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Disrupting Vestibular Activity Disrupts Body Ownership

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Abstract

People are more sensitive at detecting asynchrony between a self-generated movement and visual feedback concerning that movement when the movement is viewed from a first-person perspective. We call this the ‘self-advantage’ and interpret it as an objective measure of self. Here we ask if disruption of the vestibular system in healthy individuals affects the self-advantage. Participants performed finger movements while viewing their hand in a first-person (‘self’) or third-person (‘other’) perspective and indicated which of two periods (one with minimum delay and the other with an added delay of 33–264 ms) was delayed. Their sensitivity to the delay was calculated from the psychometric functions obtained. During the testing, disruptive galvanic vestibular stimulation (GVS) was applied in five-minute blocks interleaved with five minutes of no stimulation for a total of 40 min. We confirmed the self-advantage under no stimulation (31 ms). In the presence of disruptive GVS this advantage disappeared and there was no longer a difference in performance between perspectives. The threshold delay for the ‘other’ perspective was not affected by the GVS. These results suggest that an intact vestibular signal is required to distinguish ‘self’ from ‘other’ and to maintain a sense of body ownership.

Keywords

Cross-modal interactions, body ownership, visual perspective, body representation, vestibular cues, proprioception

1. Introduction

The representation of body in the brain, sometimes referred to as the body schema, is created through convergence of proprioceptive, haptic, and visual signals (see Serino and Haggard, 2010 for a review). Recently the vestibular system has been implicated in a previously unsuspected role in the development of the body schema (Lopez *et al.*, 2012). For example, individuals with

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vestibular disorders, such as vestibular vertigo or vestibular deafferentation, tend to misrepresent the size, shape, and location of their body parts even though the vestibular system provides no information of direct relevance to making these judgments (Lopez and Blanke, 2007; Lopez *et al.*, 2008; Sang *et al.*, 2006; Schilder, 1935). Healthy individuals with no vestibular symptoms can also be made to show degraded performance on tasks that require knowledge about their body and self by adding temporary, disruptive galvanic vestibular stimulation (GVS). For example, Bresciani *et al.* (2002) found that unilateral GVS disrupted reaching movements toward the side being stimulated and created a less accurate estimate of where the hands were in space. More remarkably, caloric vestibular stimulation affects the ability to discern the size and shape of a participant's own hands (Lopez *et al.*, 2012) and increases susceptibility to self-attribution illusions such as the rubber-hand illusion (Lopez *et al.*, 2010). Taken together, these observations suggest that intact vestibular background activity is integral for creating and maintaining a coherent representation of the self and that losing this signal undermines a person's perception of self. However, reliable, quantitative assessments of how a person perceives themselves as themselves is lacking and studies have generally been restricted to using questionnaires or self report measures.

Previous studies investigating self-recognition during active movement have found misattribution of hand movements to another agent when the participants' movements and the other agents' movements (superimposed over top of their movements) were similar and, in some instances, when there were discrepancies between the movements (Fourneret and Jeannerod, 1998; Nielsen, 1963; see Jeannerod, 2003 for a review). These results suggest the importance placed upon visual cues when making self/other judgements. Visual perspective, in particular, has been shown to modulate the ability to recognize our own body parts from others' (Conson *et al.*, 2010; Van den Bos and Jeannerod, 2002), discriminate between left and right hands (Dyde *et al.*, 2011), and experience the rubber hand illusion (Holmes and Spence, 2007). We have previously shown that visual perspective also affects the threshold for detecting a temporal mismatch between a self-generated movement (e.g., of the finger) and visual feedback of the movement (Hoover and Harris, 2012, in press). We found that when body movements are seen from a first-person perspective (e.g., when looking down at your own hands) there is a signature self advantage in detecting the delay: asynchrony is detected approximately 40 ms faster when viewed from this 'self perspective' than when movements are viewed from a perspective considered third-person or other (e.g., upside down) (Hoover and Harris, 2012, in press). Self-generated movements provided participants with efferent information as well as proprioceptive information, which are important factors in determining whether you are the agent of the action (Farrer *et al.*, 2003; Gallagher, 2000; Tsakiris *et al.*, 2005). In turn, the sense of agency is an important contributor to the sense of body ownership (Tsakiris *et al.*, 2010). The advantage in asynchrony detection thresholds suggests an enhanced sense of body ownership when an action is viewed in a self perspective. This measure can therefore be taken as an objective measure of body ownership.

Given that the vestibular system has been linked to registering spatial and temporal aspects of the self (Ferrè *et al.*, 2013; Lopez *et al.*, 2008) we examined whether disruption of vestibular activity using GVS in healthy individuals affected the self-advantage in temporal asynchrony detection.

