RESEARCH ARTICLE

Reference frames for coding touch location depend on the task

Lisa M. Pritchett · Michael J. Carnevale · Laurence R. Harris

Received: 17 July 2012/Accepted: 11 August 2012/Published online: 1 September 2012 © Springer-Verlag 2012

Abstract The position of gaze (eye plus head position) relative to body is known to alter the perceived locations of sensory targets. This effect suggests that perceptual space is at least partially coded in a gaze-centered reference frame. However, the direction of the effects reported has not been consistent. Here, we investigate the cause of a discrepancy between reported directions of shift in tactile localization related to head position. We demonstrate that head eccentricity can cause errors in touch localization in either the same or opposite direction as the head is turned depending on the procedure used. When head position is held eccentric during both the presentation of a touch and the response, there is a shift in the direction opposite to the head. When the head is returned to center before reporting, the shift is in the same direction as head eccentricity. We rule out a number of possible explanations for the difference and conclude that when the head is moved between a touch and response the touch is coded in a predominantly gaze-centered reference frame, whereas when the head remains stationary a predominantly body-centered reference frame is used. The mechanism underlying these displacements in perceived location is proposed to involve an underestimated gaze signal. We propose a model demonstrating how this single neural error could cause localization errors in either direction depending on whether the gaze or body midline is used as a reference. This model

L. M. Pritchett (🖂) Department of Psychology, York University, Toronto, ON M3J 1P3, Canada e-mail: Impritch@yorku.ca may be useful in explaining gaze-related localization errors in other modalities.

Keywords Tactile localization · Reference frames · Head · Gaze · Body representation · Posture

Introduction

The multiple sensory modalities contribute spatial information each in a unique reference frame. Visual stimuli are initially coded in retinal coordinates, tactile stimuli relative to the skin surface, and auditory stimuli relative to the head. These initial representations of stimulus location are constrained by the anatomy of sensory receptors and need to be converted to other reference frames to provide perceptually useful information such as location in space. Higher levels of processing combine information arising from different sensory modalities into a single coordinate system or else some hybrid system of multiple simultaneous reference frames (Andersen et al. 1993; Cohen and Andersen 2002; Colby 1998; Deneve and Pouget 2004). Previous studies have suggested that a gaze-based reference frame may be the most likely candidate (Azañón et al. 2010; Bolognini and Maravita 2007; Harrar and Harris 2009, 2010; Knudsen and Knudsen 1985; Röder et al. 2004, 2008).

If stimuli are coded relative to gaze, then a gaze signal is required to transform the location from the reference frame of the end organs to the central representation. Any systematic errors in coding the position of gaze would, therefore, shift the perceived location of stimuli. Indeed, several authors have demonstrated that eye position is underestimated (Harris and Smith 2008; Hill 1972; Morgan 1978) and corresponding systematic errors in localizing

L. M. Pritchett · M. J. Carnevale · L. R. Harris Centre for Vision Research, York University, Toronto, ON, Canada

various stimuli have been reported related to eye position (auditory: Lewald and Ehrenstein 1996a, b; Weerts and Thurlow 1971; visual: Bock 1986; Fiehler et al. 2010; Henriques et al. 1998; Lewald 1998; tactile: Harrar and Harris 2009, 2010). Similarly, eccentric head orientation has also been found to produce errors in localizing auditory (Lewald and Ehrenstein 1998; Lewald et al. 2000; van Goossens and Opstal 1999), visual (Kopinska and Harris 2003; Wexler 2003), and tactile stimuli (Ho and Spence 2007; Pritchett and Harris 2011).

The effects of eye and head position on tactile (Pritchett and Harris 2011) and auditory (Lewald and Ehrenstein 1998) localization are equivalent. This equivalency suggests that head and eye position may be combined into an encompassing gaze signal that may then form the reference for spatial locations. This is consistent with research showing that several monkey cortical and subcortical areas use a single signal for gaze where eye and head information is combined (Martinez-Trujillo et al. 2003).

Although it is known that stimuli are systematically mislocalized when gaze is eccentric, there are inconsistent reports on the nature and direction of these localization errors. In auditory perception, most reports are of perceived locations shifting opposite to eccentric eye or head position (van Goossens and Opstal 1999; Lewald and Ehrenstein 1996a, 1998; Lewald 1998; Lewald et al. 2000) although there are some reports of the perceived location of auditory targets shifting in the same direction as gaze (Lewald and Ehrenstein 1996b; Weerts and Thurlow 1971).

