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# Somatosensory modulation of perceptual vestibular detection

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## Abstract

1  
2 Vestibular-multisensory interactions are essential for self-motion, navigation and postural stability.  
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4 Despite evidence suggesting shared brain areas between vestibular and somatosensory inputs, no  
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6 study has yet investigated whether somatosensory information influences vestibular perception.  
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8 Here we used signal detection methods to identify whether somatosensory stimulation might  
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10 interact with vestibular events in a vestibular detection task. Participants were instructed to detect  
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12 **near-threshold vestibular roll-rotation sensations** delivered by Galvanic Vestibular Stimulation in  
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14 one half of experimental trials. A vibrotactile signal occurred to the **index fingers of both hands** in  
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16 half of the trials, independent of vestibular signals. **We found that vibrotactile somatosensory**  
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18 **stimulation decreased perceptual vestibular sensitivity.** The results are compatible with a gain  
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20 regulation mechanism between vestibular and somatosensory modalities.  
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## Keywords

28  
29 Vestibular sensation; Somatosensory processing; Galvanic Vestibular Stimulation; Multisensory  
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31 modulation.  
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## Abbreviations:

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42 GVS: galvanic vestibular stimulation; PIVC: parieto insular vestibular cortex; SII: secondary  
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44 somatosensory cortex; L-GVS: left-anodal and right-cathodal GVS; R-GVS: right-anodal and left-  
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46 cathodal GVS; **L-SHAM: left-anodal and right-cathodal SHAM; R-SHAM: right-anodal and left-**  
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48 **cathodal SHAM.**  
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## 1. Introduction

Vestibular signals are strongly integrated with information from other sensory modalities, including muscles, joints, vision, and touch (Lackner & DiZio, 2005). The vestibular system contains two distinct structures: the semicircular canals and the otolith organs, which are situated in the inner ear and detect changes in angular and linear acceleration, including gravity. Both semicircular canals and otolith organs constantly provide information to the brain regarding the sense of orientation and motion in three-dimensional space. Thus, vestibular signals are crucial to the perception of our body in the environment.

Unlike with all other sensory modalities, vestibular processing is strongly multimodal. Interactions between the canals and otoliths inputs occur immediately at the level of the first synapse in the brainstem and cerebellum. Multimodal interactions between visual, somatosensory and vestibular signals have been described in almost all vestibular relays, including the vestibular nuclei, the thalamus and several areas in the cerebral cortex (Lopez et al., 2012; zu Eulenburg et al., 2012). Electrophysiological studies have identified a widespread vestibular network whose core area is the Parieto Insular Vestibular Cortex (PIVC) (Guldin and Grüsser, 1998; Chen et al., 2010). 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 is a distributed set of regions including the anterior and posterior insula, superior temporal gyrus, temporoparietal junction, inferior parietal lobule, and somatosensory cortices (Lopez et al., 2012; zu Eulenburg et al., 2012). The right parietal operculum (area OP2) is considered the core region of the human cortical vestibular network (zu Eulenburg et al. 2012).

Somatosensory areas also receive vestibular inputs. Electrophysiological studies demonstrated that stimulating the peripheral vestibular nerve triggered neuronal responses in the secondary somatosensory cortex (SII) (Fredrickson et al. 1966). Guldin and Grüsser (1998) estimated that about 30–50% of neurons in the monkey's somatosensory area 3aV respond to vestibular stimuli. Analogous vestibular-somatosensory interactions have been described in human perception. Artificial vestibular stimulation has been shown to modulate psychophysical thresholds for tactile detection (Ferrè et al. 2011; Ferrè et al. 2013). The detection of light

1 somatosensory stimuli was estimated using a signal detection approach, to distinguish between  
2 perceptual sensitivity and response bias. Perceptual sensitivity was enhanced by artificial  
3 vestibular stimulation (Ferrè et al. 2011). This enhancement was found for tactile stimuli applied to  
4 both left and right hands. Accordingly, electrophysiological results showed an enhancement of the  
5 N80 wave of somatosensory-evoked potentials elicited by median nerve stimulation (Ferrè et al.  
6 2012). Also clinical observations described multisensory interactions between vestibular and  
7 somatosensory systems (Vallar et al. 1990; Vallar et al. 1993). Importantly, neuroimaging studies  
8 identified vestibular projections in the primary and the secondary somatosensory cortex,  
9 suggesting that these areas respond to both vestibular and somatosensory inputs (Bottini et al.  
10 1995).

