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Research reports

Disentangling the visual, motor and representational effects of vestibular input

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Abstract

The body midline provides a basic reference for egocentric representation of external space. Clinical observations have suggested that vestibular information underpins egocentric representations. Here we aimed to clarify whether and how vestibular inputs contribute to egocentric representation in healthy volunteers. In a psychophysical task, participants were asked to judge whether visual stimuli were located to the left or to the right of their body midline. Artificial vestibular stimulation was applied to stimulate the vestibular organs. We found that artificial stimulation of the vestibular system biased body midline perception. Importantly, no effect was found on motor effector selection. We also ruled out additional explanations based on allocentric visual representations and on potential indirect effects caused by vestibular-driven movements of the eye, head and body. Taken together our data suggest that vestibular information contributes to computation of egocentric representations by affecting the internal representation of the body midline.

Keywords

Vestibular system; Egocentric Representation; Multisensory Integration.

Highlights

1. Galvanic Vestibular Stimulation (GVS) biases egocentric spatial representations.
2. This bias is dissociable from GVS effects on visual perception and on motor action.
3. Vestibular signals shape egocentric body representation.

Abbreviations

GVS= Galvanic Vestibular Stimulation

L-GVS= left-anodal/right-cathodal GVS

R-GVS= right-anodal/left-cathodal GVS

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1. Introduction

Judging the position of external objects relative to the body is essential for interacting with the external environment. *Egocentric representations* describe the external world as experienced from an individual's location, according to the current spatial configuration of their body (Jeannerod and Biguer, 1987). Consider, for example, a tennis player who must quickly select a forehand or backhand shot based on the ball location relative to their body. A coherent and rapid response to the approaching ball requires combining perceptual information about the ball's trajectory relative to the player with information about the player's ever-changing posture and gaze. Such egocentric representations are thought to be essential in representing the world in relation to oneself (Bermúdez, 2005; Bermúdez, 2011; Pafel et al., 1998; Cassam, 2011).

The body midline may provide a basic reference for egocentric representation of external space (Jeannerod and Biguer 1987). Everyday descriptions of spatial locations frequently begin with "on the left..." or "on the right…". The subjective body midline is considered the internal representation of the plane that divides the body in two equal left and right parts (Bower and Heilman, 1980; Jeannerod and Biguer 1987). It remains unclear whether the subjective body midline co-ordinates are a static stored representation reflecting primarily semantic knowledge about body morphology, or rather a dynamic, continuously updated sensory datum, perhaps reflecting balance between afferent signals from lateralized receptor organs (left and right eyes, ears etc.), across changing body posture and orientation (Critchley, 1953).

Visual, auditory, somatosensory, proprioceptive and vestibular inputs could all contribute to representing the body midline (Jeannerod, 1988; Blouin et al., 1996, Blouin et al., 1998). Vestibular signals seem to be particularly relevant (Schilder, 1935; Lhermitte, 1952; Bonnier, 1905; Vallar and Papagno, 2003; Vallar and Rode, 2009). The vestibular system comprises the semicircular canals that encode rotational movements, and the otolith organs that encode translational accelerations, including the current orientation of the head relative to the gravitational vertical. Both semicircular canals and otolith organs constantly provide afferent information regarding body orientation and body movement. Since the vestibular organs on each side of the body act in a push/pull manner, a balance between vestibular signals can guide representation of the body midline. For example, a linear acceleration that produces identical signals from both otolith organs must correspond to movement aligned with the body midline, either in the straight-ahead or up-down direction. Similarly, any head rotation away from alignment with the body midline should cause equal and opposite changes in firing rate from the horizontal canals on both sides of the body. Thus, vestibular information is crucial to determine the location of environmental objects in respect to the body (Villard et al. 2005; Clement et al. 2009; Clement et al. 2012), and to specify the body midline itself.

Several clinical observations have suggested that vestibular information underpins egocentric representations. Patients with unilateral spatial neglect showed a deviation to the ipsilateral half of space when they were requested to point to an imaginary location in space straight ahead from their body midline (Heilman et al., 1983a). Critically, artificial stimulation of the vestibular system influenced this pointing error: left cold caloric vestibular stimulation temporarily reduced the rightward pointing bias characteristic of patients with left-side neglect. This suggests that vestibular inputs contribute to the subject's mental representation of space and subjective body orientation (Karnath, 1994). However, most of these studies used *motor* pointing responses to estimate *perceptual* estimates of the body midline. That is, they *assumed* that the impairment arose at the level of representation of the body midline, but they could not formally exclude the possibility that vestibular stimulation affected the motor pointing response, or some purely visual element of the experiment. Here we aimed to clarify whether and how vestibular inputs contribute to egocentric spatial representation in healthy volunteers. We have systematically investigated which processing stages along the visual-motor processing chain are modulated by vestibular signals. This method allowed us to dissociate vestibular effects on visual perception and on motor action from effects on spatial representation, seemingly for the first time.

Binaural bipolar Galvanic Vestibular Stimulation (GVS) was used 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 causes polarity-dependent modulation of sensory and cognitive functions (Utz et al., 2010). Importantly, these behavioural effects are consistent with neuroimaging evidence revealing asymmetrical cortical vestibular projections in the non-dominant hemisphere (Dieterich et al., 2003).

We hypothesized that vestibular information might play a role in shaping the online perception of the body midline, and thus contribute a basic reference for egocentric spatial representation. Accordingly, we dissociated the vestibular contributions to egocentric spatial representations from those to motor responses (Experiment 1). In a second experiment, we investigated whether GVS-induced bias on body midline could be explained by biases in visual perception, particularly in visual allocentric representation, and found that it could not (Experiment 2). Finally, we showed that effects of GVS on egocentric representation were qualitatively distinct from the effects of GVS on gaze location (Experiments 3 and 4).

2. Vestibular contribution to egocentric spatial representation

2.1. Material and Methods

2.1.1. Participants

Nineteen healthy participants (9 males, mean age ± SD: 21.8 ± 3.1 years) took part in this experiment. All the participants were right-handed (Edinburgh Handedness Inventory, Oldfield, 1971) with normal or corrected-to-normal vision. Exclusion criteria included neurological, psychiatric or vestibular conditions, epilepsy or family history of epilepsy. 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. Participants gave written informed consent.

