Experimental Brain Research
https://doi.org/10.1007/s00221-018-5346-8

RESEARCH ARTICLE

Vestibular–somatosensory interactions affect the perceived timing of tactile stimuli

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Received: 14 October 2017 / Accepted: 26 July 2018

Abstract

Passive rotation has been shown to alter temporal-order judgments for tactile stimuli delivered to the hands giving an advantage to the leading hand. Here we measure thresholds for detecting stimulus onset asynchrony for touches on the hands during tilt to the left or right and during galvanic vestibular stimulation (GVS) that evoked illusory tilt. During tilt to one side, the effect of gravity on the otoliths is equivalent to a physical acceleration away from that side (e.g., tilt left is equivalent to accelerating rightwards). We therefore predicted a "leading hand advantage" for the hand opposite to the tilt direction. Thresholds for detecting asynchronicity for left-hand-first and right-hand-first touches (defined as correct detection 75% of the time) were measured separately using interleaved adaptive staircases for 15 participants. For both physical and illusory tilt there was a temporal advantage for stimuli presented to the hand contralateral to the tilt—equivalent to the "leading hand" during passive rotation. That is, there was a temporal advantage for the upward hand (for physical tilt) and for the anodal-side hand (for illusory tilt caused by GVS). These results are discussed in terms of attention and direct sensory components evoking the "leading hand" bias. These findings add to the emerging understanding of the pervasive role of vestibular activity in many aspects of cognitive processing.

Keywords Temporal-order judgements · Detection of asynchronicity · Point of subjective simultaneity · Vestibular · Tactile · Somatosensory · Tilt · Galvanic vestibular stimulation

Introduction

As humans, we receive important information about our world through our sense of touch. In addition to resulting from reaching out and touching things, important somatosensory information is also provided from pressure at the support surface. This information is integrated with the gravity-sensing function of the vestibular system to help determine our posture and perceived orientation (Deecke et al. 1979; Jeka and Lackner 1995; Mergner and Rosemeier 1998) and our sense of self-motion (Amemiya et al. 2013; Harris et al. 2017). During tilt, the change in direction of gravity relative to the body is detected by both the vestibular and somatosensory systems. It is now becoming clear that the vestibular system is critical for many aspects of body perception (Ferrè et al. 2013; Mast et al. 2014). Of particular relevance here is that the vestibular system interacts centrally with the somatosensory system (Ferrè et al. 2011a, b, 2015) with a well-established cortical basis (Zarzecki et al. 1983; Ferrè et al. 2012; Pfeiffer et al. 2016).

Passive vertical-axis whole-body rotation that stimulates the vestibular system has been shown to enhance the detection of touches on the leading hand assessed by shifts in temporal-order judgements (TOJs) for stimuli presented on the two hands (Figliozzi et al. 2005). Rotation distorted participants' temporal-order judgements such that, even when the hands were touched at the same time, touch on the leading hand was perceived as coming first. In the present study, we assess whether using tilt to stimulate the vestibular system has similar effects as passive rotation on the processing of tactile stimuli. To do this, we measured the effects of physical body tilt by having our participants lie on their side on a wooden board tilted at 45°, and the effect of electrically stimulating the vestibular system (using galvanic vestibular stimulation, GVS) on tactile temporal-order judgments. We hypothesised that the uneven vestibular stimulus provided

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by these procedures would also alter the perceived timing of touches on the hands.

Galvanic vestibular stimulation (GVS) stimulates the vestibular system by delivering a controlled current through electrodes placed over the mastoid processes (Fitzpatrick and Day 2004). Left-cathodal, right-anodal GVS (L-GVS) increases the firing rate of the vestibular nerve on the left side and decreases it on the right side while right-cathodal, left-anodal GVS (R-GVS) has the opposite effect (Goldberg et al. 1984; Day and Fitzpatrick 2005) in both cases evoking an illusory roll towards the cathode. GVS is a purely vestibular stimulation whereas being tilted by lying on a board is a more complex situation in which participants are cognitively aware of what is happening, are aware of substantial pressure along the side of the body lying on the board, and are aware of their new position in the room. While laying on the board the position of participant's hands are very different, with the upper hand essentially free to explore the space while the downward hand is physically cramped and disadvantaged. Under these conditions, participants' attention is likely to be attracted to the side of space away from the board. GVS is a much more subtle experience with no obvious reason to attract attention from one side to the other. Measuring both the effect of GVS and the effect of physical tilt on the detection of asynchronicity on the two hands therefore allowed us to better understand the role of covert attention. If attention were the driver, we would expect only effects during physical tilt.

