

## Vestibular contributions to bodily awareness

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### ABSTRACT

The vestibular system has widespread interactions with multisensory cortical networks, including the somatosensory areas. Several clinical observations suggested that vestibular signals are essential to compute more abstract cognitive representations of the body. However, the existing literature is generally based on isolated reports. We aimed to provide both a theoretical framework, and an experimental method to investigate potential vestibular contributions to somatic cognition. Accordingly, we have investigated effects of galvanic vestibular stimulation (GVS) on the localisation of a stimulus on the skin of the hand (a process that we define as somatoperception) and on the implicit representation of the hand size and shape (involving a different process which we define as somatorepresentation).

Vestibular input influenced the localisation of tactile stimuli on the hand: touches on the dorsum of the hand were perceived as shifted toward the wrist. The specific polarity of vestibular stimulation influences the localisation errors. Right anodal and left cathodal, which influences both cerebral hemispheres, induced a stronger localisation bias compared to left anodal and right cathodal GVS, which influences primarily the right hemisphere. Although our data confirmed previous findings that the body model of the shape of the hand is massively distorted, vestibular inputs do not contribute to these distortions.

Our results suggest that vestibular input influences the registration of somatosensory input onto a map of the body (somatoperception), but does not influence stored knowledge about the spatial organisation of the body as a physical object (somatorepresentation).

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### 1. Introduction

Information from the vestibular peripheral organs in the inner ear is integrated with several other classes of signals about the body, generated by eyes, muscles and joints. The resulting signals provide a coherent sense of body posture and orientation in surrounding space (Berthoz, 1996). Multiple lines of evidence indicated the importance of a functional link between vestibular and somatosensory systems. On the one hand, neuroimaging studies revealed an anatomical overlap of vestibular and somatosensory projections (Bottini et al., 1995; Fasold et al., 2000; review in Lopez, Blanke, & Mast, 2012). On the other hand, clinical reports described temporary modulation of somatosensation in brain damaged patients induced by artificial vestibular stimulation (Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990; Kerkhoff et al., 2011). Similarly, psychophysical studies showed that vestibular inputs

directly influence primary somatosensory processing: vestibular stimulation facilitates detection of faint somatosensory stimuli in healthy volunteers (Ferrè, Bottini, & Haggard, 2011) and enhances specific somatosensory evoked potential components originating in the right opercular region (Ferrè, Bottini, & Haggard, 2012). These results were interpreted as a vestibular-induced modulation in the level of primary processing of somatic stimuli, consistent with multisensory regulation of the gain in somatosensory cortical processing pathways.

However, the vestibular contribution to other, more cognitive, aspects of body perception is not yet clear. Several clinical observations suggested that vestibular signals are essential to compute more abstract cognitive representations of the body. For instance, caloric vestibular stimulation (CVS) can have dramatic effects on neurological disorders that involve altered bodily awareness, including disownership of body parts (somatoparaphrenia, Bisiach, Rusconi, & Vallar, 1991), somatoagnosia (Rode et al., 2012) and anosognosia (Cappa, Sterzi, Vallar, & Bisiach, 1987). Additionally, CVS modifies or reduces phantom limbs sensations in both paraplegic (Le Chapelain, Beis, Paysant, & André, 2001) and amputees patients (André, Martinet, Paysant, Beis, & Le Chapelain, 2001).

Here we have focussed on a cardinal aspect of somatosensory representation, namely the localisation of somatosensory stimuli,

**Abbreviations:** GVS, galvanic vestibular stimulation; CVS, caloric vestibular stimulation; PIVC, parieto-insular vestibular cortex; TPJ, tempo parietal junction; SI, primary somatosensory cortex

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and their relation to the sense of one's own body. Sensory information from the body surface projects to the well-known sensory homunculus of the primary somatosensory cortex. The neurons in this area form an ordered, though characteristically distorted, map of the contralateral body surface. This map is often thought to underlie the perception of where on the skin a sensory stimulus is located. To give just one well-known example, appropriately-timed presentation of two nearby stimuli on the skin can produce the percept of a third stimulus located at the midpoint of the two. This illusion was accompanied by a somatosensory cortical response in a cortical region midway between the projections of the two actual stimuli (Friedman, Chen, & Roe, 2008). Interestingly, the same somatosensory cortical maps may underlie the sense of one's own body, as well as the sensation of a bodily stimulus. Thus, anaesthesia or amputation of the digits affects both the organisation of primary somatosensory cortex (Gandevia & Phegan, 1999) and also produces a feeling of enlargement or distortion of the relevant body parts.

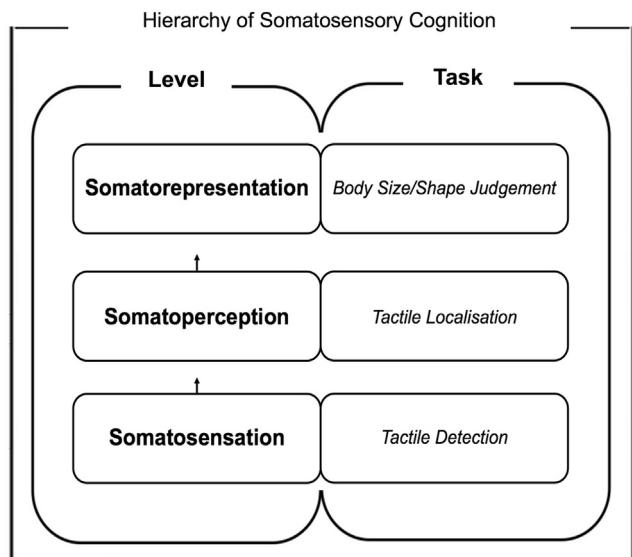
However, both tactile localisation, and the sense of one's own body require a range of other cognitive processes in addition to primary somatosensation. In a recent review, Longo, Azañón, and Haggard (2010) distinguished between two such processes. These were (i) somatoperception: 'the processes of constructing percepts and experiences of somatic objects and events, and of one's own body' and (ii) somatorepresentation: knowledge about 'the body's character as a physical object in the external world' (Longo et al., 2010). Somatoperception involves an on-line percept of the state of the body, based on the integration of multisensory inputs, while somatorepresentation involves both explicit and implicit knowledge related to body, which may be less directly related to immediate input.