Most pertinent to the current study are the contrasting directions of tactile mislocalization found in response to head position. Ho and Spence (2007) reported that when participants localized vibrotactile stimuli presented on the waist while holding an eccentric head orientation, tactile localization was biased in the direction opposite to head position. In contrast, results from this laboratory have demonstrated that brief touches presented on the forearm were mislocalized in the same direction as eye (Harrar and Harris 2009, 2010) and head position (Pritchett and Harris 2011). The current study was therefore conducted to resolve this discrepancy.

Comparing the studies on tactile localization errors related to head position (Ho and Spence 2007 vs. Pritchett and Harris 2011) is not straightforward as the studies differ along important dimensions. First, different types of touch stimuli were used and thus different sensory pathways could potentially lead to differences in the subsequent position coding. Ho and Spence (2007) used vibrotactile stimuli at 250 Hz which are primarily detected by the deep layer Pacinian corpuscles that have large receptive fields (Jänig et al. 1968). Pritchett and Harris (2011) used brief discrete solenoid touches that are detected primarily by surface layer Merkel receptors with receptive fields substantially smaller than Pacinian corpuscles (Johansson and Vallbo 1979). There is evidence that information from these different receptor types may be coded in different cortical maps (Friedman et al. 2004) that may underlie the different results reported using these different tactile stimuli. Second, Ho and Spence (2007) tested tactile localization on the front of the waist while Pritchett and Harris (2011) tested the forearm. These two body parts utilize different body landmarks as tactile reference frames, which may lead to unique localization biases (Cholewiak and Collins 2003 for abdomen, Cholewiak 2004 for forearm). Finally, in addition to type and place of stimulation, the studies used different experimental procedures. Different task demands could lead to different locationencoding mechanisms. In the study by Ho and Spence (2007) participants both received stimuli and made their responses while their heads were eccentrically positioned, while Pritchett and Harris (2011) had participants return to straight ahead before responding.

We first replicated and extended the Ho and Spence (2007) studies using the same kind of stimulation (250 Hz vibration) and body part (torso) with the participants both receiving stimuli and making responses with an eccentric head position. In Experiment 2, we used the same stimuli and body part but a protocol similar to that of Pritchett and Harris (2011) where participants received tactile stimuli in an eccentric head position but returned to center before responding. Results indicated that it was the type of task that determined the direction of localization errors and ruled out the other possible factors listed above.

Experiment 1 and 2 method

Participants

Eight participants (4 male, 4 female, mean age 28 years) volunteered to participate in Experiment 1. Experiment 2 had eight participants (4 male, 4 female, mean age 31 years), six of whom also participated in Experiment 1. All reported having a normal sense of touch and normal or corrected-to-normal vision. All experiments were approved by the ethics board of York University and followed the guidelines of Helsinki.

Apparatus

The vibrotactile stimuli were presented using an array of eight tactors (Model C2, Engineering Acoustics, Florida, USA) for all experiments. The tactors were mounted on a belt worn around the participant's waist. The eight-tactor array was centered on the participant's belly button with the center of each tactor 4 cm from the next. The vibrotactile stimuli were at 250 Hz and were of 50 ms duration. The intensity of each touch was randomly chosen from four possibilities (37.5, 50, 62.5, or 75 % of maximum intensity) in order to keep participants from distinguishing the tactor locations by learning any subtle differences in their intensities.

Head and eye position were manipulated by fixation points positioned in space and a laser mounted on a hat worn on the participant's head. During testing participants were seated in a darkened room in a chair chosen for its high supportive back extending above the head. Participants maintained a seated upright posture in all experiments. Each experiment used a slightly different set up of chair position and fixation points to facilitate the different experimental procedures (see Fig. 1). The details specific to each procedure are described below.

A 21-inch LCD computer monitor was used to display a visual scale (described below) for recording the perceived location of touches and to display fixation points. For all experiments, the computer monitor was 55 cm from the viewer when the visual scale was presented. Participants used a cordless optical mouse to indicate the perceived location of the touch on the scale.