There is a range of stimulus onset asynchronies (SOAs) where touches to the two hands appear simultaneous. On each side of this range there is a threshold SOA for detecting when the left hand is touched first and a threshold SOA for detecting when the right hand is touched first. Beyond these thresholds, the SOA is sufficient for asynchronicity of touch between the two hands to be correctly determined more than 75% of the time. Any less of an SOA and the touches are perceived as occurring simultaneously. If one hand were to obtain an advantage and be processed faster, we would need to add less delay to the other hand's touch to reach the threshold SOA for asynchronicity to be detected. Conversely, we would need to add more delay to a touch on the advantaged hand to offset the advantage when the stimulus was presented first to the disadvantaged hand. Any advantage in processing time for either hand can thus be quantified. This logic is illustrated in Fig. 1.

For each tilt condition (physical or illusory), we ran two interleaved psychometric procedures: one where the left hand was always touched first with the right hand delayed by a variable amount, and one where the right hand was always touched first with the left hand delayed. Two interleaved Bayesian adaptive staircases honed in on the SOA between the touches on the hands at which the participant correctly detected the asynchronicity 75% of the time. Stimulus onset asynchronies less than these threshold values were perceived as simultaneous and defined the window of simultaneity, also referred to as the temporal binding window (Spence and Squire 2003).

Materials and methods

Participants

20 right-handed (as indicated by the Waterloo Handedness Questionnaire) adults (10 male, $m = 30$ years, $SD = 13$ years) volunteered to participate in this study. All participants completed both the physical tilt and GVS stimulation conditions and gave informed consent. This experiment was approved by the York University office of research ethics and followed the guidelines of the Declaration of Helsinki.

Stimuli

Tactile stimuli were presented using two tactors (Model C2, Engineering Acoustics, Florida, USA) for both experiments. The tactors were secured to the back of the participants' hands using medical tape. Vibrotactile stimuli were 200 ms bursts of 250 Hz vibration at an intensity that was clearly above threshold but not uncomfortable.

Physical tilt

Physical vestibular stimulation was generated by asking participants to lie on a custom-made padded board tilted at 45° with their arms pointing directly in front of them supported by an armrest (see insert to Fig. 2). Their head was arranged to be aligned with their body and was supported by a foam headrest.

Galvanic vestibular stimulation

Direct vestibular stimulation was generated by galvanic vestibular stimulation (GVS) stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada) with electrodes positioned over the mastoid process behind each of the participants' ears and a reference electrode positioned on the forehead. The GVS system was triggered through MatLab (The MathWorks, Inc.) with the polarity of the stimulation constant within a block of trials. The GVS ramped up to 2 mA over 500 ms and was then maintained (either left-cathodal, right-anodal or left-anodal, right-cathodal) constantly for the duration of a block of trials (approximately 10 min). Participants stood upright unsupported during GVS stimulation. Some participants indicated perceiving a roll towards the cathode side; however, no visible tilt was noticeable during the stimulation.