11 Although there is growing evidence for multisensory perceptual interactions between  
12 vestibular and somatosensory signals, it is not yet clear whether somatosensory information might  
13 modulate vestibular processing. This modulation might have a functional relevance for balance  
14 and postural control. For instance, Lackner et al. (1999) demonstrated that patients with balance  
15 disorders regained postural control by touching a stationary surface with their fingers. More  
16 recently, Hashimoto et al. (2013) described better balance control during artificial vestibular  
17 stimulation when light touches were delivered to the fingers. These results suggest that  
18 somatosensory signals may regulate vestibular responses to maintain body posture (Hashimoto et  
19 al. 2013).

20 In the present study, we investigated bimodal interactions between the somatosensory and  
21 vestibular systems. Participants were instructed to detect near-threshold vestibular stimuli that  
22 occurred in one half of experimental trials. In the other half of the trials the vestibular stimulus was  
23 not present. A simultaneous vibrotactile signal occurred to the index finger of both left and right  
24 hands in half of all trials at random. The vibrotactile signal was therefore completely irrelevant to  
25 the participant's vestibular detection task. Galvanic vestibular stimulation (GVS) was used to  
26 deliver vestibular stimuli. GVS involves a weak direct current passing between surface electrodes  
27 placed on the mastoid behind the ear (Fitzpatrick & Day, 2004). GVS modulates the firing rate of  
28 vestibular afferents with perilymphatic cathodal currents causing an increase in firing rate and  
29

1 anodal currents causing a decrease (Fitzpatrick & Day, 2004). Critically, bipolar binaural GVS  
2 evokes a net pattern of firing across both vestibular organs that mimics a head motion in space, in  
3 particular a sensation of roll-rotation (Goldberg et al., 1984; Day & Fitzpatrick 2005). The direction  
4 of the of roll-rotation is polarity-specific: participants experience a roll-rotation towards the anodal  
5 side. The polarity of stimulation can be reversed, producing opposite effects on firing rate in the  
6 two vestibular organs, and thus reversing of direction of the apparent roll rotation (Day &  
7 Fitzpatrick 2005). Moreover, placing the GVS electrodes away from the mastoids allows a sham  
8 stimulation, which produce the same skin sensations under the electrodes as real GVS, but without  
9 effective stimulation of the vestibular organs.

10 We wanted to compare patterns of multisensory interaction between somatosensory and  
11 vestibular modalities to make plausibly different predictions about the effects on vestibular  
12 sensitivity. Importantly, these patterns represent the possible behavioural outcomes driven by  
13 interactions between somatosensory and vestibular stimuli. Thus, they describe behavioural  
14 effects, rather than being related to specific neurons or overall firing rate of areas. Artificial  
15 vestibular stimulation consistently increased perceptual sensitivity to cutaneous mechanical and  
16 electrical stimuli to the hands (Vallar et al. 1990; Vallar et al. 1993; Kerkhoff et al., 2011; Ferrè et  
17 al., 2011; Ferrè et al., 2014). Thus the two sensory signals might combine along the lines of these  
18 reported multisensory interactions, resulting in an enhancement of vestibular sensitivity.  
19 Alternatively, somatosensory and vestibular signals might interact through inhibitory connections.  
20 Inhibitory interactions between visual and vestibular signals have been largely described for in  
21 maintaining and controlling gaze (Brandt et al., 1998; Wenzel et al. 1996; Deutschländer et al.  
22 2002). For example, Bense and co-workers (2001) showed that artificial vestibular stimulation  
23 bilaterally deactivated the occipital visual cortex, including primary areas (BA 17-19). A model  
24 based on inhibitory connections between somatosensory and vestibular inputs might predict  
25 multisensory inhibition of vestibular sensitivity. Disentangling these different possibilities provides  
26 a novel insight into interactions between somatosensory and vestibular systems, and may clarify  
27 whether there is a functional influence of somatosensory information on vestibular perceptual  
28 sensitivity.

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## 2. Materials and Methods

### 2.1. Compliance with Ethical Standards

The experimental protocol was approved by the local ethics committee (Royal Holloway University of London) and the study was conducted in line with the Declaration of Helsinki (1995). Participants gave written informed consent to participate in the experiment before inclusion in the experiment.