2. Methods

2.1. Participants

Nine right-handed adults, with a mean age of 29 (± 12 SD) years, participated in this study. The experiment was approved by the York University office of research ethics and followed the guidelines of the Declaration of Helsinki. Handedness was determined by an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971).

2.2. Galvanic Vestibular Stimulation

The vestibular stimulation consisted of a small current applied through electrodes positioned on the mastoid processes behind the ears. A reference electrode was placed in the centre of the forehead. The electrodes were 3.25 cm diameter round carbon-conductor electrodes (9000 series electrodes; Empi Recovery Sciences, St. Paul, MN, USA). The vestibular stimuli were generated by a GVS system (Good Vibrations Engineering Ltd., Nobleton, ON, Canada) controlled by a PC. Our vestibular stimulus was a sum-of-sines waveform with dominant frequencies at 0.16, 0.32, 0.43, and 0.61 Hz (maximum current limited to ± 5 mA) which has shown to be disruptive to the vestibular system (MacDougall *et al.*, 2006; Moore *et al.*, 2006). Bilateral, bipolar stimulation was applied in 5-min blocks interleaved with 5-min blocks without stimulation so that data collected with and without GVS were interleaved over the total experimental time of 40 min.

2.3. Apparatus and Stimuli

Participants sat on an adjustable chair at a table with their head on a chinrest 50 cm away from a LCD display (HP Fv583AA 20′ widescreen monitor; 1600×900 pixels; 5 ms refresh response time) centred at eye level as shown in Fig. 1. They placed their hand on the table shielded from view by a black cloth. A PlayStation Eye camera (SCEI; resolution 640×480 @ 30 Hz) was mounted on the front of the chinrest and pointed down at their hand. The

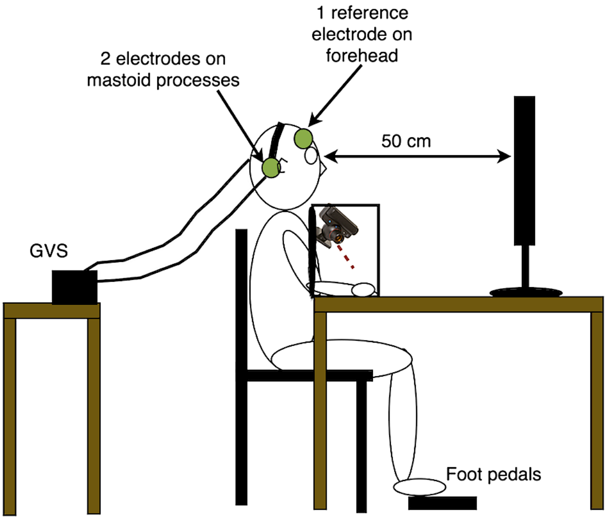

Figure 1. Participants sat on an adjustable chair at a table 50 cm from an LCD screen centred at eye level. The right hand was placed on the table shielded from direct view by a black cloth. A PlayStation Eye camera was mounted on the front of a chinrest and pointed down to capture the view as seen from a natural self perspective. Two stimulating electrodes were placed on the mastoid processes behind the ears and one reference electrode was placed on the center of the forehead. The electrodes were connected to a GVS generator. Foot pedals were used to make responses. This figure is published in colour in the online version.

camera was angled to capture the view as seen from a 'natural' egocentric perspective as if participants were looking down at their own hands.

The video signal from the camera was fed into a computer (iMAC11, 2, mid 2010), read by MATLAB (version R2009_b) and played through the LCD screen at either a minimal delay, or with an added delay of between 33 and 264 ms. To calibrate the system we had the camera view a flashing LED and compared the voltage across it with its appearance on the screen measured by a light sensitive diode. This revealed a minimum delay of 85 ms ± one-half camera refresh duration and confirmed the delay values we introduced with the software.

We asked participants to perform a single flexion of the right index finger through approximately 2 cm. They made the movement as soon as they saw their hand on the screen in a given trial. Participants avoided touching the table or other fingers with their index finger during the movement so as to not introduce additional tactile cues. To reduce between-subject differences in the speed and type of movement, all participants went through a 15-trial practice phase during which the experimenter observed and corrected movement prior to testing. Video images were manipulated using the Psychophysics Toolbox extension of MATLAB subroutine *PsychVideoDelayLoop* (Brainard,

