

Touch used to guide action is partially coded in a visual reference frame

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Received: 31 January 2010 / Accepted: 8 April 2010 / Published online: 29 April 2010
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Abstract The perceived location of touch on the skin is affected by the position of the eyes in the head, suggesting that it is at least partially coded in a visual reference frame. This observation was made by comparing the perceived location of a touch to a visual reference. Here, we ask whether the location of a touch is coded differently when it guides an action. We tested the perceived position of four touches on the arm (~5 cm apart) while participants adopted one of four eccentric fixations. A touch-sensitive screen was positioned over the stimulated left arm and subjects pointed, using their right arm, to the perceived touch location. The location that subjects pointed to varied with eye position, shifting by 0.016 cm/deg in the direction of eye eccentricity. The dependence on eye position suggests that tactile coding for action is also at least partially coded in a visual reference frame, as it is for perception.

Keywords Touch · Gaze · Fixation · Localization · Action · Perception · Reference frames · Visual coordinates · Reaching · Haptic · Pointing

Introduction

The discovery of stimulus localization errors in multiple modalities systematically related to the position of the

eyes has led to the hypothesis that the locations of stimuli perceived in several modalities are all coded in an egocentric visual reference frame (Cohen and Andersen 2000). When the head is not centred on the body or the eyes are not centred in the head, there are errors in the perceived positions of objects sensed visually (Kopinska and Harris 2003; Rossetti et al. 1994; Harris and Smith 2008), auditorily (Lewald and Ehrenstein 1996; Lewald and Ehrenstein 1998; Weerts and Thurlow 1971), and proprioceptively (Henriques et al. 1998; see Cohen and Andersen 2002 for a review). Recent evidence on the perceived location of touch shows a similar dependence on eye-in-head position and supports the suggestion that an eye-centred frame of reference is universal. Ho and Spence (2007) found that the location of a touch on the body is affected by the position of the head on the body, and the present authors have reported eye-position-related tactile shifts for eccentric eye positions (Harrar and Harris 2009). These effects are found when touch is measured perceptually. Tactile information can be used for two distinctly different purposes: it can report the location of a touch on the skin as part of the tactile exploration of the world, or it can be used to guide actions.

Since Goodale and Milner's (1992) letter-posting experiments, considerable evidence has accrued for at least a partial dissociation between the processing of visual information for the control of action and processing for perception. In their study, Goodale and Milner presented data from two sets of clinical patients with different functional disabilities. One subject was not able to perceptually match the angle of a mailbox opening with a line but was able to flawlessly post a letter (requiring matching the hand to the angle of the mailbox). Another subject was just the opposite and could not post a letter but was able to perfectly

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match the angle with a line in a perceptual task. Paillard (1999) suggested a similar parallel dissociation for the processing of tactile information. He presented data from two clinical patients who showed a double dissociation between the ability to localize a touch on the body and the ability to point to it, suggesting essentially that there may be at least two representations of touch on the body—one for perception and one for action. Here, we test whether the representation of touch for action is also coded in a visual reference frame in the same way as the representation of touch for perception appears to be (Ho and Spence 2007; Harrar and Harris 2009). To test for this, we had subjects point to (i.e., make an action towards) the perceived location of a touch on the arm that was delivered during eccentric fixation. We measured errors in tactile localization and compared these errors to previous studies of the effect of eye position on the perceived location of touch. Eye-position-related errors in touch-guided pointing would suggest that the coding systems for both touch for action and touch for perception use not only a body-based reference frame to code the location of a touch on the body, but also the common visual reference frame.

Methods

Participants

There were 10 participants (four women, six men) with a median age of 28 years. Each participant completed an informed consent agreement, which conformed to the ethical guidelines of York University and the Treaty of Helsinki.

Touch apparatus

Touch stimulators (tactors) were made from small solenoids mounted on a plate with the pins facing upwards. Solenoids were controlled by amplified 5-volt signals from a CED1401 controlled by a PC that extended the pins about 2 mm for 50 ms and then withdrew them. Four tactors were used, separated by (starting from the leftmost tactor) 5, 5.2, and 5.4 cm (see a, b, and c in Fig. 1a). The tactors were positioned in the same location as in Harrar and Harris (2009) in order to facilitate comparison across studies (see “Discussion”). Participants placed their left arm on the plate in front of their chests such that the distance from the middle of their forearm to the middle of their forehead was 33 cm. A piece of paper initially covered the tactors so that their locations could not be seen by the participants. The paper was removed only when the arm obscured the tactors from view. Participants aligned the creases on their wrists with a reference point on the box (a star, as depicted in Fig. 1a). Participants wore headphones to reduce any auditory cues from the tactors and used a chinrest to maintain head position.