### 2.2. Participants

Twenty naïve paid right-handed healthy volunteers (eight males, mean age:  $20.33 \pm 0.48$  years; mean  $\pm$  SD) participated in the experiment. Exclusion criteria were any history of neurological or psychiatric disorders. The sample size was set in advance of testing, and was also used as data-collection stopping rule. No participants withdrew from the study.

### 2.3. Galvanic Vestibular Stimulation (GVS)

Bipolar GVS was applied to deliver a boxcar pulse of 0.7 mA with 250 msec duration using a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, ON, Canada). This GVS intensity has been largely considered as sub-threshold (Kerkhoff et al., 2011; Oppenländer et al., 2015). Carbon rubber electrodes (area  $10 \text{ cm}^2$ ) were placed binaurally over the mastoid processes and fixed in place with adhesive tape. The areas of application were first cleaned with cotton wool soaked in surgical spirit, and electrode gel was applied to reduce the impedance. Left-anodal and right-cathodal GVS configuration is named 'L-GVS' (Figure 1b). The inverse polarity, namely right-anodal and left-cathodal GVS configuration, is named 'R-GVS' (Figure 1b). This GVS configuration is known to induce illusory perception of motion and evoke clear roll-rotation sensations towards the anodal side (Day et al., 1997). Sham stimulation was also administered

1 using electrodes placed on the neck about 5 cm below the GVS electrodes. Left-anodal and right-  
2 cathodal SHAM configuration is named 'L-SHAM' (Figure 1b), while right-anodal and left-cathodal  
3 SHAM configuration, is named 'R-SHAM' (Figure 1b). The sham stimulation evoked a tingling skin  
4 sensation that was similar to GVS, and so functions as a control for non-specific effects.  
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#### 10 2.4. Experimental design

11 Data from each participant was gathered in a single session. Verbal and written  
12 instructions about the task were given to participants at the beginning of the session. The  
13 experimental procedure and timing was controlled by custom-made software. To reduce the  
14 postural consequences of GVS pulse, the experiment was conducted in a comfortable sitting  
15 position.  
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24 Somatosensory vibrotactile stimulation was delivered by two identical vibrators (Hitachi,  
25 Tokyo, Japan) attached on a support, vibrating at 100 Hz, on the palmar surface of the first  
26 phalanx of both right and left index fingers (Figure 1a).  
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31 Our design factorially combined somatosensory and vestibular signals. The vestibular  
32 detection task was designed to follow a signal detection approach (Macmillan & Creelman, 1991).  
33 It consisted of a 2 (vestibular stimulus present/absent) x 2 (somatosensory stimulus  
34 present/absent) design, with the following trial types: 30 vestibular only trials (vestibular stimulus  
35 present and touch stimulus absent); 30 vestibular and touch trials (vestibular stimulus present and  
36 somatosensory stimulus present); 30 touch only trials (vestibular stimulus absent and  
37 somatosensory stimulus present); and 30 no stimulus trials (vestibular stimulus absent and  
38 somatosensory stimulus absent). Thus, a total of 120 trials were performed divided in six blocks.  
39 Half of the vestibular present trials was presented with L-GVS and the other half with R-GVS.  
40 Sham stimulation (L-SHAM and R-SHAM) was administered in the vestibular absent trials. Trial  
41 order was randomized, so that participants could not predict stimulus presence or stimulus polarity.  
42 Participants were blindfolded throughout the task. For somatosensory present trials, vibrotactile  
43 stimulation was delivered after a variable interval between 250 ms and 500 ms from an acoustic  
44 beep sound. Vibrotactile stimulation was followed by 1000 ms of delay and then the GVS/SHAM  
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1 pulse, if present, was administered. A double beep sound indicated the end of the trial after 500  
2 ms of delay from the GVS/SHAM pulse. In each somatosensory present trial the overall duration  
3 of vibrotactile stimulation was 1500 ms. Somatosensory absent trials had an identical timing, but  
4 no actual vibrotactile stimulation occurred. The overall timing of the experiment was based on  
5 previous studies (Ferrè et al. 2013). Participants made unspeeeded verbal responses ('yes'/'no').  
6 They were only required to indicate whether or not they felt a vestibular sensation of roll-rotation,  
7 and did not report which ear was stimulated. Data for each trial were recorded and analysed later.  
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### 17 2.5. Data analysis