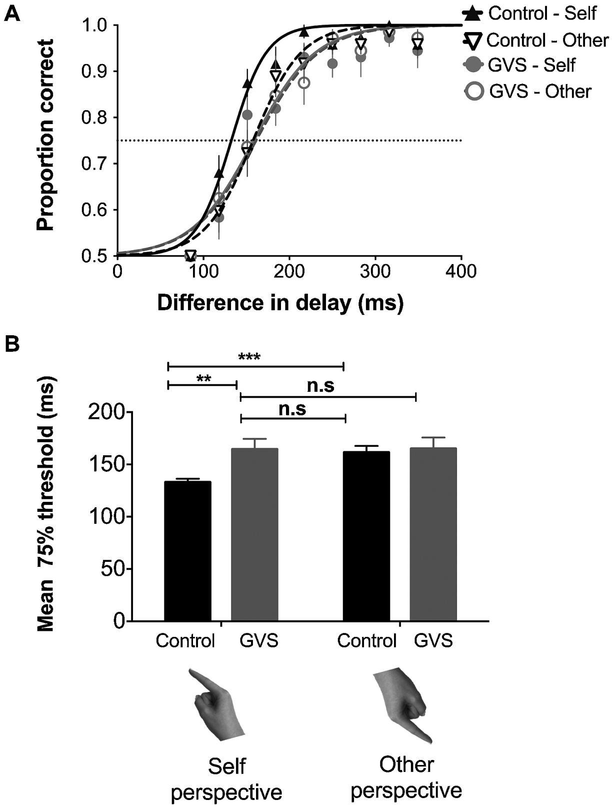

Figure 2. (A) Thresholds for detecting an imposed visual delay in the visual feedback concerning a self-generated movement. The mean proportion correct is plotted as a function of the imposed visual delay. The curves are psychometric functions fitted through the data for the 'self' perspective (solid black line and black triangles), the 'other' perspective (dashed black line and inverted white triangles), GVS 'self' perspective (solid grey line and grey circles), and GVS 'other' perspective (dashed grey line and white circles). (B) The mean 75% thresholds averaged from the fits to the individual participant's data in the control condition (black bars) and the GVS condition (grey bars) for the 'self' and 'other' perspectives. Error bars are SEMs. n.s. $p > 0.05$; $^{**}p = 0.01$; $^{***}p = 0.001$.

1997; Pelli, 1997). Participants were presented with two views of their movements: (1) a 'self' perspective (the expected first-person perspective), and (2) an 'other' perspective (the unexpected third-person perspective where the video images were flipped around the x and y axes so that they were upside down and back to front). Examples of these views are shown in insets in Fig. 2.

2.4. Procedure

To assess the thresholds for detecting temporal synchrony, a two-interval forced choice (2IFC) discrimination paradigm was used. Each trial consisted of two 1 s periods separated by an inter-stimulus interval of 100 ms: in one period a minimal-delay presentation of the movement was shown and in the other, the presentation was delayed by a variable amount. Whether the minimal-delay presentation or the delayed presentation was displayed first was randomly chosen by MATLAB. There were nine possible differences in visual delays in any given trial: 0, 33, 66, 99, 132, 165, 198, 231, and 264 ms corresponding to a delay of an integral number of video frames. Participants indicated which presentation was delayed using foot pedals (Yamaha FC5): left for first and right for second. The experiment was run in a block design where GVS was applied in five-minute blocks interleaved with five minutes of no stimulation for a total of eight blocks taking 40 min in total. Five participants started with a control block and four participants started with a GVS block. In total, the nine differences in visual delay were presented eight times for the two visual perspectives in a random order with and without GVS resulting in a total of 288 trials.

2.5. Data Analysis

To explore differences in performance across conditions we fitted a cumulative Gaussian curve to the proportion of times participants correctly chose the delayed period as a function of the delay using:

$$y = 0.5 + \frac{0.5}{1 + \mathrm{e}^{-((x - x_0)/b)}}, \tag{1}$$

where x is the delay, x_0 is the 75% threshold and b is the standard deviation. The statistical analysis comprised of repeated measures analysis of variances (ANOVAs) and paired t-tests. For all tests, alpha was set at $p < 0.05$.

3. Results

Figure 2 shows the mean proportion of trials in which the participants correctly identified the presentation with the delay, plotted as a function of the total delay (system delay plus added delay), averaged across the nine participants for the two experimental conditions (with and without GVS) and the two perspectives of the movement (‘self’ and ‘other’). Illustrative psychometric functions are plotted through these average data for the four conditions. Threshold values for detecting the added visual delay were defined as the 75% point of this curve. Each participant’s performance was analysed separately for the statistical tests. The mean thresholds and standard errors are shown in Table 1.