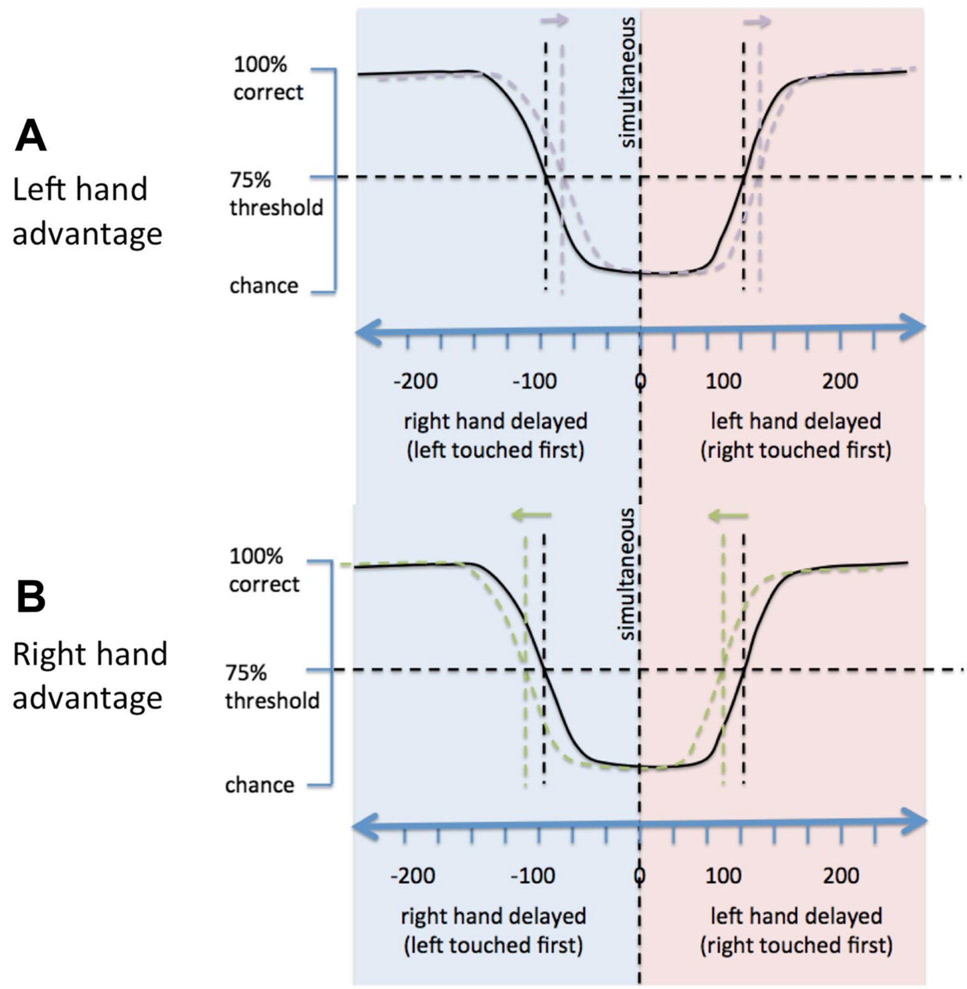

Fig. 1 Threshold curves for detecting tactile asynchronicity between the hands are expected to shift in opposite directions depending on whether the left or right hand obtains an advantage. The black curves indicate the percentage correct performance as touches the right hand are progressively delayed relative to the left (negative SOAs, blue shaded area) or touches on the left hand are progressively delayed relative to the right (positive SOAs, red shaded area). The horizontal dashed line indicates threshold performance (75%). If touch to the left hand was to obtain an advantage (**a**), then touch on the right hand would need to be less delayed for the SOA to reach threshold on the "left touched first" side of the function (shaded in blue) and more delay would need to be added to touch on the left hand for the "right touched first" side of the function (shaded in red), resulting in the function shifting to the right as shown by the dashed purple line. If touch to the right hand were to obtain an advantage (**b**), then the function (dashed green line) would shift in the opposite direction

General procedure

A two-interval forced choice paradigm was used for both the physical tilt and GVS conditions. Participants were asked to keep their eyes closed and look straight ahead during all trials. Each trial consisted of two periods. In one period a tactile stimulus was presented on one hand followed by a second tactile stimulus presented on the other hand, separated by a variable stimulus onset asynchrony (SOA) under control of a QUEST staircase procedure (Watson and Pelli 1983). In the other period, the stimuli were presented simultaneously. The participant chose the interval in which the two stimuli were not simultaneous. The two QUESTs were setup to determine the SOA at which participants were 75% correct in determining in which interval the two stimuli were not simultaneous: one QUEST was constrained to test only negative SOAs (corresponding to left hand touched first) and the other was constrained to test only positive SOAs (corresponding to right hand touched first). Participants verbally indicated in which interval the stimuli were not simultaneous and the experimenter fed their response back into the QUEST control program that then scored the response as correct or incorrect and determined the next SOA to be presented for that particular staircase. The QUEST algorithm assumes the observer's psychometric function follows a Weibull distribution and adaptively determines the next SOA to be presented on the basis of the participant's response to the previous trials. As the experiment progresses, knowledge on the observer's psychometric function accumulates. Each QUEST[1] procedure terminated after 50 trials. Each participant completed the left tilt, right tilt, L-GVS, and R-GVS conditions in separate blocks, the order of which was counterbalanced between participants. Each block took about 10 min and there was a 10-min break between each GVS block. Trials were separated by a 1000 ms inter-trial interval.