2.1.2. Galvanic Vestibular Stimulation

Bipolar GVS was applied to deliver a boxcar pulse of 1 mA using a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada). Postural studies confirm that this level of GVS activates the vestibular organs without effects persisting beyond the period of stimulation (Fitzpatrick and Day, 2004). 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 impedance. Both left-anodal/right-cathodal (L-GVS) and right-anodal/left-cathodal (R-GVS) configurations were used (Fig. 1B). We also applied a sham stimulation using electrodes placed on the left and right side of the neck, about 5 cm below the GVS electrodes (Ferrè et al., 2013a, Ferrè et al., 2013b), with a left-anodal/right-cathodal configuration. This sham stimulation evoked similar tingling skin sensations to GVS, and so functioned as a control for non-specific effects.

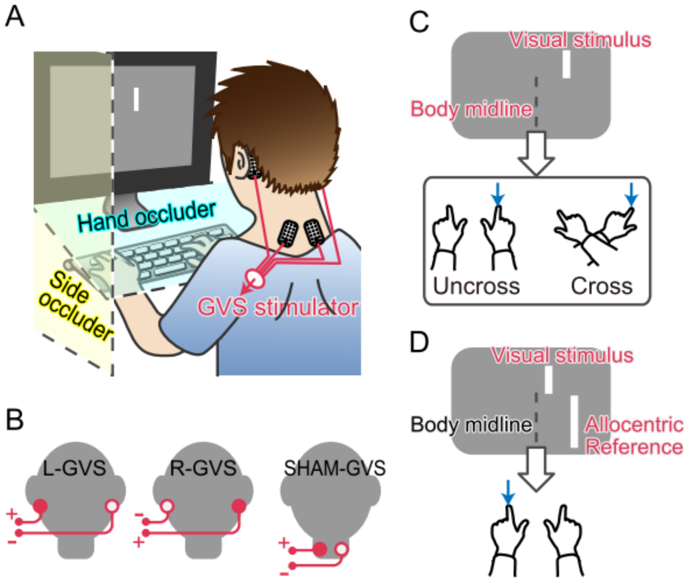

Figure 1. Experimental setup and methods.
A. Apparatus. B. GVS polarities and electrodes configurations. C. Experiment 1: Participants localized visual stimuli relative to their body midline. The task was performed with the hand uncrossed or crossed. The blue arrows indicate participant's judgment. If participant judges "right", they are instructed to press the right-side button in the both hand conditions. D. Experiment 2: Participants localized visual stimulus relative to an allocentric reference.

2.1.2. Procedure

Verbal and written instructions were given to participants at the beginning of the session. Participants were seated in front of a computer monitor (eye-monitor distance: 50 cm) with hands on a keyboard (Fig. 1A). Participants were instructed to not move their body and head during the task. The participants' posture was monitored throughout the experiment to ensure that the body midline was always aligned with the center of the monitor. A red LED was attached to the solar plexus area of participants. The position of the light, and therefore participants' posture, was recorded using a camera. To prevent the use of external visual cues, participants' vision was restricted by cardboard baffles placed to the left and right, as well as above the hands, and the experiment was completed in darkness (Fig. 1A). Visual stimuli were presented with Cogent Graphics (MATLAB, refresh-rate: 60 Hz). To prevent any influence of gaze direction on judgements, participants were asked to look straight ahead. No fixation markers were provided to avoid additional cues regarding body midline and monitor center location.

On each trial, a vertical line (0.5 x 2 cm) was presented for 80 ms at a randomly selected location ±3.2 cm from the center of the monitor. The stimulus was randomly presented in eleven locations (-3.2, -1.6, -0.8, -0.4, -0.2, 0, 0.2, 0.4, 0.8, 1.6, 3.2 cm) with respect to the center of the monitor. Twenty trials were used for eccentric locations (-3.2, -1.6, -0.8, 0.8, 1.6, and 3.2 cm), 30 for middle locations (-0.4 and 0.4 cm), and 40 for central locations (-0.2, 0, and 0.2 cm). The stimuli were shown 4 cm above the center of the monitor at the eye-line of the participants. Participants judged whether the visual target was located to the left or right of their body-midline by pressing buttons located on their left or right side. Participants were instructed to press the buttons as fast and accurately as possible. Both accuracy and reaction times were recorded from target presentation to the response.

In half of the blocks participants completed the task with their hands uncrossed, such that the left hand pressed the left-sided button and the right hand pressed the right-sided button. In the other half the hands were crossed so that the left hand pressed the right-sided button and vice versa (Fig. 1C). This allowed us to disentangle any potential effects of GVS on the motor response from effects on egocentric representation. For example, if the principal locus of GVS effects was to bias responding towards one hand, then performance on the localization task should be strongly affected by crossing the hands.

GVS polarity and hand position were combined in a factorial design, resulting in 6 experimental conditions. Each condition was repeated twice giving 12 separate blocks of 150 trials, lasting approximately 4-5 minutes each, and with GVS/sham stimulation applied continuously. The order of blocks was counterbalanced within and across participants.

2.2. Results

Trials with implausibly short reaction times (< 183 ms: corresponding to 1 % of trials) were excluded from analysis. The proportion of right responses was estimated for each condition. Reaction times did not differ significantly (Sham = 410 ± 59.0 ms, L-GVS = 409 ± 56.6 ms, R-GVS = 413 ± 60.9 ms, one-way ANOVA: $F(2,18) = 0.166$, $p = 0.848$).

Figure 2A shows averaged responses of participants with fitted logistic psychometric functions. The point of subjective equality (PSE) and just-noticeable difference (JND) were calculated from the functions for each participant in each condition. Following previous studies (Ferre et al., 2013b), we analysed the data using planned comparisons, to distinguish between general, non-specific effects of GVS, and effects of GVS that are specific to the polarity of stimulation, and thus to our hypothesis regarding shifts of the body midline. This approach is justified because of the clear mechanistic link between the polarity of GVS stimulation and the predicted direction of any spatial effects.

Generic vestibular effect. First, we checked whether the PSE for SHAM was significantly different from 0. A direct comparison showed no differences ($t(18)=-1.52$, $p=0.147$). To assess general effects of GVS independent of polarity the average of L-GVS and R-GVS conditions was compared to sham stimulation in a 2 (Stimulation: generic vestibular, sham stimulation) x 2 (Hand: uncrossed, crossed) ANOVA. No significant main effects of Stimulation ($F(1,18) = 1.52$; $p = 0.23$), Hand ($F(1,18) = 0.62$; $p = 0.44$) or interactions emerged ($F(1,18) = 0.002$; $p = 0.96$) (Fig. 2B).