A 2 × 2 repeated measures ANOVA revealed a significant interaction between the perspective of the hand (‘self’ *vs.* ‘other’) and whether GVS was applied or not, $F_{(1,8)} = 12.54$, $p = 0.008$, $\eta_{\mathrm{p}}^2 = 0.61$. In the absence of GVS,

Table 1.
Mean detection thresholds averaged across all participants, with SEs

	GVS	Control
‘Self’ perspective	165 ± 10 ms	133 ± 3 ms
‘Other’ perspective	165 ± 11 ms	162 ± 6 ms

The values were obtained by adding the system delay (85 ms) to the delay added to the video.

when participants saw their hand in the expected ‘self’ perspective they were better at detecting the delay, showing a self-advantage of 29 ms on average compared to when the hand was viewed in the ‘other’ perspective ($t_{(8)} = 5.70$, $p = 0.001$, $d = 4.03$). The presence of disruptive GVS increased the threshold to detect asynchrony in the ‘self’ perspective by 32 ms compared to the no-GVS condition ($t_{(8)} = 3.17$, $p = 0.01$, $d = 2.24$) thus eliminating the self advantage that was apparent in the control condition. Critically, GVS did not affect performance while participants viewed their movements in the ‘other’ perspective: the GVS ‘self’ perspective showed no significant difference in performance from either the control or the GVS ‘other’ perspective (GVS ‘self’ *vs.* GVS ‘other’ $t_{(8)} = 0.10$, $p = 0.92$, $d = 0.07$; GVS ‘self’ *vs.* control ‘other’ $t_{(8)} = 0.46$, $p = 0.66$, $d = 0.35$).

Analysis of the slopes of the psychometric functions (b, see Methods) showed no significant effect ($F(3, 316) = 2.40$, $p = 0.07$), although there was a trend in which the ‘self’ perspective without GVS tended towards being lower (20.3 ± 3 ms) than the other three conditions (GVS ‘self’ = 35.9 ± 6 ms; GVS ‘other’ = 36.5 ± 5 ms; and control ‘other’ = 27.9 ± 5 ms).

4. Discussion

Here we showed that disruptive vestibular stimulation affected the ability to detect temporal asynchrony between a self-generated movement and visual feedback about the movement but solely when self-generated movement was seen in the expected ‘self’ perspective. We replicated our previous finding of a self-advantage where one is more sensitive to a temporal mismatch when the hand is shown in the expected ‘self’ perspective and showed that this self-advantage is completely abolished by disruptive GVS. Since threshold for detecting a delay for movements seen from the ‘other’ perspective were unaffected by GVS, the GVS was clearly not exerting its effect by, for example, degrading the visual scene by eye movements or any other such indirect influence. Does this effect indicate a reduced sense of body ownership or a reduced sense of agency?

The sense of agency — the sense of being in control of your intended actions (Gallagher, 2000) — contributes to the sense of body ownership (Van den Bos and Jeannerod, 2002) but can be dissociated from it. Patients with vestibular disorders have reported that they experience a lessened sense of agency (Sang *et al.*, 2006) and sense of agency can be felt for objects that are not seen as part of the body (such as using a computer mouse to control a cursor on a screen; Balslev *et al.*, 2007). The current study required participants to compare efferent and proprioceptive information concerning the self-generated finger movement with visual information. It may be that the noisy vestibular information from the artificial vestibular stimulation may have caused participants to be less aware of their movements — reducing the sense of agency. However, one would expect that if our effect disrupted the ability to compare visual with proprioceptive/efferent signals (i.e., the sense of agency), both the ‘self’ and ‘other’ perspectives would be equally affected. Since this was not the case and the ‘other’ judgments were unaffected, it seems improbable that the disruptive GVS affected the sense of agency but rather that our task is probing the sense of body ownership.

The fact that disruptive vestibular stimulation only affected performance when the hand was seen from the first-person perspective suggests that the vestibular system plays a role in providing some kind of grounding information to the multisensory representation of the body in the brain. This is inline with other research investigating the contribution of the vestibular system to the ownership of a body part seen in a first-person perspective. Ferrè and colleagues (2014) found that in the presence of vestibular stimulation, participants were more apt to identify characters drawn on their forehead as being from the self-perspective rather than from the third-person perspective. This propensity for responding to the first-person perspective during a graphesthesia task also suggests, but in a more indirect way than the present study, that vestibular inputs are an integral component of the development of the body representation in the brain.

When movements are seen in the ‘self’ perspective, the self-advantage we report here of 29 ms (comparable to the 40 ms we reported previously — Hoover and Harris, 2012), provides a quantitative example of how the sense of body ownership aids performance (Gallagher, 2000). This enhancement suggests that participants are better able to detect temporal asynchrony between making a movement and seeing the movement when the visual information matches their internal representation of their hand moving. When disruptive GVS is applied, it seems that the disruption of the vestibular signal creates a reduced sense of body ownership, thus eliminating the self advantage. Under this interpretation our observation provides a quantitative measure of the effect of vestibular input on body ownership which is consistent with other more qualitative reports of vestibular stimulation leading to a lessened sense of self (Ferrè *et al.*, in press; Lopez, 2013; Lopez *et al.*, 2008) and being more susceptible to the rubber hand illusion (Lopez *et al.*, 2010).

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