[1] QUEST staircase initial parameters: ±60 ms (this is the initial "best guess" of the thresholds which determines which SOA it should test first); standard deviation 37.5 ms (the authors of the QUEST algorithm suggest a liberal standard deviation of the guesses to improve accuracy), step resolution 1.5 ms. The minimum SOA was set to 0.15 ms.

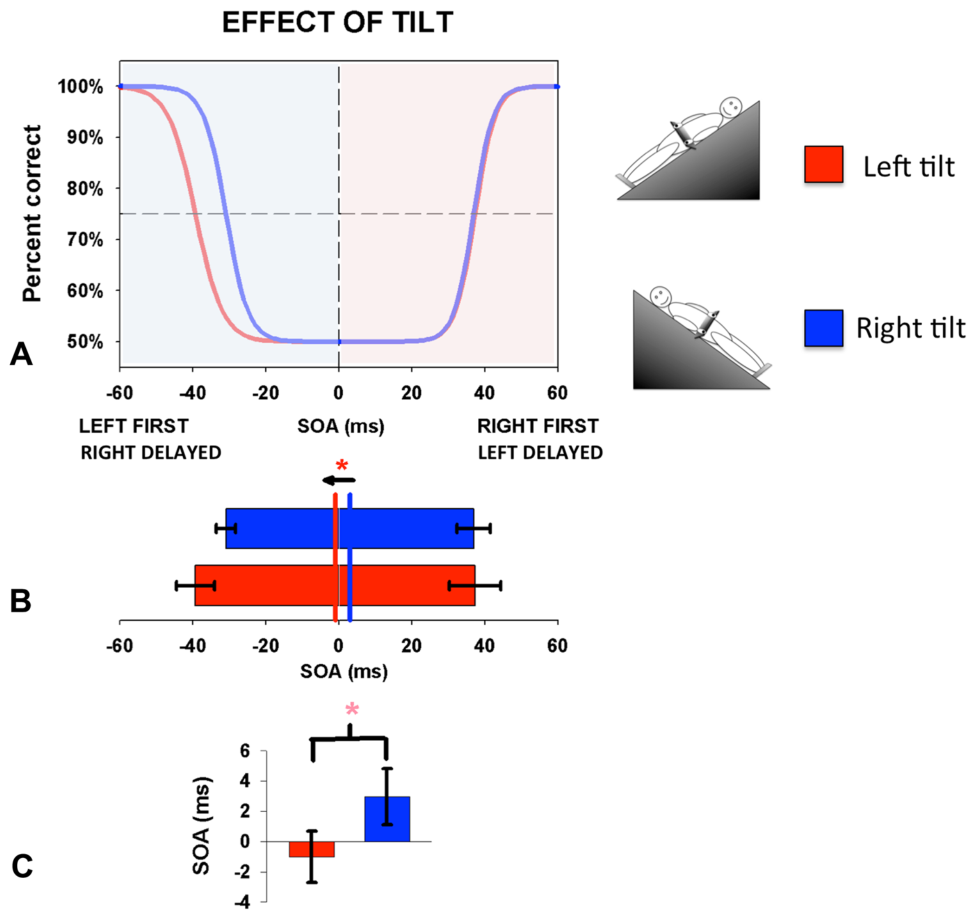

Fig. 2 The effect of physical tilt to the left or right side on the detection of asynchronicity between the left and right hands. **a** The average psychometric curve for left (red) and right (blue) tilts constructed using the mean threshold and slope values for logistic functions fitted through each participant's left-hand-first (blue shaded area) and right-hand-first (red shaded area) data. **b** The temporal binding window is the range of SOAs between the left-hand-first and right-hand-first 75% threshold values. The midpoints between the thresholds (points of subjective simultaneity, PSS) are indicated by vertical lines. **c** The midpoints (PSSs) of the temporal binding windows for the left (red) and right (blue) tilt conditions. Standard errors are also shown

Data analysis

To visualize and confirm the QUEST's performance, the participant's decisions (1 = correct, 0 = incorrect) were plotted against the SOA used for each trial and fitted with a logistic function (Eq. 1) using the curve fitting toolbox in MATLAB:

$$\text{Decision} = 0.50 + 0.50/\left(1 + \exp\left(-\left(x - x_0\right)/b\right)\right), \qquad (1)$$

where x_0 is the 75% threshold value, x is the SOA tested and b is an estimate of the slope of the function. The slope of the psychometric function provided by the QUEST is not reliable but this method, using all the data collected, provides an independent estimate of the slope (b). Five participants were removed from further analysis at this point because such a curve could not be fitted, indicating that the staircase had not adequately converged within 50 trials.