Visual scale for reporting perceived touch location

Before beginning each experiment, the vibrotactile stimuli were delivered from each tactor in order from the furthest right to the furthest left. Participants were instructed to memorize the location of the end points of the array and to use the end points of a white bar $(35.3^{\circ} \times 0.62^{\circ} \text{ visual})$ angle) presented on the screen to represent those locations (as in Ho and Spence 2007). Participants reported the perceived location of touches by moving a sliding bar $(0.51^{\circ} \times 0.77^{\circ}$ visual angle) along the scale by means of a mouse. The bar could be moved by dragging it, by clicking on the desired location on the scale, or by clicking the left or right spaces at the end of the scale. When the participant was happy with the positioning of the vertical bar they clicked on an "OK" button at the bottom of the screen. This response method is the same as used by Ho and Spence (2007).

The unique details for each experiment are described below.

Experiment 1

The first experiment was a replication of Ho and Spence (2007). One change from their protocol was the use of the head laser to enable participants to reliably position their heads in all conditions. Participants were arranged with their head either 90° left, 90° right or straight with the screen straight ahead of them (Fig. 1). Each trial began

with a fixation cross displayed centered on the screen, the head-mounted laser was illuminated and the participant fine adjusted their own head position. This was done to make the conditions as similar as possible between all the experiments. After 2 s the fixation cross and laser were turned off and a vibrotactile stimulus was presented from a randomly chosen tactor along the array. The visual scale was displayed on the screen 500 ms later and the participant indicated the perceived location of the touch. Clicking the "OK" button led to the beginning of the next trial. Each of the eight tactors was presented 12 times which took about 7 min. Once the block was complete, the experimenter moved the chair into the next position (see Fig. 1) and the next block of trials commenced until all three head conditions had been run. Running order was counterbalanced across participants.

Experiment 2

The second experiment followed a procedure similar to Pritchett and Harris (2011) but with the vibrotactile stimulation on the torso and the response measure (the visual scale) that was used by Ho and Spence (2007). The chair was positioned so that the participant looked at the computer monitor with their head and eyes straight ahead. Target LEDs to indicate required eye and head position were positioned 90° to the left and 90° to the right of the participant.

Each trial began by directing the participant to the fixation position for that trial. If it was a head-centered trial, the fixation cross on the screen was presented. If it was a left or right head condition trial, an arrow was displayed on the screen pointing in the appropriate direction, left or right. The participant was given 2 s to turn their head to the specified direction and to align their head-mounted laser to the illuminated LED at 90°. After 2 s the fixation point was removed, the head laser turned off, and the vibrotactile stimuli were presented from a randomly chosen location on the tactor array. The head laser then turned on again and the participant turned their head back to align the laser with a centered fixation point before reporting the location of the touch on the visual scale. The next trial began when they clicked the "OK" button. Each of the eight tactors was presented 12 times for each head condition for a total of 288 trials. The experiment was approximately 21 min in duration.

Data analysis

Participants reported the perceived location of touches on a linear scale. The furthest left end was coded as 0, and the furthest right end was coded as 1. Data were transformed into cm from navel by multiplying by 28 cm, the distance



Fig. 1 Head and body positions during touch delivery and response are illustrated for each experiment. In Experiment 1, head position was manipulated in a blocked design as in Ho and Spence 2007, the head was eccentric for touch delivery and during reporting perceived touch location. In Experiment 2, head position was manipulated in a randomized design, and the head was always returned to the center to report touch location. In Experiment 3, the touch was always delivered with head centered and the

head then turned before responding. In **a**, **c** and **e** perceived locations (related to the body midline at 0) of the 8 tactors under head left (*dotted line*, *square symbol*), head right (*dashed line*, *triangle symbol*) and head center (*solid line*, *diamond symbol*) are shown for each of three experiments. Standard error bars are the size of the symbols. In **b**, **d** and **f** the difference between the head-eccentric and head-centered locations are illustrated for the three experiments. *Error bars* show one standard error of the mean

between the first and last tactor and subtracting 14. For each participant the mean reported position for each touch location at each head position was averaged over 12 trials. This perceived location data were subjected to a two-way repeated-measures ANOVA. The effect of head position was quantified by calculating the difference between the perceived location of a touch during the eccentric head condition and the perceived position of the same touch during the centered head condition. This absolute difference from center data was used as an index of the magnitude of the effect of head position. It was also subjected to a two-way repeated-measures ANOVA for each of the three experiments.