Therefore, we can propose a hierarchy of somatosensory cognition (Fig. 1), extending from primary somatosensation, to somatoperception and finally somatorepresentation. This hierarchy does

not correspond directly to the somatosensory afferent pathway. In particular, somatosensation is a necessary condition for somatoperception, because perceiving the current state of the body will always involve integrating a range of somatosensory afferent signals. In contrast, somatorepresentation can persist in the absence of any particular somatosensory input: one knows what one's body is like even in the absence of any tactile afferents (Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013). We suggest that each level of the hierarchy can be tapped by different somatosensory tasks: tactile detection measures the first, somatosensory level, tactile localisation the somatoperceptual level, and judgements about body part size, or shape the somatorepresentational level (Fig. 1). Previous work already showed strong vestibular modulation of somatosensory detection (Ferré et al., 2011). Here we investigate whether vestibular input can also influence the somatoperceptual and somatorepresentational levels.

Experiment 1 investigated the vestibular influence in recognising the location of a stimulus on the skin surface (topognosis). Clinical reports described brain-damaged patients unable to indicate where they have been touched, though their ability to detect that they had been touched was unimpaired (Head & Holmes, 1911). On the basis of these observations, it has been proposed that the ability to localise stimuli on the skin is subserved by a cognitive representation of the body surface, namely the superficial schema. Localising the activation produced by a stimulus within a somatotopic map is, in fact, not by itself sufficient to identify its position on the body surface. Rather, a two-stage process is required (Longo et al., 2010). First, the stimulus-evoked activity is localised within the somatotopic map. Second, the somatotopic location must be mapped onto a corresponding bodily location. This second step requires a body model, relating the receptor surface of the skin to locations on the body, and thus involves at least an implicit somatoperception according to the definition of Longo et al. (2010). Consistent with this two-step model for somatoperception, localising a tactile stimulus involves both the somatotopic maps in the primary somatosensory cortex (SI) (Seyal, Siddiqui, & Hundal, 1997), and also additional somatosensory processes in parietal areas posterior to SI (Porro et al., 2007; Van Boven, Ingeholm, Beauchamp, Bikle, & Ungerleider, 2005). Interestingly, recent studies in patients (Rapp, Hendel, & Medina, 2002) and in healthy volunteers (Mancini, Longo, Iannetti, & Haggard, 2011) highlighted systematic biases in localizing tactile stimuli on the hand. In healthy volunteers, these biases involved a distal and radial shift of the estimated spatial locations for stimuli delivered on the dorsum of the hand and on the proximal segments of the fingers, but not on the middle segments of the fingers. Patients with left parietal lesions, in contrast, showed a proximal shift, mainly on the fingers (Rapp et al., 2002).

Second, we assessed whether vestibular inputs interact with a model of body size and shape (Experiment 2). No peripheral receptors are directly informative about the size and shape of body parts. Thus, the knowledge about these features are linked to an internal stored model of the body's metric properties (Longo & Haggard, 2010). It has recently demonstrated that this 'body model' is strongly distorted (Longo & Haggard, 2010). At least for the hand, these distortions included a radial-ulnar gradient of magnification of the digits and shrinkage toward the proximo-distal axis. These internal models appear to be independent of any specific somatosensory input for two reasons. First, people can judge the configuration and location of the body, including its metric properties, in the absence of specific somatosensory stimulation (Longo & Haggard, 2010). Second, these metric properties are accessible even for congenital phantoms (Longo, Long, & Haggard, 2012). For this reason, the internal body model involves a level of somatorepresentation, independent of any particular somatosensory event or stimulus.



**Fig. 1.** The hierarchy of somatosensory cognition. The hierarchy of somatosensory cognition extends from primary somatosensation, to somatoperception and finally somatorepresentation. Somatosensation represents the first stage of somatosensory processing, resulting from activation of tactile receptors in the skin. Somatoperception involves an on-line percept of the state of the body, based on the integration of multiple somatosensory inputs. Finally, somatorepresentation involves both explicit and implicit knowledge related to body, which may be less directly related to immediate input. Each level of the hierarchy can be tapped by different somatosensory tasks: tactile detection measures the somatosensory level, tactile localisation measures the somatoperceptual level, and judgements about body shape, size and configuration measure the somatorepresentational level.