Tactile 75% thresholds (below which stimuli were perceived as simultaneous) were assessed separately for left-tactor-first and right-tactor-first stimuli for both left and right physical tilts and GVS-induced illusory tilts. This is equivalent to using a two-criterion window model of the PSS (Cravo et al. 2011; Yarrow et al. 2011; Rohde et al. 2014). The values correspond to the two edges of the temporal binding window (Fig. 2a). Two-tailed paired t tests were conducted to compare 75% asynchronicity thresholds, points of subjective simultaneity (PSS; corresponding to the midpoint between the thresholds) and slopes (standard deviation) of the psychometric curves for the left and right physical tilt and L-GVS and R-GVS conditions. Effect sizes are reported as Cohen d values. One-way t tests were conducted to compare the points of subjective simultaneity (PSS) for each direction of tilt (left and right) and each direction of GVS (left and right) to zero.

Results

The mean values and slopes for all the data collected are given in Table 1.

Effect of physical tilt

Figure 2a illustrates tactile asynchronicity thresholds for left-tactor-first (negative SOAs) and right-tactor-first data (positive SOAs) for both left and right physical tilt conditions. There was no significant effect of tilt on either of these

Table 1 The mean left-hand-first and right-hand-first 75% asynchronicity detection thresholds that define the edges of the temporal binding window

	Left-first 75% threshold	Right-first 75% threshold	Midpoint (PSS)	Left-first standard deviation (slope)	Right-first standard deviation (slope)
45° left tilt	−39.3 ± 5.2	37.2 ± 7.1	−1.0 ± 1.7	3.7 ± 1.2	2.7 ± 0.6
45° right tilt	−30.9 ± 2.6	36.9 ± 4.5	3.0 ± 1.9	3.1 ± 1.0	2.7 ± 0.7
L-cathode-GVS	−36.9 ± 3.9	36.4 ± 5.6	−0.2 ± 1.7	1.7 ± 0.5	5.6 ± 1.6
R-cathode-GVS	−32.3 ± 2.4	39.5 ± 4.6	3.6 ± 1.6	2.2 ± 0.5	3.1 ± 0.8

The midpoint between these thresholds corresponds to the point of subjective simultaneity (PSS). A negative PSS corresponds to an advantage for tactile stimuli on the right hand while a positive PSS corresponds to an advantage for tactile stimuli on the left hand. Standard deviations correspond to the slopes of the functions shown in Figs. 2a and 3a. All values in ms ± SE. Negative values correspond to left hand stimulated first

thresholds (left first, left tilt vs. right tilt: $t(14) = -1.685$, $p = 0.114$, $d = 0.52$, right first, left tilt vs. right tilt: $t(14) = 0.078$, $p = 0.939$, $d = 0.02$).

The midpoint between the thresholds for left-tactor-first (negative SOAs) and right-tactor-first (positive SOAs) thresholds corresponds to the middle of the temporal binding window—the point of subjective simultaneity (PSS). The PSS's for left tilt and right tilt were significantly shifted relative to each other (Fig. 2b, c) indicating an advantage to the "upward" hand: right perceived earlier during leftward tilt and visa versa (c.f., Fig. 1) $t(14) = -2.596$, $p = 0.021$, $d = 0.29$. The PSS's for both left and right tilt were not significantly shifted relative to zero (left tilt: $t(14) = -0.605$, $p = 0.550$, $d = 0.15$; right tilt: $t(14) = 1.607$, $p = 0.130$, $d = 0.42$). Figure 2c illustrates the PSS for the left and right tilt conditions.

Slopes (standard deviations) of the psychometric curves were obtained from fitting a logistic function to each participant's performance (see "Materials and methods"). There was no significant difference in the slopes between tilt conditions (left first: $t(14) = 0.504$, $p = 0.622$, $d = 0.18$; right first: $t(14) = -0.066$, $p = 0.948$, $d = 0.02$).

Effect of galvanic vestibular stimulation

The same experiment was carried out using GVS instead of physical tilt. Figure 3a illustrates 75% tactile thresholds for left-tactor-first and right-tactor-first data for both left-cathode and right-cathode GVS conditions. There was no significant difference between L-GVS and R-GVS thresholds (left first, L-GVS vs. R-GVS: $t(14) = 1.708$, $p = 0.110$, $d = 0.32$; right first, L-GVS vs. R-GVS: $t(14) = 0.890$, $p = 0.399$, $d = 0.16$).