Experiment 1 and 2 results

Experiment 1

The mean perceived location of touch with the head held eccentric is plotted in Fig. 1a. A significant effect of touch location (F(7, 49) = 248.67, p < 0.001) confirmed that the touch locations could be discriminated. A main effect of head position was also found (F (2, 14) = 15.92,p < 0.001) indicating that the perceived position of a touch was influenced by head position. A trend analysis indicated that the effect of head position was linear (F(1, 7) = 25.06), p = 0.002), meaning that left and right head position affected touch location similarly in magnitude but in opposite directions. Touches were perceived furthest to the left in the right head condition (M = 1.03 cm left), more medially in the centered head condition (M = 0.12 cm)left), and furthest to the right in the left head condition (M = 0.60 cm right). There was not a significant interaction of head position and touch location (F(14, 98) = 1.45,p = 0.147).

Further analysis of the effect of head position was conducted using the difference between the perceived position of each touch during the head-eccentric trials (left or right) and the perceived position of the same touch during the head-centered trials (Fig. 1b). The average unsigned difference between eccentric and centered head position was used as an index of the magnitude of the effect of head position. These data were subjected to a two-way repeated-measures ANOVA. The main effect of head position was not significant (F < 1, ns), indicating that left and right head position effect touch location similarly in magnitude. Additionally, the touch location main effect was not significant (F(7, 49) = 2.23, p = 0.11), suggesting that the magnitude of the effect was the same across touch locations. However, a significant interaction of touch location by head position was found (F(7, 49) = 5.75,p = 0.013). As can be seen in Fig. 1b, head position had a larger effect on touches that were located on the same side of space. Thus, when the head was positioned to the left the touches on the left were affected more (M = 11.3 mm left tactors, M = 6.0 mm right tactors) and when the head was positioned to the right the touches on the right were affected more (M = 16.0 mm right tactors, M = 8.7 mm left tactors).

We hypothesized that holding the head eccentrically for several minutes might lead to some kind of adaptation, which might affect the coding of touch location. Therefore, we calculated correlations between the perceived position of touch and the time in seconds since the participant had began that head condition. Pooling across and controlling for touch location, no evidence for a drift in perceived position of touch was found for either left (r (766) = -0.009, p = 0.80) or right (r (766) = 0.055, p = 0.13) head positions.

Experiment 2

The localization data from Experiment 2 where the head returned to center before the response was made is plotted in Fig. 1c. These data were analyzed using a two-way repeated-measures ANOVA. A significant effect of tactor location (F (7, 49) = 244.83, p < 0.001) confirmed that touch location could be discriminated. A significant effect of head position (F(2, 14) = 17.36, p = 0.004) indicated that the perceived position of a touch was affected by head position. As in Experiment 1, the effect of head position was found to be linear (F (1, 7) = 17.82, p = 0.004), indicating that left and right head positions affected perceived touch location equally in magnitude but opposite in direction. Touches were perceived furthest to the left when the head was positioned to the left (M = 1.13 cm left), more medially when the head was centered (M = 0.11 cm left), and to the right when the head was right (M = 1.06 cm right). A significant interaction of head position by touch location was found (F(14, 98) = 8.57,p < 0.001), indicating that the effect of head position was different at the different touch locations. This effect is further explored in the analysis of the difference-fromcenter data (Fig. 1d).

The unsigned difference data were subjected to the twoway repeated-measures ANOVA. The main effect for head location was not significant (F(1, 7) = 2.31, p = 0.17), indicating that the size of the head orientation effect was equal for the left (M = 1.14 cm) and right (M = 1.34 cm) head orientations. A main effect of tactor location indicated that the effect of head position was different depending on the location of the touch (F(7, 49) = 6.29, p = 0.003). The head position by touch location interaction was also significant (F(7,49) = 9.062, p = 0.002). This indicated that touches on the same side as the eccentric head position were affected more (head left, left touches M = 1.62 cm; head right, right touches M = 1.94 cm) than those on the opposite side (head left, right touches M = 0.66; head right, left touches M = 0.74 cm).

Experiment 1 and 2 discussion

The results of Experiment 1 replicate Ho and Spence (2007), showing that when touches are localized under eccentric head conditions the perception is shifted in the opposite direction of head eccentricity. The results of Experiment 2 are consistent with the results of Pritchett and Harris (2011), demonstrating that when a touch is applied under eccentric head position but reported under centered head position the perception is shifted in the same direction of head eccentricity.

We can therefore conclude that the opposing results are not due to the different body parts tested (torso vs. arm) or to the type of touch stimuli used (vibration or tap). We can also rule out adaptation affects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time.