Fixations

Four fixation LEDs were placed in a straight line 29 cm away, at eccentricities of -20.8° , -5.9° , 9.6° , and 23.3° (negative indicates left of straight ahead). The LEDs were positioned in the same location as in Harrar and Harris (2009) in order to facilitate comparison across studies (see “Discussion”). The LEDs were not visible except when they were illuminated (they were under a layer of tinted

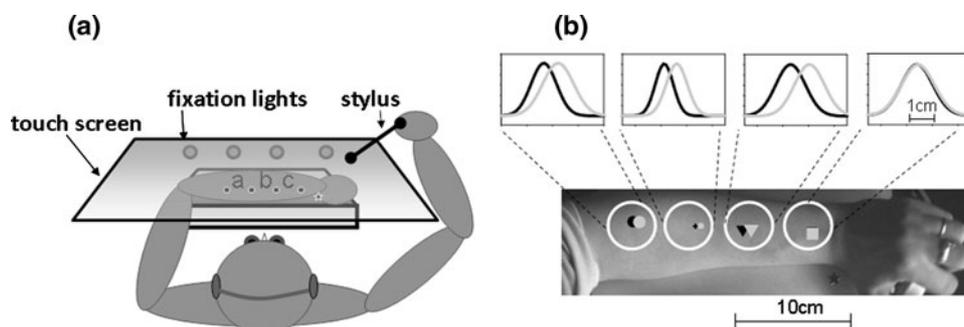


Fig. 1 Pointing to a touch. **a** A stylized representation of the posture of the participants and how it related to the four fixation lights, the four touches, the touch screen, and the stylus used by subjects to report the perceived location of the touch. The *left* arm was placed under a transparent touch-sensitive screen. Participants fixated one of four LEDs placed under the touch screen hidden when not illuminated by tinted plastic. Participants used a stylus in their right hand to indicate the perceived location of the touch on the screen. **b** The mean location subjects pointed for each of the four touches when fixating *left* (black) and *right* (grey) are shown superimposed on a photograph of a typical arm

(the placement of the touches on this photograph is only a rough approximation for schematic understanding). This mean location pointed to depended on both where they were actually touched and where subjects fixated. For clarity, locations corresponding to subjects fixating on the *left* are drawn in black (average perceived locations for the two leftmost fixations), and fixations to the right are drawn in grey (average perceived locations for the two rightmost fixations). To further pull out the effects, Gaussians of the distributions of the locations pointed to are plotted for the pooled left-fixations (black) and right-fixations (grey) with standard errors used as the width of the curves

plastic). The luminance of the LEDs when they were illuminated was 3.1 cd/m².

Procedure

Each trial was initiated by one of the four fixation LEDs illuminating for 1–1.5 s. Subjects were instructed to fixate the light and maintain fixation even after it turned off. Within a variable delay of 100–450 ms following the offset of the LED, one of four touches was presented for 50 ms. Following the offset of the touch, participants were allowed to move their eyes to the location of the touch. We allowed each subject to freely view both the stimulated and pointing arms. Participants were instructed to normally view their pointing hand as they pointed to the location of the touch using a stylus on a touch-sensitive transparent screen. The touch screen (43 x 33 x 0.3 cm, Keytec Inc., Garland, TX) was positioned 10 cm above each subject's left arm (Fig. 1a). Participants could reposition the stylus on the touch screen multiple times and indicated their final answer by lifting their foot from a foot pedal. The computer then stored the stylus' position.¹ The next trial was initiated when the foot pedal was depressed again.

Results

Participants indicated where they felt touches on their forearms by pointing to them. The results are plotted in Fig. 1b, which shows that when subjects fixated to the left (black symbols, black curves), the pointed to position of the touches was shifted to the left compared to when subjects fixated to the right (grey symbols, grey curves). Touches on the left arm were displaced towards the wrist when looking to the right and towards the elbow when looking to the left.

A two-way repeated-measures ANOVA was conducted (with Huynh–Feldt correction) with two independent variables: touch location (4) × fixation position (4). There was a significant linear main effect of fixation ($F_{1,9} = 5.092$, $P = .050$, $\eta_p^2 = .361$) showing that the location of the touch varied with the eye position, shifting by 0.016 cm/deg of eye position (depicted by the linear regression line in Fig. 2). The data points in Fig. 2 represent the mean response at each fixation position (averaged across the four touch locations), and error bars representing the standard error of the mean. There was no significant interaction between the touch location and fixation ($F = 1.589$,

¹ This step was necessary since some participants had a tendency to touch the screen with their fingers and hands at the same time as the stylus. Participants heard a “beep” for every touch on the screen and could therefore adjust the position of the stylus if the screen had recorded a finger point instead of the stylus point.