The midpoints between the tactile thresholds (corresponding to the middle of the temporal binding window—the central point of subjective simultaneity, PSS) for the left-first and right-first thresholds in the L-GVS and R-GVS conditions were significantly shifted relative to each other. This indicates an advantage to the hand on the anodal side (c.f., Fig. 1), $t(14) = 2.565$, $p = 0.022$, $d = 0.59$. The PSS for R-GVS was significantly different from zero, $t(14) = 2.308$, $p = 0.037$, $d = 0.60$, while the PSS for L-GVS was not, $t(14) = -0.140$, $p = 0.891$, $d = 0.04$. Figure 3c illustrates the PSS for the tilts evoked by L- and R-GVS.

Slopes (standard deviations) were obtained by fitting a logistic function to each participant's performance. There was no significant difference between GVS conditions (left-tactor-first: $t(14) = 0.755$, $p = 0.463$, $d = 0.31$; right-tactor-first $t(14) = 1.177$, $p = 0.259$, $d = 0.49$).

Discussion

Vestibular stimulation created either by left or right physical tilt or by left or right illusory tilt induced by GVS affected the minimum SOA needed to detect asynchronicity between the hands. In both cases, the point of subjective simultaneity shifted in a way consistent with the upward hand being processed faster. Figure 1 shows how if perceiving a touch on one hand were faster than for the same touch applied to the other hand, it would result in changes to thresholds for detecting asynchronicity and produce an overall shift the temporal binding window (TBW). Because these effects are expected to be symmetrical on either side of the function (left hand leading and right hand leading), we did not expect any changes in the width of the TBW: just a shift of both edges of the TBW (the threshold SOAs) such that touch to the advantaged hand needed to be delayed more relative to touches on the disadvantaged hand for the disadvantaged hand to be perceived as first, and visa versa. Our results indicate that physical tilt to the left shifted the PSS by 4 ms relative to physical tilt to the right, and L- GVS shifted the PSS by 3.8 ms relative to R-GVS. A direct quantitative comparison with Figliozzi and colleagues (Figliozzi et al. 2005) is difficult because of how they report their data and differences in their method. However, the results of the two experiments are consistent in terms of movement if we consider that physical or illusory tilt to one side is consistent with a linear acceleration. When tilted to one side, the gravity vector can be decomposed into one component aligned