Specific vestibular effect. We directly compared L-GVS and R-GVS conditions to investigate differences in how vestibular projections in each hemisphere might influence egocentric representation. The effect of GVS polarity was analyzed using a 2 (GVS polarity: L-GVS, R-GVS) x 2 (Hand posture: uncrossed, crossed) ANOVA. A significant main effect of GVS polarity was found ($F(1,18) = 16.2$; $p = 0.0008$, Partial $\eta^2 = 0.47$, Effect size $f = 0.95$), in which the PSE shifted leftwards (0.75 cm hands uncrossed and 0.68cm hands crossed) under L-GVS relative to R-GVS (Fig. 2B). There was no significant main effect of Hand posture ($F(1,18) = 0.31$; $p = 0.58$) or interaction between GVS polarity and Hand posture ($F(1,18) = 0.14$; $p = 0.71$). In addition, we also subtracted SHAM from R-GVS and L-GVS, and directly compared the absolute magnitude of GVS effect between both polarities. No statistically significant difference emerged (paired T-test, $t(18)=1.231$, $p = 0.234$).

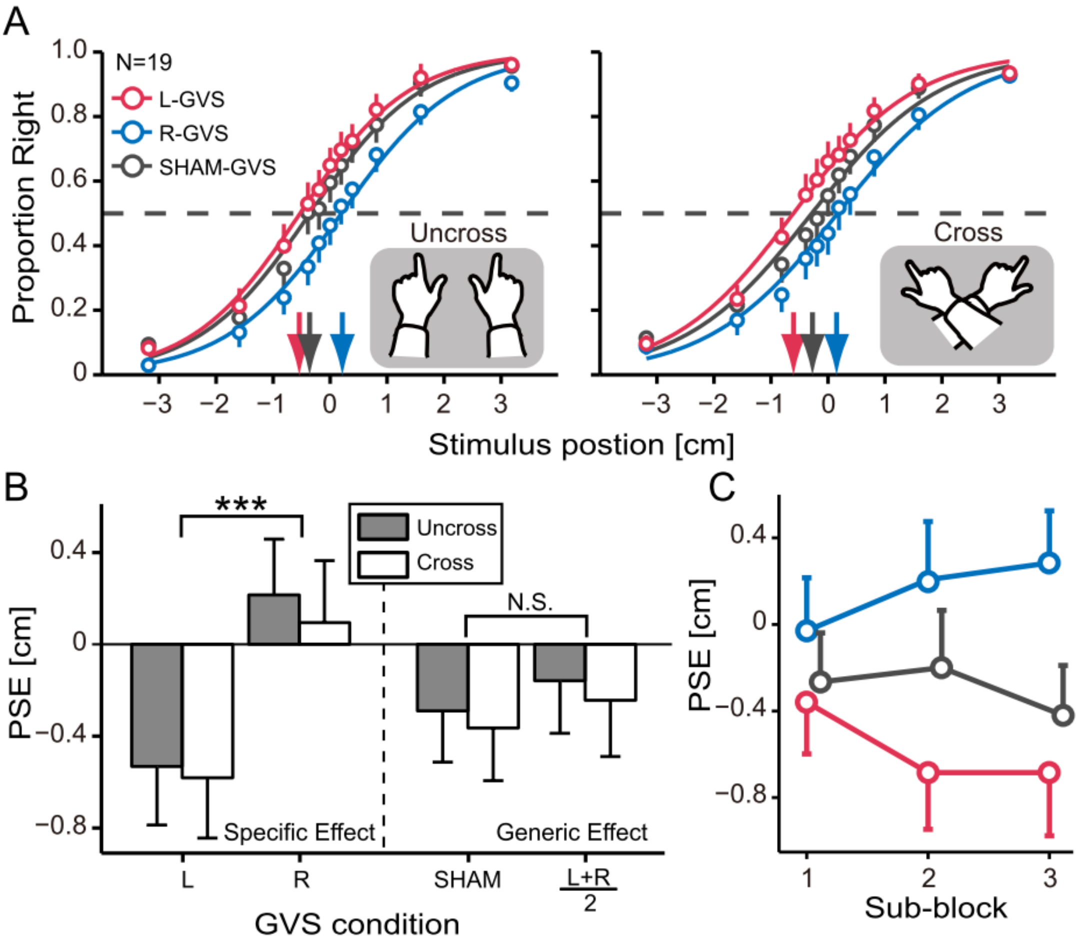

Figure 2. Results of Experiment 1.

A. Ensemble judgment as the function of the stimulus location with psychometric curves. The data were shown for hand uncrossed (left panel) and crossed (right panel). The arrow indicates the value of PSE for each GVS condition. Error bar indicates standard error of mean. B. Averaged PSEs for all the conditions. Three asterisks: significance at $p < 0.001$. N.S.: not significant. C. Temporal change in the PSE as the function of the sub-block. The PSE gradually varied according to the GVS condition. Colours denote the GVS condition as shown in panel 2A.

Temporal effect. We also performed an exploratory analysis of the time-course of GVS effects within each block. We divided the data in each stimulation condition (150 trials, lasting approx. 4min.) into three sub-blocks having 50 trials. That is, we defined first, second, and third sub-blocks consisting of trials 1-50, 51-100, and 101-150. Since each stimulation block was repeated twice in our experimental design, we could then calculate an estimate of PSE at each window position based on 100 trials. The choice of sub-block length was arbitrary, but reflected a trade-off between the need to keep the datapoints independent for statistical analysis, and the need to have enough trials per sub-block to ensure stable fitting of the psychophysical function. Since we found no influence of hand posture, the data for uncrossed and crossed hand postures were collapsed. The sign of L-GVS data was inverted and a two-way (sub-block and GVS polarity) ANOVA was conducted. A significant main effect of sub-block was found ($F(2,36) = 6.55$; $p = 0.004$; Partial $\eta^2 = 0.27$; Effect size $f = 0.60$) indicating that the PSE gradually shifted over the course of the block (Fig. 2C).