Here we aimed to clarify whether and how vestibular signals contribute to body models in healthy volunteers. Bilateral bipolar galvanic vestibular stimulation (GVS) was used to non-invasively stimulate the vestibular receptors (Fitzpatrick & Day, 2004), including both otoliths and semicircular canal afferents (Stephan et al., 2005). In this GVS configuration, 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, Smith, & Fernandez, 1984). Because we hypothesised two distinct levels of somatosensory representation, we reasoned that these could show different degrees of lateralisation. For example, tactile localisation might rely on integrating a purely contralateral map of the skin with a more bilateral body model. In this case, effects of GVS on tactile localisation might be hemisphere specific, while effects of GVS on direct tests of the internal representation of the body model might be more bilateral. For this reason, we planned to compare GVS stimulation of both hemispheres against sham stimulation (to test a bilateral hypothesis), and we also planned to compare the effects of GVS between the two hemispheres (to test a contralateral hypothesis). These comparisons are described in detail in Section 2.3.2.

## 2. Methods

### 2.1. Participants

Twelve naïve right-handed participants volunteered in the study (6 male, mean age  $\pm$  SD:  $26 \pm 4.32$  years) with ethical committee approval, and on the basis of written informed consent. Subjects with a history of sensory or neurological disorders were excluded. The study was designed according to ethical standards of the Declaration of Helsinki. Participants took part in both Experiment 1 and Experiment 2. The tasks were administered in a counterbalanced order between participants. Data from one participant were lost for technical reasons.

### 2.2. Galvanic vestibular stimulation procedure

Bipolar GVS was applied to deliver a boxcar pulse of 1 mA with 8 s of duration, using a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada). Carbon rubber electrodes (area  $10 \text{ cm}^2$ ) 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 with surgical spirit-soaked cotton wool and electrode gel was applied to the electrodes to reduce the impedance. The left anodal and right cathodal configuration is named 'L-GVS' following previous convention (Ferré, Vagnoni, & Haggard, 2013), and predominantly stimulates the right hemisphere. The inverse polarity, namely left cathodal and right anodal configuration, is named 'R-GVS', and predominantly stimulates the left hemisphere (Fig. 2A). A 'PSEUDO-GVS' stimulation, based on that used by Lopez, Lenggenhager, and Blanke (2010), was applied attaching the electrodes on the left and right side of the neck, about 5 cm below the GVS electrodes, with left anodal and right cathodal configuration (Fig. 2A). This causes a similar tingling skin sensation to real GVS, and it functions as a control for non-specific alerting effects. In our experiment, such non-vestibular effects could include the skin sensations generated by the GVS electrodes, and also the knowledge that an unusual stimulation is occurring. Other forms of sham GVS have also been proposed, such as onset-only sham stimulation (Utz, Dimova, Oppenlander, & Kerkhoff, 2010). However, we used short trial lengths that precluded an onset-only stimulation.

### 2.3. Experiment 1: vestibular effects on tactile localisation

#### 2.3.1. Procedure

Blindfolded participants sat with their left hand palm down on a table aligned with their body midline. Electrodes for GVS and PSEUDO-GVS were placed at the beginning of the session and remained in place for the entire duration of the experiment. The electrodes used and the polarity of stimulation were selected under computer control at the start of each stimulation.

A camera was suspended on a tripod directly above the centre of the table. The camera captured JPEG images ( $1280 \times 960$  pixels) and saved them for off-line coding. Participants pointed with a wooden stick held in the right hand, to touch the location on the left hand where they had perceived a tactile stimulus applied by the experimenter.

Sixteen landmarks were used: six points on the dorsum of the hand and two points for each finger, located approximately at the midpoint of the two proximal segments, as shown in the figure (Fig. 2D and E). Three blocks for each type of stimulation (L-GVS, R-GVS, PSEUDO-GVS) were administered in random order. Each block was composed of 16 trials, one of each landmark, in random order. On each trial, L-GVS, R-GVS or PSEUDO-GVS was delivered after 1000 ms from the beginning of the trial (Fig. 2B). Then, after 1 s, the experimenter touched the designated skin location with a definitively suprathreshold von Frey nylon filament. Participants were instructed to point after a tone and to maintain the pointing location until a different tone occurred 3.5 s later. The image was captured in concomitance to this second acoustic cue. Each trial lasted for 10 s and the total amount of stimulation was 8 s. No adjustments in the pointing were allowed after the initial attempt, to prevent participants from exploring the skin surface to reproduce any sensory quality of the original sensation. Tactile locations were marked with a non-permanent felt-tip pen at the beginning of the session. The participant did not see these marks at any point during the experiment, because of the blindfolding. The experimenter continuously checked that the touched hand had not moved during the block.

#### 2.3.2. Data analysis

The X-Y pixel coordinates of each actual location and of the corresponding pointing judgement on the images were coded using ImageJ software (<http://rsbweb.nih.gov/ij/>). Two sets of coordinates were coded in each block, representing the actual and perceived stimulus locations of each landmark. The two-point registration method developed by Bookstein (1991) was used to define a common coordinate frame, based on the mean actual and mean judged locations of two fiducial landmarks: the knuckle of the little finger was defined as point (0,0) and the knuckle of the index finger as point (1,0). This method defines unit length relative to the size of each participant's hand. Therefore individual differences in overall hand size were removed, allowing averaging across participants.