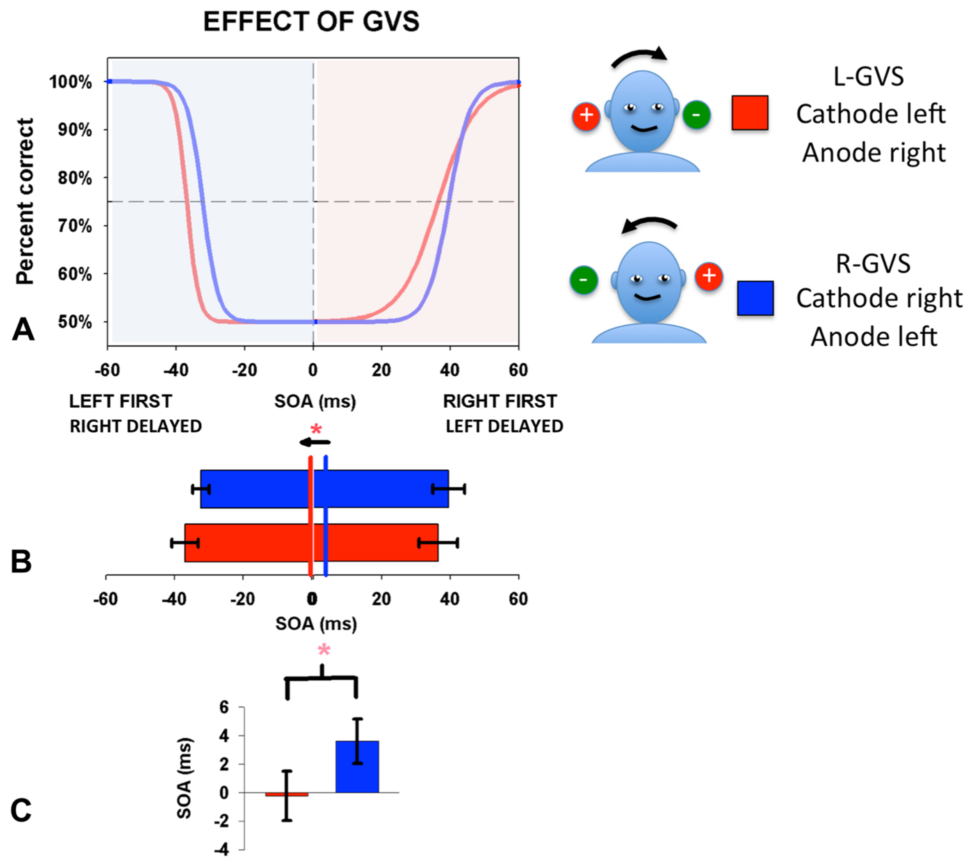

Fig. 3 The effect of maintained simulated tilt to the left using galvanic vestibular stimulation cathode left (L-GVS, red curve) or to the right using cathode right (R-GVS, blue curve) on asynchronicity detection thresholds and PSSs between the left and right hands. Format as for Fig. 2

with the body and an acceleration vector orthogonal to this (as shown in Fig. 4a). Thus, right tilt stimulates the otoliths in a way consistent with accelerating to the left (Fig. 4b). Using this line of reasoning, the advantage that Figliozzi et al. (2005) observed for the leading hand during rotation (Fig. 4c) is consistent with the advantage that we observed for the "upward" hand.

Can the results be explained by an attention shift?

Figliozzi et al. (2005) suggested that their observation could be explained by a shift of attention towards the leading hand in which tactile signals from one hand gain an advantage by a variation of prior entry (Spence et al. 2001). A similar explanation has been posited to explain a corresponding change in auditory TOJs during self-motion created by vection (illusory visually induced self-motion) (Teramoto et al. 2008). However, when Figliozzi and colleagues (2005) repeated their experiment with the hands crossed, rather than continuing to find an advantage on the leading hand, the facilitatory effect largely disappeared. This observation argues against an explanation based on attending to the leading hand as this hypothesis would predict that the new leading hand should now experience the advantage. Indeed, vestibular stimulation

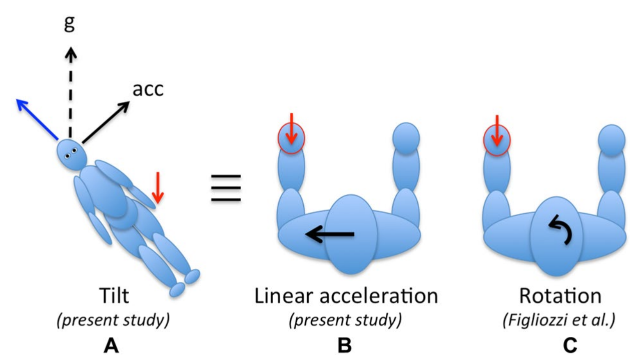

Fig. 4 **a** Redirecting gravity by tilt stimulates the vestibular system in a way comparable to acceleration towards the upward hand (**b**). **c** Figliozzi et al. (2005) demonstrated that rotation gave a temporal advantage to the leading hand during rotation. The advantaged hand is indicated by a red arrow in each case (*g* gravity, *acc* acceleration)

alone, for example, when evoked by caloric irrigation,[2] does not affect covert attention (Rorden et al. 2001). Rorden and colleagues (2001) found no shift in covert visual attention

[2] Caloric irrigation involves irrigating the external auditory meatus with warm or cold water; thus inducing convection currents in the vestibular endolymph and stimulating the vestibular apparatus without physical motion.

corresponding with the side of caloric irrigation in control participants when completing a visual task typically sensitive to attention. Furthermore, passive rotation has been shown to enhance tactile thresholds on both hands not just on the leading hand (Ferrè et al. 2014). Thus, the "leading hand advantage" associated with rotation may not be a consequence of a shift of attention when measuring direct vestibular–somatosensory interactions (Ferré et al. 2014).