2.3. Discussion

These results suggested that GVS changed the participants' egocentric spatial representation, with the perceived body midline shifting towards the anodal side. There was no effect of crossing the hands, ruling out alternative explanations based on GVS affecting the selection or efficiency of lateralized motor output processes. Our data therefore support a body-related theory suggesting that GVS selectively modulates our egocentric spatial representations (Fig. 3A). In a second experiment, we tested whether our results could be alternatively explained by a GVS modulation of allocentric visual representations, unrelated to the body midline (Fig. 3A).

3. Vestibular contribution to allocentric spatial representation

3.1. Material and Methods

3.1.1. Participants

Nineteen healthy, right-handed participants (6 males, mean age ± SD: 21.9 ± 3.0 years) took part in this experiment. None of the participants had participated in the previous experiment. Exclusion criteria were as Experiment 1.

3.1.2. Procedure

Participants were asked to judge whether the visual targets (as in Experiment 1) appeared to the left or right of a visual reference. This reference was a 20 cm vertical line presented at a fixed location 3 cm to the left or to the right of the center of the monitor (Fig. 1D). Thus, the task required a visual allocentric representation, centred on the reference, and egocentric location was irrelevant. Peripheral presentation of the reference ensured that the task difficulty was equal between both experiments. As there was no main effect of hand position in Experiment 1, participants completed this task with hands uncrossed. The two reference locations (left and right) and three GVS polarities (L-GVS, R-GVS and sham stimulation) gave six conditions, repeated twice to give 12 blocks of 150 trials. The experimental setup and all other procedures were as Experiment 1.

3.2. Results

As in Experiment 1, we excluded trials with reaction times less than 283 ms (1 % of trials). No statistical difference emerged between GVS conditions (Sham = 453 ± 53.1 ms, L-GVS = 450 ± 50.3 ms, R-GVS = 441 ± 48.2 ms, one-way ANOVA, $F(2,18) = 2.52$, $p = 0.09$).

Generic vestibular effect. To assess general effects of GVS independent of polarity the average of L-GVS and R-GVS conditions was compared to sham stimulation in a 2 (Stimulation: generic vestibular, sham) x 2 (Reference: left, right) ANOVA. A significant main effect of Reference emerged ($F(1,18) = 9.89$, $p = 0.006$, Partial $\eta^2 = 0.35$, Effect size $f = 0.74$). No significant main effect of Stimulation ($F(1,18) = 0.36$, $p = 0.36$) or interactions between factors was found ($F(1,18) = 2.38$, $p = 0.14$) , suggesting a tendency to mislocalise according to the location of reference, but irrespective of stimulation conditions (Fig. 3B).

Specific vestibular effect. The effect of GVS polarity was analyzed using a 2 (GVS polarity: L-GVS, R-GVS) x 2 (Reference: left, right) ANOVA. A significant main effect of GVS polarity ($F(1,18) = 8.80$, $p = 0.0082$, Partial $\eta^2 = 0.33$, Effect size $f = 0.70$) was found: the PSE shifted leftward for R-GVS, and rightward for L-GVS (Fig. 3B). Thus, GVS affected allocentric visual localization in a polarity-dependent manner in the opposite direction to Experiment 1. In addition, the main effect of Reference was significant ($F(1,18) = 12.72$, $p = 0.0022$, Partial $\eta^2 = 0.41$, Effect size $f = 0.84$). However, no significant interaction was found ($F(1,18) = 4.17$, $p = 0.056$), suggesting that the mislocalization was independent of GVS polarity.

Temporal effect. Data were analysed as Experiment 1. No significant temporal pattern of GVS emerged (*F*(2,36) = 0.24; *p* = 0.79) (Fig. 3C).

Further, we compared the effects of GVS between Exp.1 and Exp.2. We performed a two-way ANOVA with Stimulation (L-GVS and R-GVS) as within factor and Experiment (Exp.1 and Exp.2) as between factor. For this analysis, we subtracted Sham-GVS from R-GVS and L-GVS as shown in Figure 3D. In addition to a significant main effect of GVS (F(1,1) = 11.5, p = 0.0017, Partial η^2 = 0.24, Effect size *f* = 0.56), significant interaction (GVS x Experiments) emerged (F(1,36) = 20.4, p = 0.0001, Partial η^2 = 0.36, Effect size *f* = 0.75). These data indicate that GVS effect differ between experiments.