18 Vestibular detection results were analysed using signal detection analysis (Macmillan &  
19 Creelman, 1991). We considered the number of hits (number of vestibular stimulus present trials  
20 in which participants said 'yes'), false alarms (number of vestibular stimulus absent catch trials in  
21 which participants said 'yes'), misses (number of vestibular stimulus present trials in which  
22 participants said 'no') and correct rejections (number of vestibular stimulus absent catch trials in  
23 which participants said 'no'). Hit rates [P('yes'|vestibular stimulus present), proportion of hit trials to  
24 which participant responded 'yes'] and false alarm rates [P('yes'|vestibular stimulus not present),  
25 proportion of trials in which there is not actually the stimulus to which subject responded 'yes']  
26 were calculated. These were used to obtain the perceptual sensitivity ( $d'$ ), a measure of  
27 discriminability in detecting the signal. The  $d'$  is the difference between the z-transformed  
28 probabilities of hits and false alarms, and was therefore calculated as  $d' = z(\text{Hit}) - z(\text{False Alarm})$ .  
29 The tendency to report stimuli as present ( $C$ , response bias) was also obtained as  $C = - [z(H) +$   
30  $z(F)]/2$ . Sensitivity and response bias were calculated for each GVS polarity, and each  
31 somatosensory condition.  
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### 55 3. Results

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A  $2 \times 2$  repeated measures ANOVA with factors of Somatosensory Stimulation (present vs absent) and GVS polarity (L-GVS vs R-GVS) was applied to VSDT estimates of perceptual sensitivity ( $d'$ ) and response bias ( $C$ ).

Analysis of  $d'$  showed a significant effect of Somatosensory Stimulation ( $F(1,19) = 10.820$ ,  $p = 0.004$ , Partial  $\eta^2 = 0.363$ ), with lower vestibular sensitivity when somatosensory stimulation was present than when it was absent. There was no effect of GVS polarity ( $F(1,19) = 0.012$ ,  $p = 0.914$ ) and no interactions between factors ( $F(1,19) = 0.890$ ,  $p = 0.357$ ).

$C$  values showed a significant main effect of Somatosensory Stimulation ( $F(1,19) = 6.469$ ,  $p = 0.02$ , Partial  $\eta^2 = 0.254$ ). Participants showed the tendency to be more liberal in the somatosensory present condition compared to somatosensory absent condition. No significant effect of GVS polarity ( $F(1,19) = 0.493$ ,  $p = 0.491$ ) or interaction between factors were found ( $F(1,19) = 0.296$ ,  $p = 0.593$ ).

--- Insert Figure 1 about here ---

### 3. Discussion

Vestibular projections in the human brain are widespread and highly interconnected with other sensory areas, including the somatosensory cortices. Here we wanted to compare patterns of interaction between somatosensory and vestibular signals. Based on anatomical evidence, we made two contrasting predictions. First, the two sensory signals might combine resulting in an enhancement of vestibular sensitivity, as reported for other multisensory interactions (Vallar et al. 1990; Vallar et al. 1993; Ferrè et al. 2012). Alternatively, somatosensory and vestibular signals might interact through inhibitory connections. Our results support this second hypothesis: vestibular sensitivity decreased when concurrent, yet irrelevant, somatosensory inputs were also present. That is, participants were worst in detecting GVS-induced roll-rotation sensations when vibrotactile stimuli were applied to the fingers, compared to a condition in which the tactile stimuli