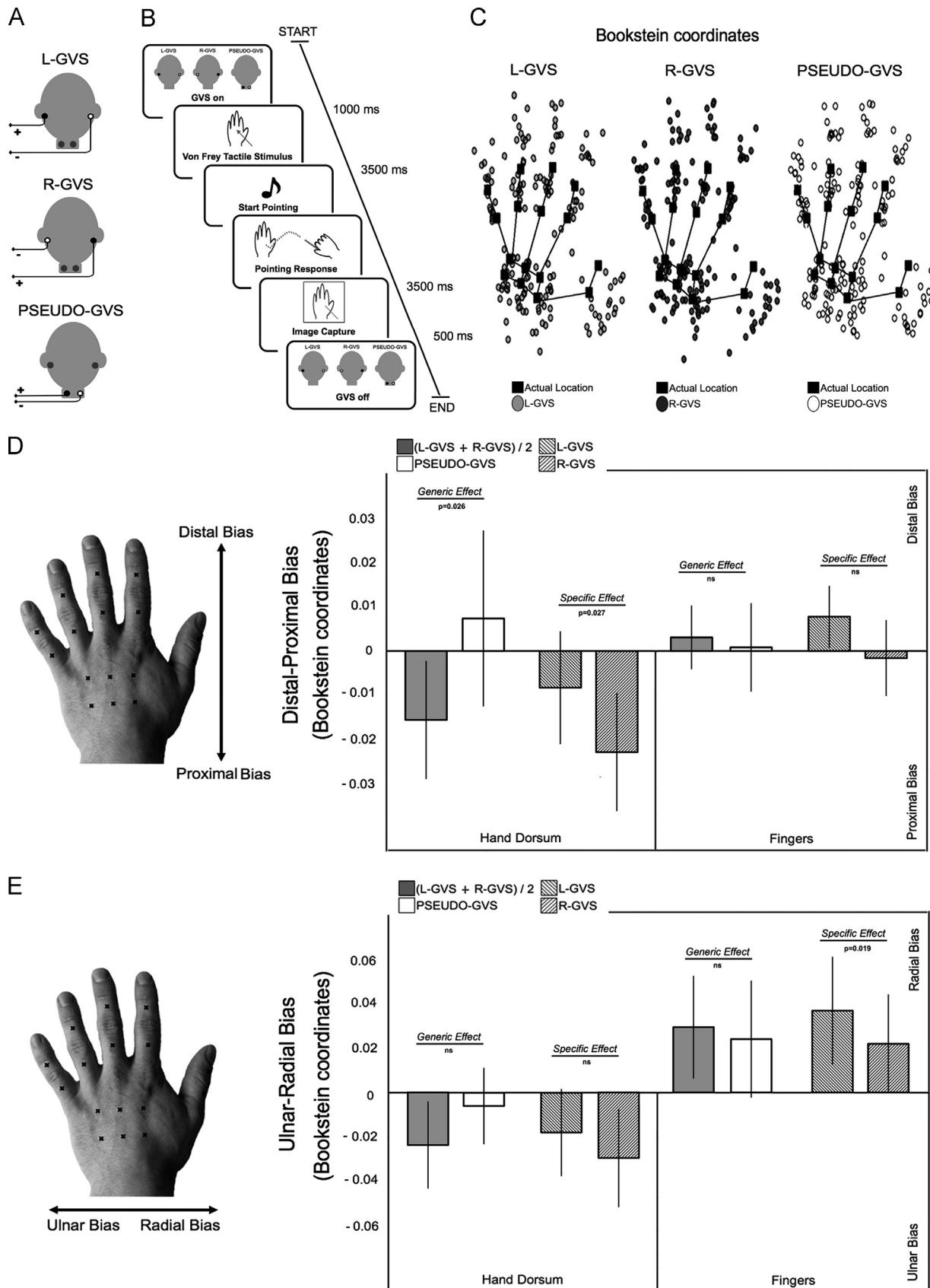
We then calculated localisation error, considered as the combination of constant error (bias in localisation, defined by the error vector between actual location and the mean judged location), and variable error (imprecision of localisation, defined by the standard deviation of repeated attempts to judge location). Constant and variable errors are logically independent: for example, it is possible to be biased, but precise. Here we focussed on vestibular effects on constant error, rather than variable error for both theoretical and methodological reasons. We aimed to investigate whether vestibular inputs might bias somatosensory representations, and constant error is the natural measure of bias. In contrast, variable error is an index of the precision during localisation. This does not directly reveal the content of somatosensory representation, though they may indicate the quality of representation, or how effectively it is used. Second, estimating variable error requires measuring variability across an appropriate number of trials in each condition. Since GVS is a relatively unpleasant experience, we wished to keep the number of trials low, and this meant our design could not reliably estimate variable error.

In order to evaluate the direction of the bias, the constant error vector was decomposed into two components, one aligned with the proximo-distal axis of the hand and the other aligned with the ulnar-radial axis. Several previous studies have motivated this decomposition. Healthy participants show direction-specific tactile localisation biases (Mancini et al., 2011). There is a distal and radial shift in the estimated spatial locations for stimuli on the dorsum of the hand, but not for the fingers (Mancini et al., 2011). In contrast, patients with left parietal lesions showed a strongly proximal shift on the fingers (Rapp et al., 2002), but a reduced bias in the palm. Accordingly, we independently computed the constant errors for the fingers and the dorsum of the hand.