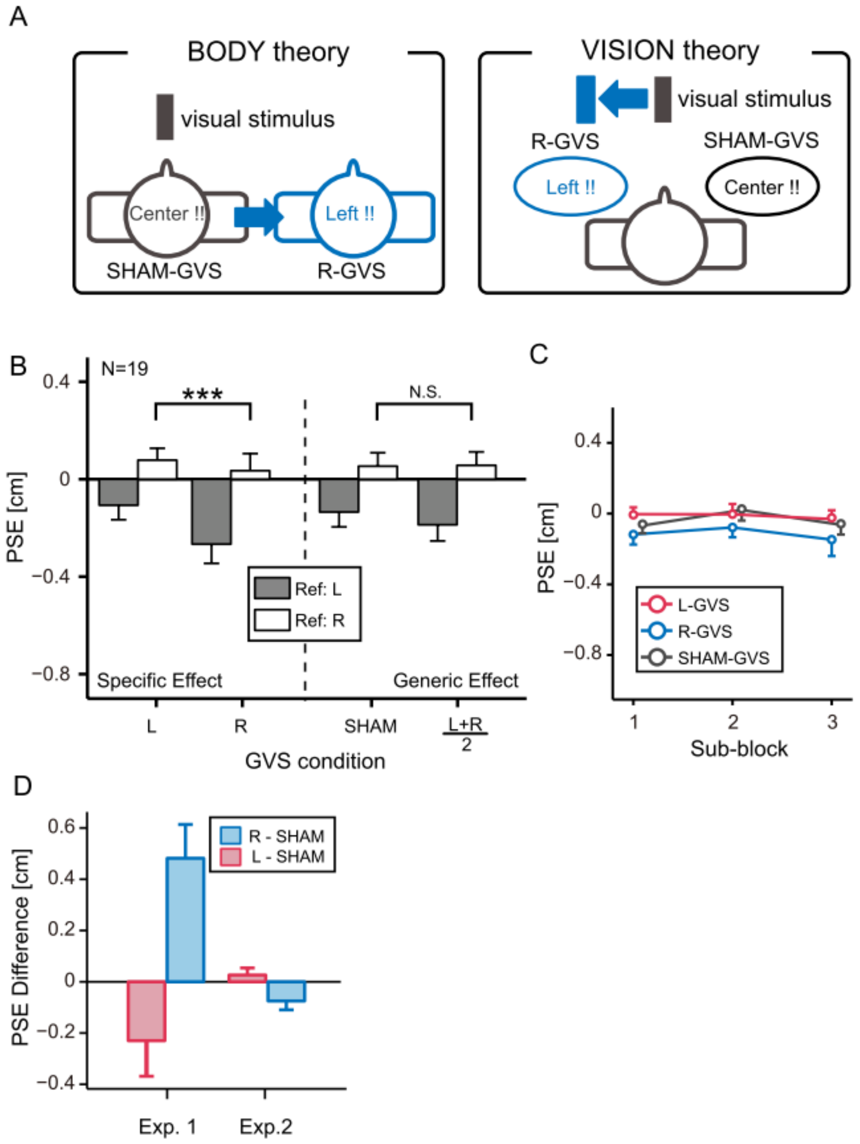

Figure 3. Body vs Vision theory and results of Experiment 2.
A. Two contrasting theories for interpreting results of Experiment 1. Consider the scenario in which the visual stimulus is at the body-center, and participants judge its location “Center” for Sham-GVS. The BODY theory would explain the observed results as a rightward shift in egocentric body representation induced by R-GVS. Center-stimuli would then be judged “Left”. The VISION theory proposes a direct shift in the visual representation induced by R-GVS, without any change in the representation of the body egocentre. B. Averaged PSEs for all the conditions for Experiment 2. C. Temporal change in the PSE as the function of the sub-block. D. A direct comparison of GVS effect observed in the first and second experiment. We subtracted Sham-GVS from R-GVS and L-GVS.

3.3. Discussion

GVS significantly biased allocentric visual localization in the opposite direction compared to the egocentric localization bias of Experiment 1 (Fig. 3D). The effect of GVS on allocentric representations may be explained by a GVS-induced modulation of spatial attention and “foveal mislocalisation”, in which briefly-presented peripheral targets are perceived as closer to the foveal location than their true location (Müsseler J. et al., 1999). This effect could be observed as a positive or negative bias in the PSE depending on the location of the reference (Figure 3B). For example, when R-GVS is applied, an increase in activity in the left hemisphere directs spatial attention towards the right side. This shift in attention would subsequently increase foveal mislocalisation for visual stimuli presented on the left, and reduce mislocalisation for stimuli on the right. Hence, GVS biased allocentric representations towards the left for R-GVS and towards the right for L-GVS.

Taken together, our results highlight the relationship between vestibular information and egocentric body representation. Our experimental paradigm and procedures carefully and systematically ruled out other explanations based on GVS affecting body motion, the effector selection process, and allocentric visual localization. A final alternative explanation is that GVS could induce a change in gaze location which may have affected the egocentric judgement task. Thus, in two final experiments we examined the relationship between GVS, gaze shift, and egocentric body representation.

4. Comparison of effect on egocentric representation between vestibular stimulation versus gaze shift

We conducted two experiments to examine 1) gaze behaviour during the egocentric judgment task with GVS (Experiment 3) and 2) the direct effect of gaze location on egocentric body representation (Experiment 4).

4.1. Experiment 3

4.1.1 Materials and Methods

Participants

Thirteen participants took part in Experiment 3 (3 males, mean age ± SD: 21.1 ± 3.4 years). The sample size was a priori decided based on a power analysis with $t = 4.03$, $\alpha =$

0.05 and power = 0.80 (G*Power; Faul, Erdfelder, Lang, & Buchner, 2007). None of the participants had participated in the previous experiments. Exclusion criteria were as the previous experiments.

Procedure

Participants completed the egocentric localization task with GVS while their gaze location was recorded. The task was completed with hands uncrossed. Only L-GVS and R-GVS polarities were used. The two conditions were repeated twice giving 4 blocks of 150 trials. Participants were fixed in a chin-rest during each block. Gaze location was measured from continuous recording of the right eye using a video-based eye-tracking system (ASL5000, sampling frequency of 60 Hz). Procedures were otherwise as Experiment 1.

4.1.2 Results

A significant difference between L-GVS and R-GVS was found ($t(12) = 5.72$, $p = 0.001$, Effect size $dz = 1.44$) (Fig. 4A). The PSE was shifted leftwards by 1.04 cm during L-GVS versus R-GVS, replicating the results of Experiment 1.

Eye-tracking data were processed by manual inspection and exclusion of trials with eye-blinks. Figure 4B shows a fixation map, obtained from a representative participant. Areas with longer fixation are shown with warmer colours (i.e. red). The fixation map indicates that gaze location was concentrated on the left of the body midline (vertical pink line) for L-GVS (top panel in Fig. 4B), and at the right side for R-GVS (middle panel in Fig. 4B). Averaged gaze location was statistically significant between both GVS polarities as shown in the bottom panel of Figure 4B ($t(12) = 3.80$, $p = 0.003$, Effect size $dz = 1.05$). The average gaze location at each successive 30s time-window within a block was then calculated (average block length was 217 ± 19.7 s). Figure 4C shows the change in gaze location across time, averaged across participants. A significant difference in gaze location was found at each time window, with R-GVS shifting gaze location rightwards and L-GVS shifting gaze location leftwards (multiple comparison with Holm-Bonferroni correction: $t(12)$ =

[4.08, 4.07, 3.88, 3.48, 3.44, 3.26, 3.06, 3.96], p_{adj} = [0.02, 0.021, 0.019, 0.013, 0.022, 0.011, 0.012, 0.011] at each time window).

4.2. Experiment 4

4.2.1 Materials and Method

Participants

Thirteen participants took part in Experiment 4 (7 males, mean age ± SD: 36.1 ± 6.2 years, based on the same power calculation as for Experiment 3. None of the participants had participated in the previous experiments. Exclusion criteria were as the previous experiments.

Procedure

Participants completed the egocentric localization task while their gaze was directed left or right. On each trial, participants were required to direct their gaze ±4cm from the centre of the monitor. This magnitude of shift was chosen based on the results of experiment 3, computing the mean ± 2SD of the gaze shift observed in Exp.3. Instead of a fixation marker, sound feedback was given when the gaze was in an incorrect location. After holding the correct fixation for 0.7s, the visual target was briefly flashed. No GVS was applied. Procedures were otherwise as experiment 3. Gaze location was recorded with an Eyelink 2000 eye-tracker (sampling frequency 1 kHz). Right or left gaze condition was fixed for each block (150 trials), and 4 blocks were conducted in randomized order.