Other differences between the two procedures are that the scale used for response in Experiment 1 was viewed with the head-eccentric and that it was necessary to remember and update the location of the touch after moving the head in Experiment 2. Experiment 3 was therefore designed to test the possible contribution of these two factors. In Experiment 3, touches were delivered while the head was centered, but the response was made with head-eccentric; thus, the scale was viewed with headeccentric (as in exp 1), and it was necessary to remember the location of the touch during a movement (as in exp 2), but the touches were delivered with the head and eyes centered.

Experiment 3

Participants

Eight participants (4 males, 4 females, mean age 28 years) completed Experiment 3. Five of them had also completed both Experiments 1 and 2.

Method

Participants were arranged with their body pointing either to the left, right, or straight toward the screen for each block of trials. In conditions where the participant was not facing the monitor, an LED was placed directly in front of the participant as a fixation point; when facing the monitor, a cross displayed on the screen was used. To begin each trial the central fixation point and the head-mounted laser were illuminated and participants aligned their eyes and head with this point. After 2 s the fixation and headmounted laser were turned off, and a touch was presented from a randomly chosen tactor on the array. Next, the laser and a fixation cross on the computer monitor were illuminated. Participants were given 2 s to align the head laser with the fixation cross. Next the visual scale was displayed on the screen. The participant reported the perceived location of the touch on the scale and clicked the "OK" button. This triggered the beginning of the next trial. The participant turned their head back to the centered location and aligned the laser and their eyes with the fixation point ready for the next trial. Each of the 8 tactors was presented 12 times before the block terminated in approximately 7 min. The chair was then repositioned, and the next head condition was run until all three had been completed. Conditions were counterbalanced across participants.

Results

The localization data from Experiment 3 are plotted in Fig. 1e, f and were analyzed using a two-way repeatedmeasures ANOVA. The main effect of touch position was significant (F(7, 49) = 539.10, p < 0.001), indicating that the touches could be discriminated. The main effect of head position was not significant (F(2, 14) = 2.56, p = 0.12), indicating that the touches were perceived similarly regardless of the position of the head at the time when the location was reported. Finally, the touch location by head position interaction was not significant (F(14, 98) = 0.77, p = 0.54). These results indicate that there was no effect of head position on the response. This suggests that there were no effects of eccentrically viewing the scale in Experiment 1 or of moving the head in Experiment 2.

General discussion

The experiments described here confirm that there is a systematic effect of head position on perceived touch location and that this depends critically on the procedure used to measure it. We have successfully reproduced the effect of shifting touch in the opposite direction of eccentric head position when following the procedure of Ho and Spence (2007). And we replicate the effect of shifting perceived touch location in the same direction as head position when following procedures more similar to Pritchett and Harris (2011).

The present experiments allow us to rule out some explanations for the opposing effects. The difference is not





Fig. 2 Model of how an eccentric head position may shift perceived touch location in either the same or opposite direction as head position. *Solid lines* represent accurate locations, *dashed lines* represent perceived locations (of body and gaze in \mathbf{a} and of touch in \mathbf{b} , \mathbf{c}). \mathbf{a} Illustrates different consequences of an underestimated gaze angle. The perceived body center is shifted toward gaze and

perceived gaze is shifted toward the body (see text for details). **b** The result of coding relative to a shifted body midline is that the perceived location of touch is shifted in the direction opposite to head position. **c** The result of coding relative to a shifted gaze direction is that the perceived location of touch is shifted in the same direction as head position

simply due to type of touch (vibration or tap) or to the body part tested (torso vs. arm). We can rule out adaptation effects during the blocked head condition trials of Experiment 1 as no systematic drift in perceived touch location was found across time. Finally, the null results of Experiment 3 demonstrate that the difference cannot be simply explained as resulting from eccentric viewing of the scale in Experiment 1, or from moving the head in Experiment 2. Instead, the results point to different mechanisms for encoding, storing, or retrieving touch location in the two experimental situations.

Lewald and Ehrenstein (1996a) argued that auditory localization was only found to move in the direction opposite to gaze when a visual reference was used and that the effect of gaze on visual localization was larger than it was on auditory. This combination can, therefore, make it appear as if auditory localization is shifted in the same direction as gaze because of the opposing effects of gaze on the sound stimulus and on the visual reference used to measure it. Our control study rules out effects of the probe scale as an important contributor to the results reported here. We offer another explanation for opposite effects of gaze on the perceived location of touches in different situations.

Why are gaze-induced localization errors found in opposing directions?