These values were compared across different stimulation conditions using planned contrasts. We hypothesised that vestibular stimulation might influence tactile localisation in two distinct ways (Ferré et al., 2013), and we expressed these hypotheses as planned contrasts. First, we hypothesised that any activation of the vestibular system might influence the localisation of touches on the skin surface, independent of the polarity of the stimulation, and of any hemispheric effects. To test this generic hypothesis, we compared the average of the L-GVS and R-GVS conditions to the PSEUDO-GVS condition, for each dependent variable. Second, we hypothesised that the effects of vestibular stimulation could be specific to the hemisphere activated. This hemisphere-specific hypothesis was tested by directly comparing localisation in the L-GVS and R-GVS conditions. This analysis in terms of generic and specific elements is an established method of describing effects of interventions (Schmidt et al., 2013). We preferred planned contrasts reflecting generic and hemisphere-specific hypotheses to univariate ANOVA, because the former clearly sets out predictions in advance about the action of GVS. Our approach also avoids the risks of capitalising on arbitrary levels of statistical significance that can occur if an inference about a single research question is based on the significance of one test and non-significance of another (Nieuwenhuis, Forstmann, & Wagenmakers, 2011).

#### 2.3.3. Generic vestibular effects on tactile localisation

The generic vestibular effect, defined as  $(\text{L-GVS} + \text{R-GVS})/2$ , was compared to the PSEUDO-GVS condition. Investigation of the bias in the proximal-distal axes



**Fig. 2.** Vestibular contribution to superficial schema: procedure and results. (A) Bilateral bipolar galvanic vestibular stimulation (GVS) was delivered by placing an anode and cathode on the left and right mastoid, or vice versa. Left anodal and right cathodal configuration is named 'L-GVS'. The inverse polarity was named 'R-GVS'. Sham stimulation was applied in which the electrodes were placed on the left and right side of the neck ('PSEUDO-GVS'). (B) Trial timeline. (C) Raw tactile localisation data (average across experimental conditions). (D) Localisation bias in the distal-proximal axis. Note the significant proximal bias induced by both L-GVS and, more strongly, R-GVS. (E) No localisation bias in the ulnar-radial axis was found, apart from a slight radial bias in the fingers. Error bars represent between-subject variability (expressed as SEM).

revealed a significant generic vestibular effect in the localisation of tactile stimuli on the dorsum of the hand ( $t_{(10)}=2.604$ ,  $p=0.026$ , effect size—Cohen's  $d=0.44$ ) (Fig. 2D). On the contrary, the shift induced in the fingers was not significantly different between conditions ( $t_{(10)}=-0.375$ ,  $p=0.716$ ) (Fig. 2D). We explored this bias qualitatively by grouping touches located in the dorsum and in the fingers. This analysis highlighted a spatial gradient in the localisation error, so that touches located in the dorsum were shifted in the proximal direction, while stimuli located on the finger were shifted in the distal direction.

Testing the hypothesis of a generic vestibular effect on the ulnar–radial axes did not reveal significant difference either in the dorsum ( $t_{(10)}=-1.489$ ,  $p=0.167$ ) and the finger of the hand ( $t_{(10)}=0.463$ ,  $p=0.653$ ) (Fig. 2E).

### 2.3.4. Specific vestibular effects on tactile localisation

To test our hypothesis of hemisphere-specific effects of GVS, we directly compared L-GVS and R-GVS conditions. This planned comparison was designed to reveal how vestibular projections in each hemisphere might influence the cognitive processes involved in tactile localisation. We found a significant difference in touches located on the dorsum of the hand ( $t_{(10)}=-2.596$ ,  $p=0.027$ , effect size—Cohen's  $d=0.34$ ). R-GVS induced a larger proximal displacement than L-GVS (Fig. 2D). No differences were found comparing touches located on the fingers ( $t_{(10)}=-1.527$ ,  $p=0.158$ ) (Fig. 2D).

Investigation of the specific differences between GVS polarities in the ulnar–radial axes showed no significant differences in stimuli applied to the dorsum of the hand ( $t_{(10)}=0.794$ ,  $p=0.445$ ) (Fig. 2F), while touches delivered on the finger were perceived as shifted less radially during R-GVS than L-GVS ( $t_{(10)}=2.779$ ,  $p=0.019$ , effect size—Cohen's  $d=0.19$ ) (Fig. 2E).

### 2.3.5. Discussion

The ability to localise touches on the skin surface is essential to successfully interact with the surrounding environment. Here we show that vestibular input, in general, interfered with the localisation of touches on the dorsum of the hand. However, the bias induced by vestibular inputs was selective for the proximal–distal axis: stimuli on the hand were shifted toward the wrist. This shift followed a clear spatial gradient, with a bias toward the proximal direction for touches located on the dorsum. In contrast, stimuli located on the finger were shifted in the distal direction. This selectivity of the bias might be not surprising: localising touches involves the somatotopic maps in the primary somatosensory cortex and it is well known that fingers are better represented in the somatosensory cortical maps compared to other body parts, such as the hand dorsum. This difference in cortical representation may explain the differential influence of vestibular stimulation.

Additionally, specific polarities of vestibular input, associated with activation of vestibular projections in each hemisphere separately, had differential effects on localisation of touch. In particular, our data revealed that the proximal shift in tactile localisation was stronger during R-GVS than L-GVS. Furthermore, R-GVS induced a slight radial bias compared to L-GVS for touches located on the fingers. Hemisphere-specific effects might arise because one polarity of GVS might be stronger than the other. In fact, 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). R-GVS decreases the firing rate of the vestibular nerve on the right side and increases it on the left side (Fitzpatrick & Day, 2004; Goldberg et al., 1984), and vice versa for L-GVS. Neuroimaging studies using monaural stimulation methods have revealed asymmetrical cortical vestibular projections, suggesting that the core region of the vestibular network is primarily located in the non-dominant right hemisphere in right-handed subjects (Dieterich et al., 2003). Additionally, hemisphere-specific effects might be due to the potential hemispheric lateralisation of tactile localisation ability. Clinical observations described patients affected by left parietal lesions showing distorted errors of tactile localisation in the contralesional hand (Rapp et al., 2002). These localisation errors preserved the somatotopic arrangement of the hand, but systematically misplaced each point toward the proximal direction (Rapp et al., 2002). Finally, a combination of both these factors, such as stronger polarity of GVS and task hemisphere-specificity, cannot be excluded.