4.2.2 Results

Figure 4D shows average PSEs across participants while gaze was directed either leftwards or rightwards. We verified that the gaze was directed to the correct location by estimating the average gaze location during the period from the onset of the target to the response (mean ± SD: gaze-left = -3.9 ± 0.26 cm; gaze-right 4.0 ± 0.36 cm). There was no significant difference in the PSE between gaze conditions [$t(12)=0.65$, p=0.53].

4.3. Discussion

The results of Experiment 3 showed that GVS can bias not only egocentric body representations (Fig. 4A), but also shift horizontal gaze location (Fig. 4B). Thus, one might argue that this GVS-induced shift in gaze location could have indirectly driven the bias in egocentric body representation, without any direct effect of GVS. However, in Experiment 4, egocentric judgements were not significantly altered when participants were explicitly asked to direct their gaze leftwards or rightwards by an amount equivalent to the GVS-induced bias (Fig. 4C). Taken together, these results therefore suggest that the indirect effect of GVS mediated by gaze shifts is minimal or absent. Thus, the strong biasing effect of GVS on egocentric body representations is independent of changes in gaze location, and appears to represent a direct vestibular input to spatial representation of the body midline.

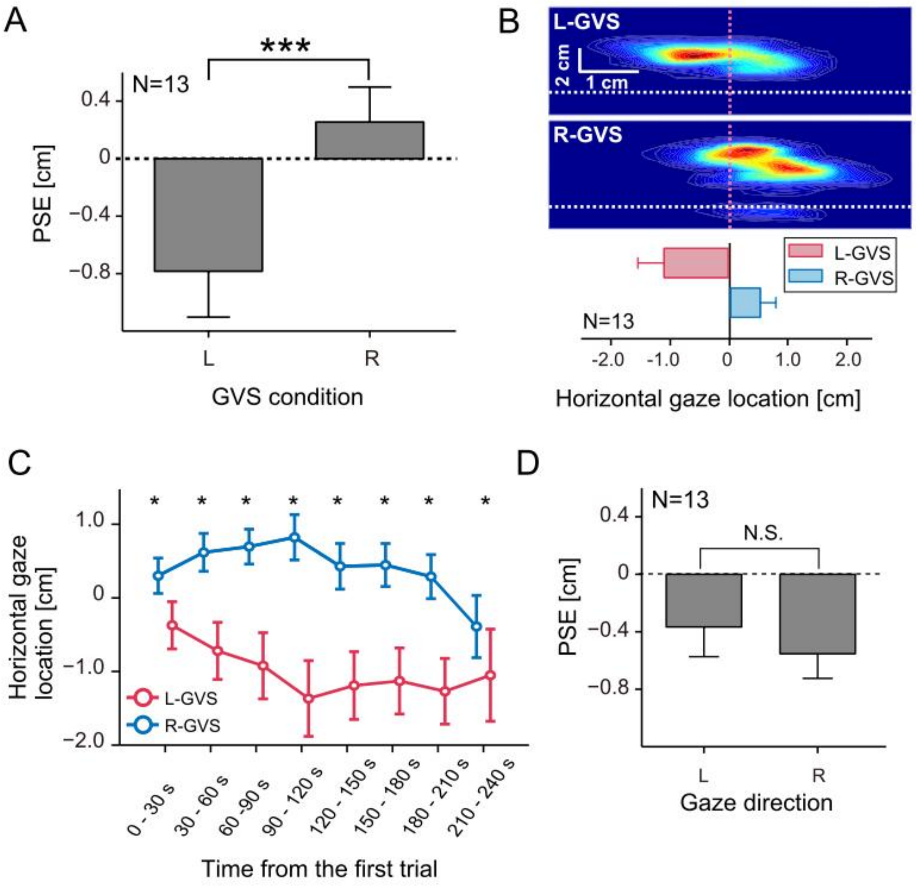

Figure 4. Results of Experiment 3 and 4.
A. Averaged PSE for each GVS condition in Experiment 3. Right-left judgment of the visual target relative to body-midline was biased by GVS. B. "heat map" of gaze locations obtained from a single participant for L-GVS (top panel) and R-GVS (middle panel). Vertical pink line: center of the monitor, corresponding to true body midline. Horizontal white line: vertical position of stimulus presentation. Bottom panel: Averaged gaze location across participants. C. Temporal change in horizontal gaze location during one block. D. Averaged PSE for each gaze direction in Experiment 4.

5. General Discussion

In many situations appropriate motor responses must be chosen rapidly based on the location of external objects relative to the body midline. Figure 5 depicts a conceptual model for these vision-body-action chains. In this schematic, the retinal location of a visual target is integrated with other sensory signals, and with a representation of the body itself, and particularly of the body midline, to localize the target with an egocentric frame of reference. Motor responses are then selected based on this egocentric localization. Our research has been concerned with the origin of this representation of the body midline, and particularly with the possibility that it may depend on vestibular signals. The specific vestibular contribution to egocentric body representation has proved difficult to study because of potential confounding effects of vestibular interactions with visual and motor systems. In this series of studies, we systematically investigated the contribution of vestibular signals to egocentric spatial representations. In Experiment 1 we found that artificial stimulation of the vestibular system biased body midline perception based on GVS polarity. Importantly, no effect was found on motor effector selection. In experiments two and three we ruled out additional explanations based on allocentric visual representations and on potential indirect effects caused by vestibular-driven movements of the eye, head and body. Thus, our data suggest that vestibular information contributes to computation of egocentric representations by affecting the internal representation of the body midline.