Holding the eyes eccentrically shifts the perceived body straight ahead in the same direction as the eyes (Harris and Smith 2008; Hill 1972; Morgan 1978). Similar results have also been found when the head rather than the eyes is held eccentrically (Yamaguchi and Kaneko 2007). That is, the angle between the body and eye straight ahead is underestimated. As shown in Fig. 2a, an underestimated representation

of gaze eccentricity can be described as perceiving the body straight ahead as shifting toward gaze, that is, in the same direction as head position (as in Hill 1972 Experiment 2 and 3). Or, it may be regarded as the location of gaze moving closer to the actual body, that is, a shift in the direction opposite to head position (as in Hill 1972 Experiment 4). Thus, which direction the perceived touch location shifts may be dependent on the frame of reference (body or gaze) to which it is attached.

As shown in Fig. 2b, if the body midline were shifted in the same direction as head position, any location coded relative to body midline would show errors in the direction opposite to head position. In contrast, Fig. 2c shows that if perceived gaze were shifted in the opposite direction of head position, then any stimuli coded relative to gaze would show errors in the same direction as eccentric position. We therefore conclude that the opposing effects of gaze eccentricity described here may be the result of coding stimuli relative to the body in Experiment 1 and relative to gaze in Experiment 2.

This explanation is consistent with work in the auditory domain. Numerous reports exist of auditory perception shifting in the direction opposite to gaze (Kopinska and Harris 2003; Lewald and Ehrenstein 1996a, b, 1998). The explanation offered for this shift has been that it is linked to a shifted perceived median of the head. When participants were asked to adjust a dichotic sound until it sounded as if it were in the middle of the head while their eyes (Lewald and Ehrenstein 1996a, 1998) or head (Kopinska and Harris 2003; Lewald and Ehrenstien 1998) were turned, participants consistently adjusted the sound such that it was more intense in the ear on the same side as gaze. This indicated that they perceived the sound as shifted in the direction opposite to gaze.

Mechanism

Touch location is initially coded by a labeled-line system where the nerve endings in the skin transmit information to the primary somatosensory tactile homunculus. If the conscious perception of touch arose from that representation, then no systematic errors related to gaze position would be expected: perceived touch location should correspond directly to actual touch location. However, the parietal cortex contains many spatial representations that are responsive to tactile as well as visual and auditory stimulation (Avillac et al. 2005; Cohen and Andersen 2002; Galati et al. 2001; Mullette-Gillman et al. 2005; Schlack et al. 2005). These multisensory maps are thought to code space in different coordinate systems. For example, the lateral intraparietal area (LIP) of the monkey seems to code space not only in an eye-centered representation but also relative to head-centered and intermediate reference frames (Mullette-Gillman et al. 2005; Stricanne et al. 1996), while the ventral intraparietal area (VIP) seems to code space in a body-centered representation (Sereno and Huang 2006). Converting touch information from a body representation into head, eye, or gaze frames requires taking eye and head position into account. Inaccuracies in the representation of head, gaze, or eye position thus get passed along as tactile space is converted into such a frame.

Why are our effects asymmetrical?

A noticeable feature of our data is the asymmetry of the effects on the left and right sides of the body (Fig. 1b, d). When the head was turned to the left the touches on the left side of the body were more affected, and when the head was turned to the right the touches on the right side of the body were more affected. This is true for both Experiment 1 and 2 as can be clearly seen in the data of Fig. 1a, b. It seems that only the touches on the same side of the body as the direction of gaze are affected. When interpreted in the context of the frame conversion model, this might suggest that only touches within the current visual field are recoded relative to the body midline or gaze. The non-affected touches, which are outside the visual field, may remain coded in the original somatotopic reference frame. This is consistent with other work showing that vision affects coding of touch location (Haggard et al. 2007; Kennett et al. 2001; Sathian and Zangaladze 2002; Tipper et al. 2001). Another possibility is that touches on the side of the body opposite to gaze are coded in both gaze- and body-centered coordinates simultaneously with equal weighting. In that case, the opposite-directed errors could cancel out.