Finally, in our tactile localisation task participants were asked to point to the location of the stimulated skin surface a few seconds after the tactile stimulus. This procedure is slightly different from the tactile localisation tests used clinically, where the patient points to the skin immediately after touch. Thus, our tactile localisation procedure may also include a working memory component, in maintaining the trace of the location of the touches. However, the working memory demand is constant across experimental conditions. There is no obvious reason why the specificity of the observed bias in the tactile localisation should arise merely from interaction with memory processes.

## 2.4. Experiment 2: vestibular contribution to metric body models

### 2.4.1. Procedure

The methods were based on those of Longo and Haggard (2010). Participants sat with their left hand palm down on a table aligned with their body midline. A camera viewed the table as in Experiment 1. The hand was covered by an occluding surface during the experiment. Participants used a wooden stick to

indicate with their right hand the perceived location of verbally-identified landmarks on their occluded left hand. Ten landmarks were used: the knuckle at the base of each finger and the tip of each finger (i.e., the centre of the fingernail). Before each block a picture was taken without the board to record actual hand size and shape of the hand. On each trial, a recorded voice cued the participant as to which landmark to judge. Participants were instructed to point after a first acoustic tone and to maintain the pointing location until a second acoustic tone, and to avoid ballistic pointing movements. To avoid hysteresis effects, participants moved the tip of the baton to a green dot at the edge of the occluding board before the start of each trial. To avoid ambiguities in the coding of knuckle location from the photos, a small green mark was made on the centre of each of the participant's knuckles with a no-permanent felt-tip pen at the beginning of the session. This mark was not seen during the experiment.

Three blocks for each type of stimulation were administered. Each block was composed of 10 trials, one of each landmark, in random order. Each trial lasted for 10 s; after 1 s from the beginning of the trials the stimulation starts. Then the recorded voice was played after 1 s and then 3.5 s the pointing 'start' cue was delivered. After 3.5 s the trial ended. The total GVS duration was 8 s. Just before each block, a picture was taken without the occluder so that the actual size, shape, and location of the hand could be determined. The experimenter also checked that the hand had not moved during the block by means of adhesive dots applied on the table aligned with the fingertips.

### 2.4.2. Data analysis

X-Y pixel coordinates of each landmark on the images of the actual hand and the corresponding judged locations were coded using ImageJ software. Mean coordinates were computed for each landmark. Finger length was computed by calculating the distance between the knuckle and the fingertip of each finger. Hand width was measured as the distance between the knuckles of the index and little fingers. Two sets of coordinates were coded in each block: one for actual hand shape, the other for the hand shape represented in the internal body model, as revealed by judgements of landmark locations. Combining the judged location of different landmarks allowed an overall model of the hand to be built. We then computed the difference between this model and actual hand shape using methods developed previously (Longo & Haggard, 2010). For example, the judged positions of the index knuckle and fingertip were used to calculate represented index finger length, which could then be compared with values derived from the actual hand image. These values were compared across different stimulation conditions, according to planned comparison (see Section 2.3.2).

### 2.4.3. Generic vestibular effect in body size and shape task

As in Experiment 1, we computed a generic vestibular effect, defined as (L-GVS + R-GVS)/2, to identify whether generic vestibular input influences the perception of body size. Then we compared it to the PSEUDO-GVS condition. Finger length values did not vary with the hemisphere stimulated by GVS ( $t_{(10)}=-1.426$ ,  $p=0.184$ ) (Fig. 3A). Similarly, hand width did not differ according to the hemisphere stimulated by GVS ( $t_{(9)}=-0.888$ ,  $p=0.398$ ) (Fig. 3B).

### 2.4.4. Specific vestibular effect in body size and shape task

We also compared the perception of hand shape between L-GVS and R-GVS conditions. This planned comparison revealed no significant difference in finger length ( $t_{(10)}=0.758$ ,  $p=0.466$ ) or in finger width ( $t_{(9)}=-1.002$ ,  $p=0.342$ ) (Fig. 3A and B).

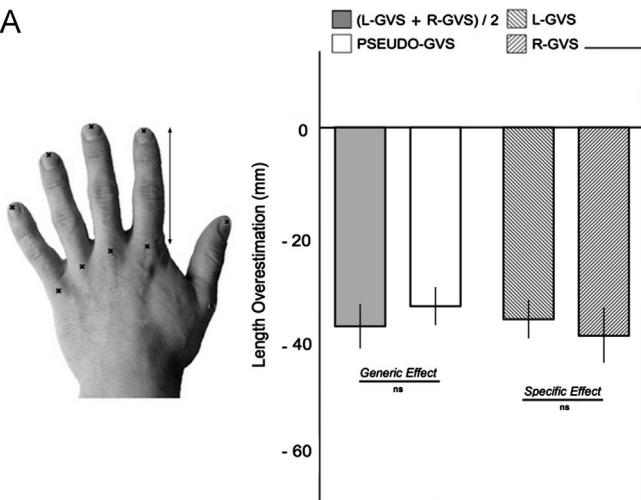
### 2.4.5. Discussion

We found a systematic underestimation of the finger length across all conditions, replicating Longo and Haggard's previous results (2010). However, no differences between stimulation conditions were found. In contrast, knuckle spacing was generally overestimated (Longo & Haggard, 2010), but vestibular stimulation again did not influence the width component of the hand representation. In conclusion, our data confirmed previous findings that the body model of the hand is massively distorted (Longo & Haggard, 2010), but vestibular inputs apparently did not contribute to these distortions.