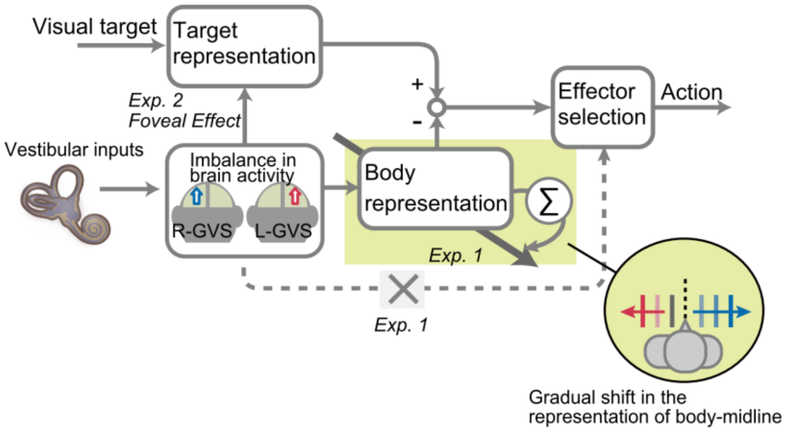

Figure 5. A hypothetical model of the mechanisms underlying the effect of vestibular signals on vision-body-action processing. See text for explanation.

Previous research investigating the perception of the body midline involved asking participants to point straight ahead without visual information. In particular, this task has shown a systematic bias towards the ipsilesional side in patients with hemispatial neglect. This bias has been successfully remediated by artificial vestibular stimulation, suggesting that the vestibular system contributes to body representation (Cappa et al., 1987; Vallar et al., 1993; Karnath et al., 1994). However, the use of this task cannot rule out alternative explanations based on vestibular contributions to motor control (Pizzamiglio et al., 2000; Heilman et al., 1983b). Indeed, vestibular-motor interactions have been found for posture control (Horstmann et al., 1988; Cullen, 2012) and arm-reaching/ocular movements (Itō, 1982; Ito 1984; Lacquaniti and Caminati, 1998; Bresciani et al., 2002). Furthermore, recent imaging studies have shown that vestibular inputs project to widespread brain regions including motor-related areas (Lopez et al., 2012). Our experiments however systematically rule out these alternative explanations, and show that a direct vestibular contribution to egocentric body representation remains, even after controlling for motor effects. Thus, in Experiment 1, hand posture did not change the GVS effect on perceptual judgments (Fig. 2A and 2B), and there was no GVS effect on reaction times. In addition, these findings are consistent with previous studies showing no effect of GVS on the use of right or left hand during free selection of manual actions (Ferrè et al., 2013a).

In Experiment 2, we aimed to disentangle the effects of GVS on egocentric and allocentric representations (Figure 3A). Previous imaging and neurophysiological studies have demonstrated the tight interaction of vestibular function with visual systems (Brandt et al., 1998; Brandt et al., 2002), however there are few studies directly examining vestibular contributions to allocentric visual localization. The results showed that GVS slightly, but significantly, affected allocentric visual localization (Fig. 3B). This effect could be ascribed to “foveal mislocalization” (Müsseler et al., 1999) and its modulation by GVS. Since GVS shifts spatial attention towards the anode, it may change the degree of mislocalization, with a direction that depends on the side of the allocentric reference relative to central fixation. Importantly, the GVS effect on allocentric visual perception was in the opposite direction from the GVS effect on egocentric localization in Experiment 1 (Fig. 3D). This suggests a clear dissociation between effects of vestibular input on visual localization and on body representations.

Finally, we confirmed that our results were not due to physical movements of the head or eye causing shifts in gaze location. In Experiment 3, we replicated the GVS effects observed in Experiment 1 even when the head movements were physically restricted by a chin-rest. Regarding eye movements, our results are consistent with previous studies reporting reflexive and weak horizontal eye movements (slow phase nystagmus) towards the anode (Cauquil et al., 2003; Curthoys and MacDougall, 2012): in Experiment 3 we found that gaze location shifted toward the anode during the egocentric judgment task (Fig. 4B and 4C). Importantly, equivalent manipulations of gaze location by instructed voluntary fixation, without GVS, did not affect egocentric localization in Experiment 4 (Fig. 4D). Voluntary gaze shift has been reported to modulate spatial representations (Cui et al., 2010). For instance, voluntary shift in gaze location influenced head-center, but not body-center, representation (Lewald & Ehrenstein, 2000). However, our results are in line with previous studies which have shown that selectively induced change in gaze, for instance with prism adaptation, did not contribute to egocentric localization (Newport et al., 2009). Although there might be differences in the neural *mechanisms* underlying involuntary and voluntary gaze control, we were able to balance the oculomotor *behavior* between experiments 3 and 4. This rules out the possibility that the vestibular effects on egocentric localization we have obtained in this study are mediated by the consequence of gaze shift. Thus our results show that vestibular modulation of egocentric localization is independent of oculomotor *behaviour*, but cannot conclusively address whether vestibular modulation of localization is independent of oculomotor *circuits*. In addition, it has been known that GVS induces torsional eye movements (Jahn et al., 2003), but it is difficult to reproduce such eye movements voluntarily, without vestibular inputs. Thus, Experiments 3 and 4 focused on the possible effects of horizontal shift in gaze on body representation. An influence in the opposite direction is, of course, also possible, with body representation influencing gaze direction: the brain may adjust gaze location according to the shift in the representation of the body-midline. Thus, how body representation, gaze location and vestibular inputs interact is an open question for further investigation.

Which brain networks are responsible for vestibular interactions with egocentric body representations? Neuroimaging studies have demonstrated that vestibular stimulation activates widely spread cortical networks, involving the posterior and anterior insula, the temporoparietal junction, the inferior parietal lobule, the somatosensory cortices, the primary motor cortex and premotor cortex (Bottini et al., 1994; Bense et al., 2001; Fasold et al., 2002; Emri et al., 2003). The right posterior parietal cortex is involved in spatial perception and/or orienting spatial attention (Corbetta et al., 1995; Mesulam, 1999). For example, left hemispatial neglect is associated with damage to the right inferior parietal or temporoparietal lobe, suggesting right-hemisphere dominance in spatial perception (Driver and Mattingley, 1998). Accordingly, neurologically normal volunteers tend to be biased toward the left-side of space in visuospatial tasks such as line-bisection, a phenomenon known as 'pseudoneglect' (Jewell and McCourt, 2000). Interestingly, we also observed a slight but nonsignificant leftward bias in body-midline localisation without vestibular stimulation (SHAM condition in Fig. 2B), analogous to pseudoneglect. A recent EEG study suggested that pseudoneglect reflects representations of near space in the right parietal cortex (Longo et al., 2015). Furthermore, an fMRI study investigated neural activation when performing a line-bisection task during GVS (Fink et al., 2003). L-GVS produced unilateral activation of the right vestibular cortex, while R-GVS activated the vestibular cortex bilaterally. In addition, posterior parietal and ventral premotor cortex were specifically activated during the bisection task with GVS, with pronounced right hemisphere activation. Finally, previous fMRI studies showed that a bilateral parietal-premotor network, with larger activations in the right hemisphere, was activated when participants performed visual localization relative to the body-midline (Galati et al., 2000; Vallar et al., 1999). Taken together, we speculate that a frontal-parietal network is involved in the egocentric localization process, and GVS induces the change in the activation of these areas in a polarity specific manner.