Conclusion

The results of the experiments described here suggest that perceived locations of tactile stimuli are coded differently depending on the situation. In the static design of Experiment 1 and Ho and Spence (2007), touch location may be coded relative to the body, while in the more dynamic conditions of Experiment 2 and Pritchett and Harris (2011), touch may be coded relative to gaze. This may be connected to using a more centralized, gaze-centered reference frame when the locations of touches need to be remembered and reconstructed after a move. These findings may have important applications in designing working environments as spatial representations may be different depending on context and task demands. Drivers, pilots or users of backhoes, for example, may interpret the location of tactile objects differently depending on the situation and where they are looking. These findings may improve our understanding of the different patterns of spatial neglect that are seen in parietal brain damage patients attempting different tasks (see Colby 1998) and may have implications for the blind.

Acknowledgments This research was funded by a Discovery Grant to Laurence Harris from the Natural Sciences and Engineering Research Council of Canada.

References

- Andersen RA, Snyder LH, Li C-S, Stricanne B (1993) Coordinate transformations in the representation of spatial information. Curr Opin Neurobiol 3:171–176. doi:10.1016/0959-4388(93)90206-E
- Avillac M, Deneve S, Olivier E, Pouget A, Duhamel J-R (2005) Reference frames for representing visual and tactile locations in parietal cortex. Nat Neurosci 8:941–949. doi:10.1038/nn1480
- Azañón E, Longo MR, Soto-Faraco S, Haggard P (2010) The posterior parietal cortex remaps touch into external space. Curr Biol 20:1304–1309. doi:10.1016/j.cub.2010.05.063
- Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. Exp Brain Res 64:476–482. doi:10.1007/BF00340484
- Bolognini N, Maravita A (2007) Proprioceptive alignment of visual and somatosensory maps in the posterior parietal cortex. Curr Biol 17:1890–1895. doi:10.1016/j.cub.2007.09.057
- Cholewiak RW (2004) Vibrotactile localization on the abdomen: effects of place and space. Percept Psychophys 66:970–987. doi: 10.3758/BF03194989
- Cholewiak RW, Collins AA (2003) Vibrotactile localization on the arm: effects of place, space, and age. Percept Psychophys 65:1058–1077. doi:10.3758/BF03194834
- Cohen YE, Andersen RA (2002) A common reference frame for movement plans in the posterior parietal cortex. Nat Rev Neurosci 3:553–562. doi:10.1038/nrn873
- Colby CL (1998) Action-oriented spatial reference frames in cortex. Neuron 20:15–24. doi:10.1016/S0896-6273(00)80429-8
- Deneve S, Pouget A (2004) Bayesian multisensory integration and cross-modal spatial links. J Physiology Paris 98:249–258. doi: 10.1016/j.jphysparis.2004.03.011

- Fiehler K, Rösler F, Henriques D (2010) Interaction between gaze and visual and proprioceptive position judgements. Exp Brain Res 203:485–498. doi:10.1007/s00221-010-2251-1
- Friedman RM, Chen LM, Roe AW (2004) Modality maps within primate somatosensory cortex. Proc Natl Acad Sci USA 101:12724–12729. doi:10.1073/pnas.0404884101
- Galati G, Committeri G, Sanes JN, Pizzamiglio L (2001) Spatial coding of visual and somatic sensory information in bodycentered coordinates. Eur J Neurosci 14:737–746. doi:10.1046 /j.0953-816x.2001.01674.x
- Haggard P, Christakou A, Serino A (2007) Viewing the body modulates tactile receptive fields. Exp Brain Res 180:187–193. doi:10.1007/s00221-007-0971-7
- Harrar V, Harris LR (2009) Eye position affects the perceived location of touch. Exp Brain Res 198:403–410. doi:10.1007/ s00221-009-1884-4
- Harrar V, Harris LR (2010) Touch used to guide action is partially coded in a visual reference frame. Exp Brain Res 203:615–620. doi:10.1007/s00221-010-2252-0
- Harris LR, Smith A (2008) The coding of perceived eye position. Exp Brain Res 187:429–437. doi:10.1007/s00221-008-1313-0
- Henriques DYP, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. J Neurosci 18:1583–1594
- Hill AL (1972) Direction constancy. Percept Psychophys 11:175–178. doi:10.3758/BF03210370
- Ho C, Spence C (2007) Head orientation biases tactile localization. Brain Res 1144:136–141. doi:10.1016/j.brainres.2007.01.091
- Jänig W, Schmidt RF, Zimmermann M (1968) Single unit responses and the total afferent outflow from the cat's foot pad upon mechanical stimulation. Exp Brain Res 6:100–115. doi:10.1007/ BF00239165
- Johansson RS, Vallbo AB (1979) Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. J Physiol 286:283–300
- Kennett S, Taylor-Clarke M, Haggard P (2001) Noninformative vision improves the spatial resolution of touch in humans. Curr Biol 11:1188–1191
- Knudsen EI, Knudsen PF (1985) Vision guides the adjustment of auditory localization in young barn owls. Science 230:545–548. doi:10.1126/science.4048948
- Kopinska A, Harris LR (2003) Spatial representation in body coordinates: evidence from errors in remembering positions of visual and auditory targets after active eye, head, and body movements. Can J Exp Pshychol 57:23–37. doi:10.1037/h0087410
- Lewald J (1998) The effect of gaze eccentricity on perceived sound direction and its relation to visual localization. Hearing Res 115:206–216. doi:10.1016/S0378-5955(97)00190-1
- Lewald J, Ehrenstein WH (1996a) Auditory-visual shift in localization depending on gaze direction. NeuroReport 7:1929–1932
- Lewald J, Ehrenstein WH (1996b) The effect of eye position on auditory lateralization. Exp Brain Res 108:473–485. doi:10.1007/ BF00227270
- Lewald J, Ehrenstein WH (1998) Influence of head-to-trunk position on sound lateralization. Exp Brain Res 121:230–238. doi: 10.1007/s002210050456