1 were absent. Additionally, participants were more liberal when tactile signals were present.  
2 Finally, no differences between the detection of GVS polarities were found.  
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4 Vestibular and somatosensory signals converge at the level of the vestibular nuclei  
5 (Waespe & Henn, 1978), at the thalamus (Magnin & Putkonen, 1978; Sans et al. 1970) and in  
6 multisensory cortical regions such as the parietal operculum and the posterior insula (Schwarz &  
7 Fredikson, 1971; Bremmer et al. 2002; Lopez, 2013;). Thus, it might not be surprising that these  
8 modalities interact. Artificial vestibular stimulation has been shown to increase the sensitivity for  
9 tactile stimuli **applied on the hands of healthy participants** (Ferrè et al. 2011; Ferrè et al. 2012). It  
10 has also been demonstrated that artificial vestibular stimulation improves tactile deficits in  
11 neurological patients (Vallar et al. 1990; Vallar et al. 1993; **Kerkhoff et al., 2011; Schmidt et al.,**  
12 **2013**). Our results demonstrate that vestibular processing in the presence of somatosensory  
13 signals is **inhibited**. Similarly, inhibitory visual-vestibular interactions have been described for  
14 maintaining and controlling gaze (Brandt et al. 1998). Accordingly, PET studies using artificial  
15 vestibular stimulation demonstrated not only an activation of the PIVC but also a decrease in rCBF  
16 of the visual cortex (Wenzel et al. 1996; Deutschländer et al. 2002). Inhibitory somatosensory-  
17 vestibular interactions might be therefore beneficial for prioritising environmental information and  
18 postural control.  
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37 Clinical reports have described a decrease in postural unbalance in vestibular loss patients  
38 when concomitant somatosensory signals were delivered, i.e. patients were asked to place their  
39 fingers on a surface (Lackner et al. 1999). Importantly, Dickstein et al. (2001) confirmed these  
40 results in a group of healthy participants: the postural sway decreased in the presence of tactile  
41 information, and not in the presence of other sensory cues, such as visual events. Our results are  
42 in line with these findings, supporting a functional relation between vestibular and somatosensory  
43 signals.  
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53 Caution is required in interpreting the non-significant difference that we found between GVS  
54 polarities. Our data suggest that the somatosensory signals have the same effects on the  
55 detection of left-anodal and right-cathodal and right-anodal and left-cathodal GVS stimuli. This  
56 lack of lateralization contrasts with previous findings using GVS, which found polarity-dependent  
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1 differences in postural, sensorimotor, and cognitive functions (Utz et al. 2010). Accordingly,  
2 neuroimaging studies identified an asymmetry in the cortical area activated by GVS. Fink et al.  
3 (2003) found that left-anodal and right-cathodal GVS produced unilateral activation of the right  
4 hemisphere vestibular projections, while the opposite polarity, i.e., left-cathodal and right-anodal  
5 GVS, activated both left and right hemispheres (Fink et al. 2003). Importantly, the lack of polarity-  
6 dependent effects might arise because of the low level processing required by our task.  
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12 Somatosensory stimuli also influenced the response bias in our vestibular detection task:  
13 participants were more liberal in the somatosensory present condition compared to somatosensory  
14 absent condition. These results were not predicted and might reflect a non-specific bias or change  
15 in the arousal in decision making when multiple stimuli are applied to the body (Johnson et al.  
16 2006). The response bias is the extent to which one response is more probable than another.  
17 Importantly, the signal detection method that we used allows a clear distinction between perceptual  
18 sensitivity and response bias. That is, the effects of somatosensory stimulation on vestibular  
19 sensitivity are independent from the effects of the somatosensory stimulation on response bias.  
20 Participants were more likely to respond that a stimulus was present, however this tendency can  
21 be dissociated from the somatosensory-induced decrease in perceptual sensitivity.  
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35 Multiple sensory stimuli applied to the body might have increased the perceptual load to be  
36 processed. Research on the role of perceptual load in dual task or selective attention was  
37 triggered by the hypothesis that perception has limited capacity (Lavie et al., 2005). Thus,  
38 increasing the number of items that need to be perceived is more demanding on attention (Lavie  
39 and Cox, 1997; Lavie et al., 2005). However, only the vestibular stimulus was relevant in our task.  
40 Participants were instructed to detect roll-rotation sensations and ignore the somatosensory stimuli  
41 applied to the fingers. Further, the somatosensory stimuli were applied 1000 ms before the *to-be-*  
42 *detected* vestibular signal to avoid distraction or other non-specific effects. Finally, the  
43 somatosensory stimulation was spatially distinct from our vestibular stimuli. It is therefore unlikely  
44 that an attentional load account can readily explain our results.  
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57 In our study, somatosensory stimulation was administered to both left and right hand. We  
58 chose this combination for several reasons. First, the strongest effects of vestibular stimulation  
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1 have generally been found when stimulating the vestibular organ and the hand (Vallar et al., 1990;  
2 Vallar et al., 1993). Second, it has been demonstrated that vestibular stimulation modulates tactile  
3 sensitivity for both hands (Ferrè et al., 2011). An interesting question is whether somatosensory  
4 stimuli applied to different body parts might induce a similar reduction in vestibular detection. One  
5 might hypothesise that somatosensory stimulation of the sole of the feet would be functionally  
6 relevant for balance and postural control. However, both electrophysiological and neuroimaging  
7 studies identified a convergence between vestibular and somatosensory inputs in the parietal  
8 operculum and secondary somatosensory cortex. Critically, a fine somatotopical organisation of  
9 body parts is less present in these areas. Future studies might investigate potential interaction  
10 between vestibular detection and somatosensory stimulation applied to different body parts.