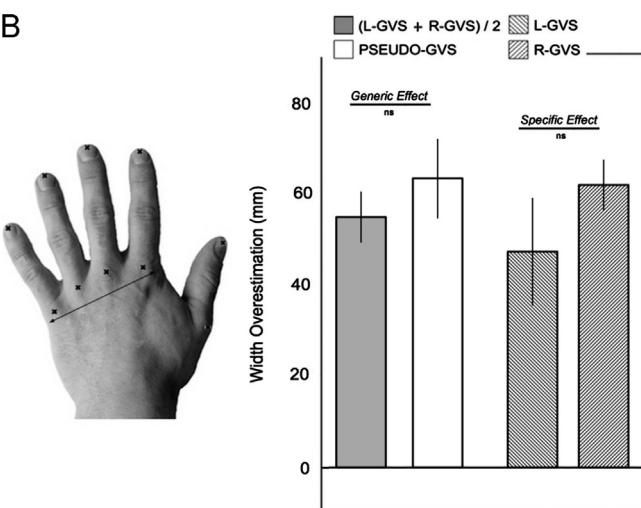
## 3. General discussion

How the brain computes a coherent representation of the body is still matter of debate. Recent models distinguish between primary sensory processing, i.e. somatosensation, and secondary somatosensory processes that involve or create more abstract representations of the body (Longo et al., 2010). In particular, two classes of higher-order mechanism beyond somatosensation have been proposed: (i) somatoperception, defined as the process of perceiving the body itself, by integrating and updating current inputs from multiple different sensory channels and (ii) somatorepresentation,

A



B



**Fig. 3.** Vestibular contribution to metric body models: results. Vestibular stimulation did not affect the metric model of body shape and size, either (A) in the length of the finger and (B) in the width of the hand. Error bars represent between-subject variability (expressed as SEM).

defined as implicit and explicit knowledge about the body, including spatial, metric, and semantic properties (Longo et al., 2010). Crucially, somatoperception involves an on-line percept of the state of the body, while somatorepresentation is a stable, relatively abstract representation of the body as a physical object.

The vestibular system has widespread interactions with multi-sensory cortical networks, including several somatosensory areas. Psychophysical studies already demonstrated that vestibular inputs influence somatosensation. Unilateral caloric vestibular stimulation (CVS) facilitates detection of faint somatosensory stimuli in healthy volunteers on both the hands (Ferré et al., 2011) and enhances the N80 component recorded over both ipsilateral and contralateral somatosensory areas, without significantly affecting other components (Ferré et al., 2012). Interestingly, this evoked component has been localised to the parietal operculum, which includes the human homologue of the monkey parieto insular vestibular cortex (PIVC). Those results suggest a strong interaction between the vestibular system and the primary somatosensory level of our somatic cognitive hierarchy (Fig. 1). Here we have investigated whether vestibular stimulation might also affect the additional levels of somatoperception and somatorepresentation. To our knowledge, this question has not previously been addressed systematically. Abnormal bodily experience has been reported as consequence of abnormal vestibular input following vestibular damage or appropriate vestibular

stimulation. Notably, direct electrical stimulation of vestibular cortical regions caused both the feeling of the self being located outside the body, and also the feeling that the body itself was contracting or folding (Blanke, Ortigue, Landis, & Seeck, 2002). However, the existing literature is generally based on isolated or anecdotal subjective reports. We aimed to provide both a theoretical framework, and an experimental method to investigate potential vestibular contributions to higher somatic processing.

Our first experiment showed that vestibular input, in general, influenced the localisation of tactile stimuli on the hand. Moreover, specific polarities of vestibular inputs, associated with activation of vestibular projections in each hemisphere, had stronger or weaker effects on tactile localisation. In particular, our data revealed a selective modulation in the proximal-distal axis: touches on the dorsum of the hand were perceived as shifted toward the wrist. The size of this shift increased from the finger to the dorsum of the hand. This shift occurred in both L-GVS and R-GVS conditions, but was larger during R-GVS. Thus, following the terminology used in our planned contrasts, it included both a generic and a specific vestibular effect. No localisation bias in the ulnar-radial axis was found, apart from a slight radial shift for touches located in the fingers during R-GVS condition. Interestingly, the relative position between different tactile locations was preserved during vestibular stimulation. Thus our results do not suggest a vestibular-induced distortion within the somatotopic map of the skin. Rather, the pattern of localisation errors suggested that GVS altered the linkage between the somatotopic map of the skin surface and the underlying body structure. Thus, we interpret this as evidence that vestibular input contributes to the somatoperceptual level of the somatic 'cognitive hierarchy'.

Interestingly, our effects are reminiscent of those described in patients following left parietal brain damage. Rapp et al. (2002) reported two patients showing a clear dissociation between an intact ability to detect faint stimuli compared to an impaired localisation of touches on the affected hand. In particular, the authors commented 'The post-lesion [tactile] mislocalisations may preserve the relative locations of the pre-lesion topography, resulting in systematically shifted and distorted somatosensory experiences'. Importantly, these deficits in localisation could not be explained by deficits in detection, confirming the dissociation between the somatosensation and somaperceptual levels (Halligan, Hunt, Marshall, & Wade, 1995; Harris, Thein, & Clifford, 2004). The effects of GVS produce a similar shift in the proximal direction.