GVS polarity-specific effects have been previously described in the literature (see Utz et al., 2010 for a review). For example, clinical studies have described a significant reduction in visuospatial neglect induced by left anodal GVS compared to right-anodal GVS. However, it is controversial to generalize these GVS polarity-specific effects to heathy participants. For instance, changing the GVS polarity did not influence the *magnitude* of errors in a line bisection task (although the *direction* of these errors did depend on polarity, as predicted; Ferrè et al., 2013c). Similarly, we did not find a significant difference in the numerical magnitude of GVS effects between R-GVS and L-GVS. Polarity effects on the magnitude, as opposed to direction, of GVS effects are often interpreted in terms of hemispheric specialization (Ferrè et al., 2013c). Our data therefore do not support hemispheric specialization effects in egocentric localization in healthy participants.

Moreover, our temporal analysis (Experiment 1) revealed that the effect induced by GVS grows with cumulating vestibular input (Fig. 2C). In fact, the perceived body midline shifted gradually with increasing GVS exposure during the course of the block. This seems to suggest that the representation of the midline is established by constant online integration of ongoing sensory input, rather than being a systematic stored knowledge about one's own body.

Our results suggest that vestibular signals contribute to a representation of the body midline, and that this representation is implicit, and continuously updated by afferent input. The representation of the body midline recalls the idea of an "egocentre". Most sensory organs are duplicated on each side of the body, yet behavioural performance suggests information is integrated into a virtual single sensory organ located closer to the midline. Thus, vision from the two eyes has been referred to a "Cyclopean eye" (Julesz, 1971), though this idea remains controversial (Erkelens and Van Ee, 2002). Proprioceptive inputs from each arm are referred to shoulder, and the perceptual properties related to each shoulder are integrated (Jola et al., 2011). Cutaneous inputs from a zone of overlap around the body midline project to both hemispheres (Manzoni et al., 1989), yet touches at the corresponding skin location are felt as one object rather than two. In the vestibular case, rotation of the head causes a velocity signal in vestibular canal afferents. Increases in firing from afferents on one side of the body are accompanied by decreases on the other side. Therefore, heading direction at rest can be computed as a direction which generates no net vestibular velocity signal. In our study, the head is fixed relative to the torso, so the body midline and heading direction are identical. Thus, for example, a visual stimulus aligned with the body midline would generate no change in canal input if a head rotation were made to fixate it. In this way, the combination of signals from lateralised vestibular organs can contribute to a purely cognitive representation of the body midline.

In conclusion, our studies highlight vestibular contributions to egocentric body representations. Although the role of vestibular signals in egocentric representation has often been suggested, the dependent measures and control conditions used as operational definitions of egocentric representation in previous studies could not rule out other explanations, based on possible vestibular influences on the visual and motor processes used to measure egocentric representation. We have shown that vestibular stimulation biases participants' perception of their body-midline location, shifting it towards the anode. Importantly, we have systematically ruled out alternative explanations based on possible vestibular influences on action selection, action execution, gaze direction, and allocentric visual representation. Thus, our results suggest that vestibular information is involved in the process of egocentric visual localization, necessary for making rapid motor actions. Our results strongly support the idea of a central, cognitive representation of egocentric space, centred on the body midline, and abstracted from specific visual input and from motor output. Vestibular signals provide an ongoing input to the cognitive process which computes and maintains the representation of the body midline.

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Figure captions

Figure 1. Experimental setup and methods.

A. Apparatus. B. GVS polarities and electrodes configurations. C. Experiment 1: Participants localized visual stimuli relative to their body midline. The task was performed with the hand uncrossed or crossed. The blue arrows indicate participant's judgment. If participant judges "right", they are instructed to press the right-side button in the both hand conditions. D. Experiment 2: Participants localized visual stimulus relative to an allocentric reference.

Figure 2. Results of Experiment 1.

A. Ensemble judgment as the function of the stimulus location with psychometric curves. The data were shown for hand uncrossed (left panel) and crossed (right panel). The arrow indicates the value of PSE for each GVS condition. Error bar indicates standard error of mean. B. Averaged PSEs for all the conditions. Three asterisks: significance at $p < 0.001$. N.S.: not significant. C. Temporal change in the PSE as the function of the sub-block. The PSE gradually varied according to the GVS condition. Colours denote the GVS condition as shown in panel 2A.

Figure 3. Body vs Vision theory and results of Experiment 2.

A. Two contrasting theories for interpreting results of Experiment 1. Consider the scenario in which the visual stimulus is at the body-center, and participants judge its location "Center" for Sham-GVS. The BODY theory would explain the observed results as a rightward shift in egocentric body representation induced by R-GVS. Center-stimuli would then be judged "Left". The VISION theory proposes a direct shift in the visual representation induced by R-GVS, without any change in the representation of the body egocentre. B. Averaged PSEs for all the conditions for Experiment 2. C. Temporal change in the PSE as the function of the sub-block. D. A direct comparison of GVS effect observed in the first and second experiment. We subtracted Sham-GVS from R-GVS and L-GVS.

Figure 4. Results of Experiment 3 and 4.

A. Averaged PSE for each GVS condition in Experiment 3. Right-left judgment of the visual target relative to body-midline was biased by GVS. B. "heat map" of gaze locations obtained from a single participant for L-GVS (top panel) and R-GVS (middle panel). Vertical pink line: center of the monitor, corresponding to true body midline. Horizontal white line: vertical position of stimulus presentation. Bottom panel: Averaged gaze location across participants. C. Temporal change in horizontal gaze location during one block. D. Averaged PSE for each gaze direction in Experiment 4.

Figure 5. A hypothetical model of the mechanisms underlying the effect of vestibular signals on vision-body-action processing. See text for explanation.