- Lewald J, Dörrscheidt GJ, Ehrenstein WH (2000) Sound localization with eccentric head position. Behav Brain Res 108:105–125. doi: 10.1016/S0166-4328(99)00141-2
- Martinez-Trujillo JC, Klier EM, Wang H, Crawford JD (2003) Contribution of head movement to gaze command coding in monkey frontal cortex and superior colliculus. J Neurophysiol 90:2770–2776. doi:10.1152/jn.00330.2003
- Morgan CL (1978) Constancy of egocentric visual direction. Percept Psychophys 23:61–68. doi:10.3758/BF03214296
- Mullette-Gillman OA, Cohen YE, Groh JM (2005) Eye-centered, head-centered, and complex coding of visual and auditory targets in the intraparietal sulcus. J Neurophysiol 94:2331–2352. doi: 10.1152/jn.00021.2005
- Pritchett LM, Harris LR (2011) Perceived touch location is coded using a gaze signal. Exp Brain Res 213:229–234. doi:10.1007/ s00221-011-2713-0
- Röder B, Rösler F, Spence C (2004) Early vision impairs tactile perception in the blind. Curr Biol 14:121–124. doi:10.1016/ j.cub.2003.12.054
- Röder B, Föcker J, Hötting K, Spence C (2008) Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans. Eur J Neurosci 28:475–483. doi:10.1111/j.1460-9568.2008.06352.x
- Sathian K, Zangaladze A (2002) Feeling with the mind's eye: contribution of visual cortex to tactile perception. Behav Brain Res 135:127–132. doi:10.1016/S0166-4328(02)00141-9
- Schlack A, Sterbing-D'Angelo SJ, Hartung K, Hoffmann K-P, Bremmer F (2005) Multisensory space representations in the macaque ventral intraparietal area. J Neurosci 25:4616–4625. doi:10.1523/JNEUROSCI.0455-05.2005
- Sereno MI, Huang R-S (2006) A human parietal face area contains aligned head-centered visual and tactile maps. Nat Neurosci 9:1337–1343. doi:10.1038/nn1777
- Stricanne B, Andersen RA, Mazzoni P (1996) Eye-centered, headcentered, and intermediate coding of remembered sound locations in area LIP. J Neurophysiol 76:2071–2076
- Tipper S, Phillips N, Dancer C, Lloyd D, Howard L, McGlone F (2001) Vision influences tactile perception at body sites that cannot be viewed directly. Exp Brain Res 139:160–167. doi: 10.1007/s002210100743
- van Goossens HHLM, Opstal AJ (1999) Influence of head position on the spatial representation of acoustic targets. J Neurophysiol 81:2720–2736
- Weerts TC, Thurlow WR (1971) The effects of eye position and expectation on sound localization. Percept Psychophys 9:35–39. doi:10.3758/BF03213025
- Wexler M (2003) Voluntary head movement and allocentric perception of space. Psychol Sci 14:340–346. doi:10.1111/1467-9280.14491
- Yamaguchi M, Kaneko H (2007) Integration system of head, eye, and retinal position signals for perceptual direction. Opt Rev 14:411–415. doi:10.1007/s10043-007-0411-8