Neuroimaging studies revealed activation of the right temporo-parietal junction (TPJ) during tactile localisation (Van Boven et al., 2005). It is widely agreed that the primary somatosensory cortex provides the neural basis of tactile acuity (Duncan & Boynton, 2007). However, we have argued that tactile localisation requires the additional computational step of somatoperception: mapping skin locations onto body locations. Based on previous results (Van Boven et al., 2005), we suggest that right TPJ activity might reflect the process of linking the somatotopic map and body-surface localisation. Right TPJ is also a core region of the human vestibular cortical network (Lobel et al., 1999; Fasold et al., 2000; Blanke & Arzy, 2005). The anatomical overlap between vestibular cortical areas and areas involved in tactile localisation supports our speculation that vestibular inputs might influence the process of registering somatotopic skin location with specific locations on the body, although this should be tested in further studies, possibly investigating tactile localisations in patients with peripheral vestibular disease.

Our data do not provide any evidence of a vestibular modulation in the metric body model that we used as an example of somatorepresentation (Experiment 2). The contrast with the positive vestibular effects in Experiment 1 is striking: the difference between the experiments is that Experiment 1 involved

pointing to locations of tactile stimuli, while Experiment 2 involved pointing to body landmarks. Experiment 2 confirmed previous results that the mental representation of hand size and shape is massively distorted, with shortened fingers and broadened hands (Longo & Haggard, 2010). Our data replicate these findings. Lopez, Schreyer, Preuss, and Mast (2012) recently showed that caloric vestibular stimulation increased the perceived length and width of the hand, implying a general scaling of somatorepresentation. However, we found no evidence of either generic or polarity-specific GVS effects in the computation of shape and size of the hand. This may because GVS effects are relatively weak compared to the CVS used by Lopez et al. (2012).

Interestingly, the errors in tactile localisation at the somato-perceptual level that we found in Experiment 1 could be mistaken for a change in the metric body model at the somatorepresentation level, if the somatoperceptual and somatorepresentational levels are not separately considered. In particular, Experiment 1 found a progressive gradient for localisation of touches on the hand: vestibular stimulation shifted touches located on the dorsum toward the proximal direction, while touches located on the fingertips did not show these shifts. Thus, we speculate that vestibular stimulation could cause a sort of tactile expansion that affects the location of stimuli on body surface. However, when we tested the representation of body parts in the absence of stimulation, in Experiment 2, we did not find any somatic expansion corresponding to the tactile expansion of Experiment 1. Importantly, in our study the sample was the same for both the tasks, suggesting that the power of statistics applied was consistent in detecting significant and/or not significant results. However, more research is required to investigate whether vestibular inputs indeed modulate the somatorepresentational level, and whether this modulation can indeed be dissociated from modulation of somatoperception, as we suggest.

Could our bias be an indirect effect of GVS, mediated by some other effect of vestibular stimulation, rather than a direct effect on tactile localisation? For example, vestibular stimulation influences postural control, producing postural sway in the direction of the anode (Fitzpatrick & Day, 2004). However, an indirect effect on somatosensation mediated by postural responses seems unlikely for several reasons. First, the effects induced by GVS on postural responses have been mainly demonstrated in standing participants, while in our study subjects were seated. Second, any GVS-induced sway of the whole body should not affect the pointing with one body part to another body part. Importantly, GVS was delivered not at the start of the localisation response, but several seconds before. Therefore, any postural adjustment should have stabilised at the time of the localisation task. Finally, an explanation based on a localisation shift caused by GVS-induced postural sway would presumably be due to a vestibular bias in pointing. However, our Experiment 2 did not show any difference between experimental conditions, despite using a pointing response similar to Experiment 1. Thus, our data do not imply a general, non-specific bias in pointing (Karnath, Himmelbach, & Perenin, 2003).

In our study we decide to investigate the GVS induced effects on only one hand. We chose to study the left hand, since vestibular projections are contralateral, and are predominately located in the right hemisphere in healthy participants. This procedure allowed us to maximize the effect induced by the vestibular stimulation on both somatoperception and somatorepresentation. Additionally, we tested right-handed participants, and we wanted them to use the dominant hand for pointing responses, to minimise error. Future studies might focus on both the hands because GVS induced polarity dependent effects. However, that would need a much larger study with a quite different design, and it would address a fundamentally different question.

To conclude, we have used a theoretical model of hierarchical cognitive processes linked to body representation to investigate the relation between vestibular input and body cognition. Our data clearly show an effect of vestibular stimulation on tactile localisation. We found systematic errors in tactile localisation in the proximal-distal axis, notably a proximal shift for stimuli on the hand dorsum. However, we found no effects of CVS on the metric body model, in contrast to another recent study (Lopez et al., 2012). We conclude that vestibular input influences the somato-perceptual level of the cognitive hierarchy, in addition to effects on primary somatosensation reported previously. Our results suggest a simple dissociation between the vestibular effects on the body superficial schema that is used for tactile localisation at the somatoperceptual level, and the metric model of the body that is used at the somatorepresentational level. However, our failure to find any influence of vestibular signals on somatorepresentation should be taken with caution: further research on this question is required.

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