily awareness. Proprioceptive drift may be appropriate in this case, because frequent, quantitative measures can be made within a randomised, event-related design. Interestingly, Rohde et al. (2011) found a proprioceptive drift in their asynchronous condition (Rohde et al., 2011, figure 3), which they interpreted was as by-product of making frequent proprioceptive judgements. Our data did not reproduce that result, even in the Pseudo-GVS condition.

5. Conclusion

We provide a behavioural demonstration that vestibular signals contribute to bodily awareness. The results can be interpreted as a vestibular modulation of the weighting of intrinsic proprioceptive signals in the process of multisensory integration of information about the body. Activating the vestibular network in the right hemisphere rapidly strengthens body awareness, by increasing the weighting of proprioceptive signals and decreasing the reliance on visual capture. Our research suggests that some neuropsychological disorders of bodily awareness and body-part ownership could reflect underweighting of the intrinsic somatosensory signals in multisensory integration. Our study also points to a potential mechanistic explanation for the striking remission from somatoparaphrenia with vestibular stimulation.

Figure 1. Experimental paradigm and results.

(A) Timeline of the experimental block. An initial proprioceptive judgement was followed by a two minutes of visuo-tactile stimulation to induce the illusion. This was followed by 9 shorter periods of visuo-tactile stimulation with concurrent GVS or Pseudo-GVS. Each period of visuo-tactile stimulation was followed by proprioceptive pointing judgement.

(B-left panel) Mean of proprioceptive drifts in L-GVS and R-GVS conditions. Drifts were larger in synchronous blocks than in asynchronous blocks for both L-GVS and R-GVS. Drifts after synchronous stroking were significantly larger after trials where R-GVS was applied than when L-GVS was used. (B-right panel) Mean of proprioceptive drifts in Pseudo-GVS and non-hemisphere-specific GVS conditions. Proprioceptive drifts were not affected by the non-hemisphere-specific vestibular effect. Error bars indicate SEM.

(C) A schematic representation of the vestibular reweighting hypothesis. Concurrent tactile and visual signals are combined, which influences the experience of one’s own body (Bodily Awareness Processor). Tactile and visual interaction induces bodily awareness with respect to the rubber hand ("the rubber hand feels like my hand"). Next, visual (Vi, i.e. rubber hand) and proprioceptive (P, i.e. real hand) signals are integrated to construct a representation of the hand location in space (“where is my hand?”). The perceived self-location is captured by the proprioceptive drift in the RHI paradigm. Vestibular signals influence the weighting function between proprioceptive and visual inputs by increasing the weight of proprioceptive signals (Wp) and decreasing the reliance on extrinsic visual signals (Wvi), thus reducing visual capture. Note that the vestibular system acts on the weighting function, rather than directly influencing the precision of raw proprioceptive signals.

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