11 We suggest that somatosensory signals inhibit vestibular sensitivity. Thus, our results  
12 suggest that providing additional tactile information may be useful to reduce vestibular related  
13 symptoms, such as dizziness and vertigo, in vestibular patients. Vestibular patients could benefit  
14 by incorporating vibrotactile cues in rehabilitation, since our data suggests that vibrotactile  
15 information can decrease vestibular signals. Future, clinical studies might investigate this question  
16 more fully.

17 In conclusion, this study provides evidence that somatosensory modulation occurs on  
18 vestibular processing, supporting that this interaction is inhibitory. Vestibular signals are inhibited  
19 in the presence of somatosensory information. These perceptual results are consistent with known  
20 neuroanatomical interactions between these two sensory modalities (zu Eulenburg et al. 2012;  
21 Lopez & Blanke, 2011).

## Acknowledgements

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**Conflict of interest**

The Authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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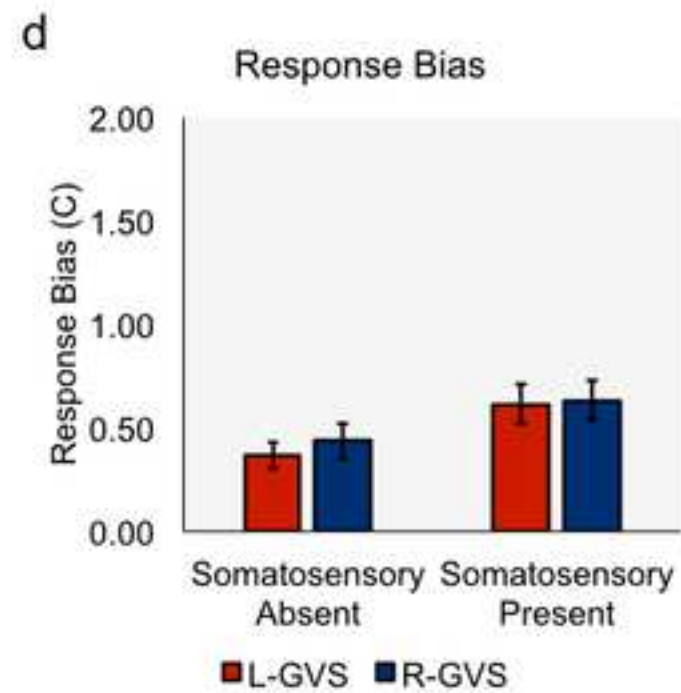
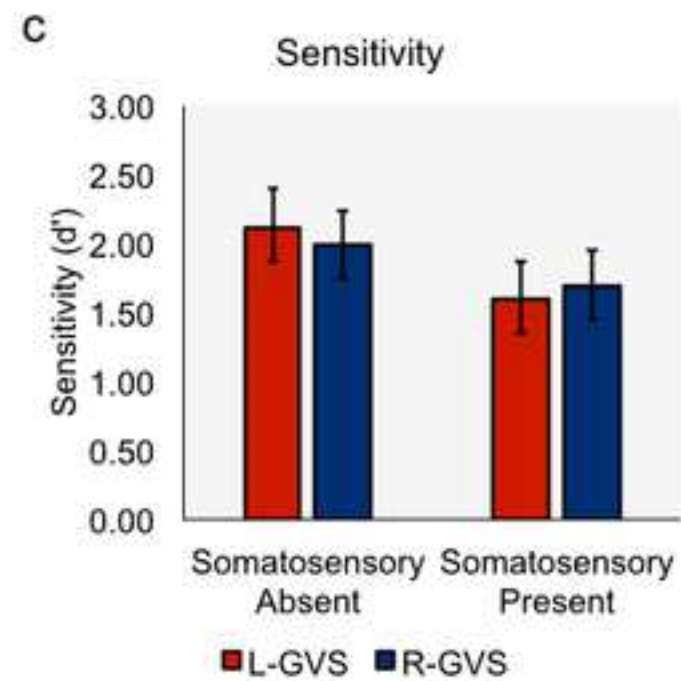
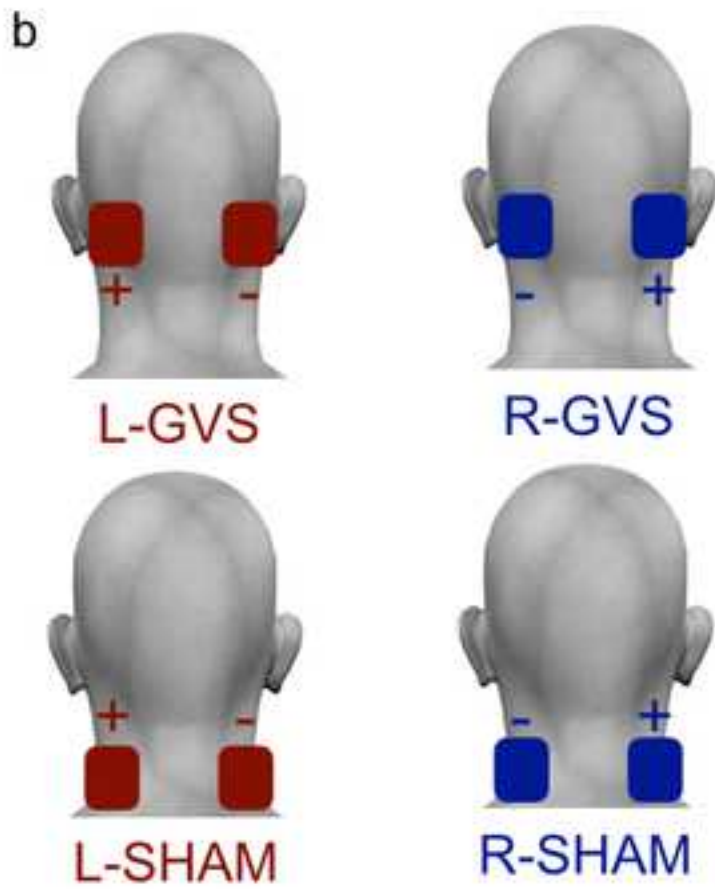
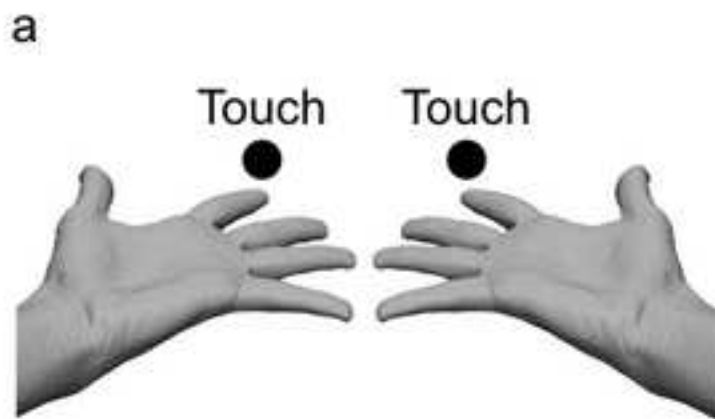
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## Legend for figures

### Figure 1. Experimental procedure and results.

(a) Somatosensory vibrotactile stimulation was delivered on the palmar surface of the first phalanx of both right and left index fingers. (b) Bipolar GVS was applied with a boxcar pulse of 0.7 mA with 250 msec. Left-anodal and right-cathodal GVS configuration is named 'L-GVS'. The inverse polarity, namely right-anodal and left-cathodal GVS configuration, is named 'R-GVS'. Sham stimulations (both L-SHAM and R-SHAM) was applied using electrodes placed on the neck about 5 cm below the GVS electrodes. (c) Vestibular detection task: sensitivity results. (d) Vestibular detection task: response bias results.





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