There are other situations where temporal-order judgements are modified without attentional manipulation. An upright person with their arms held in front of them is able to differentiate the temporal order of touches presented on the limbs with as little as 20–60 ms stimulus onset asynchrony (Yamamoto and Kitazawa 2001). But when body posture is altered by crossing arms, tactile TOJs are inverted and spatial locations are confused (Yamamoto and Kitazawa 2001; Shore et al. 2002; Craig and Belser 2006; Azañón and Soto-Faraco 2007). A comparable confusion is found when tactile stimuli are presented to crossed fingers on the same hand (Zampini et al. 2005) and even at the end of sticks that are crossed while keeping the hands in their regular spatial position (Yamamoto et al. 2005). When the spatial arrangement of the arms is varied, the just noticeable difference (JND) between tactile stimuli decreases as the physical distance between the two arms increases (Shore et al. 2005; Kuroki et al. 2010) and increases when the arms are perceived as closer together, even virtually with the use of a mirror (Gallace and Spence 2005). A plausible explanation for these modulations which we would also like to apply to our data and to those of Figliozzi et al. (2005), is the remapping of tactile sensation from skin coordinates to body-in-space coordinates (Craig and Busey 2003; Craig 2003) resulting in an extra (time-consuming) step required for their conversion (Yamamoto and Kitazawa 2001; Shore et al. 2002). Thus, it may not be necessary to evoke attention as a cause of the leading hand advantage during rotation; instead the effect may reflect the processing of mapping tactile sensations from the skin surface into a location in space—a process that would need to take motion of the limb in space into account. We postulate that both our and Figliozzi et al.'s results may arise from such a remapping mechanism based on vestibular–somatosensory interactions at the cortical level.

Vestibular–somatosensory interactions

Coding the location of a touch in space coordinates (Azañón and Soto-Faraco 2008) is required if touch is to usefully inform us about the external world. It is impossible to experience a touch without simultaneously knowing where in space that touch occurred. Achieving this requires knowledge about body posture, to know where in space the body part that received the touch is located. Such knowledge comes from a variety of sources including proprioception and vision (Longo et al. 2015). But making the jump to spatial coordinates, as opposed to body coordinates, requires additional knowledge concerning the body's position and orientation in space. The vestibular system can provide some of this information and has been shown to be an important input into the process of tactile localization (Zarzecki et al. 1983). Cortically, the vestibular system has a large distribution of projections that are typically multimodal (Lopez and Blanke 2011). Cortical activation related to body rotation, translation and tilt has been seen in the retro-insular cortex, parietal operculum and posterior insula regions where afferents from the semicircular canals and otoliths converge according to a comprehensive activation likelihood estimation meta-analysis of several neuroimaging studies (Lopez et al. 2012).

Tactile localization in space can only occur after vestibular–tactile multisensory interactions that allow the brain to calculate the location of the relevant body part. Alterations of any of the inputs may affect the process. Vestibular activation has been shown to modulate tactile detection thresholds (Ferrè et al. 2011, 2014); but why might vestibular activation have an effect on the point of subjective simultaneity (PSS) for touches on the hands? Simultaneity cannot be assessed from physical properties of stimuli, as the brain has no direct access to this information. Instead the brain must rely on sensory information, which is necessarily delayed both by physical factors and by sensory processing times. The brain, therefore, needs to learn about simultaneity from experience and it has been shown that the process is flexible (Fujisaki et al. 2004; Harrar and Harris 2008). It might be argued that perceiving touches on the two hands does not require such temporal flexibility because the distance from each hand to the brain is the same. However, being touched on the two hands is a special case. The system needs to be able to cope with touches anywhere on the body and the variations in transmission time associated with the distance that the information has to travel to reach the brain (Harrar and Harris 2005). We postulate that our "leading hand advantage" is an outcome of such central processing.

Future studies should include comparison with no-tilt, no-GVS and no-rotation conditions to investigate the possibility of natural biases that may be present independently of vestibular activation. Asymmetric activation of the vestibular system created by tilting, GVS or rotation may underlie the observed change in the perceived timing of tactile events. For example, remapping of a tactile location into a new part of space not previously occupied by a body part may be given priority by the remapping process, perhaps related to supporting exploratory behavior. It is possible that such an effect may subsequently direct attention to different body parts (Ferrè and Haggard 2015), but this would be a consequence of vestibular changes resulting from a remapping process and not the cause of them.

Acknowledgements We sincerely thank all of our participants for volunteering in this study, and Ben Shachar for his assistance in testing participants. This research was supported by the Natural Sciences and Engineering Research Council of Canada (46271-2015) Discovery Grant to LRH. SSM is supported by the Natural Sciences and Engineering Research Council of Canada, Toronto Rehabilitation's TD Graduate Scholarship for People with Disabilities, and York University.

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