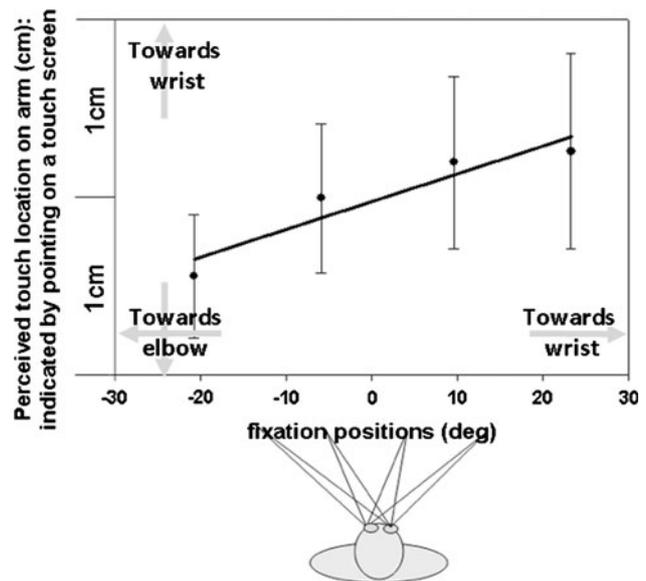


Fig. 2 The effect of eccentric fixation on tactile localization. The locations on the arm that were pointed to were averaged across participants and across the four touch locations and plotted as a function of fixation position (between-subject error bars shown). The significant linear effect (regression line through the data with a slope of 0.016 cm/deg, see text) indicates that the apparent position of the tactile target moved towards the wrist when the eyes were pointed in the direction of the wrist and in the direction of the elbow when the eyes were pointed towards the elbow

$P = 0.13$). Additionally, the main effect of touch location was significant ($F_{3,27} = 347.05$, $P < .001$, $\eta_p^2 = .975$), indicating that participants were able to distinguish between the four touches.

Discussion

Our finding of an eye-related error when pointing to a touch indicates that tactile processing for action appears to code the location of a touch at least partially in visual coordinates—the same reference frame conversion errors were found for processing of tactile location for perception (Harrar and Harris 2009). Paillard (1999) demonstrated separate brain areas associated with locating a touch on the body versus pointing to it. But our results show that both of these tasks, or the spatial mechanisms that feed into them, appear to code touch in mixed eye-centred and body-centred coordinate systems.

Dijkerman and de Haan (2007), who followed up on Paillard's work and mapped out the neurological paths for the two systems, pointed out the differences between touch and vision with respect to the dissociation between processing for perception and processing for action. One of the critical differences between the visual perception/action model and the somatosensory perception/action model,

they point out, is that for touch there appears to be considerable cortical overlap in the two processing streams. For example, the posterior parietal cortex (PPC) appears to be involved in both tactile perception and action.

The PPC appears to code spatial events in visual coordinates (Andersen 1997; Andersen et al. 1997) and, since it is known to be involved in both tactile perception and action, the PPC might be the area associated with both the effects reported here and those reported previously for perception (Harrar and Harris 2009). Since the PPC is known to also code auditory and tactile stimuli in a visual frame, Andersen (1997) suggests that a unified perception of space (containing all modalities) might specifically be due to the PPC's ability and involvement in transforming the multimodal frames into a single general representation of space. More specifically, neurological candidates include the parietal reach region (PRR) and the lateral intraparietal area (LIP), both of which have been associated with transforming (or representing transformed) stimuli from several modalities into a common visual reference frame for actions (Cohen and Andersen 2000; Cohen and Andersen 2002). Since here touch is being localized in order to guide a hand movement, its location is likely coded with respect to both the eyes and the hand. Such an intermediate body-based and eye-based reference frame is found in the dorsal area five of the PPC (Buneo et al. 2002) and the dorsal premotor area (PMd) (Pesaran et al. 2006). Coding the position of targets in a reference frame that is both visual- and body-based enables the motor signal of a hand movement towards the visually specified object to be directly derived from the target's position (no additional transformations are required) (Buneo and Andersen 2006).

Pointing to a target

When pointing to a target, errors may arise from two sources: knowing where the pointing arm is and knowing where the target is. Neurological evidence suggests that movement plans (like pointing) to visually specified targets may be coded relative to both the eye and the hand (Buneo et al. 2002; Pesaran et al. 2006). Therefore, eye-position-related errors could arise from either source. Pouget et al. (2002) describe this problem of having errors related to both the position of the hand and the position of the target, which makes it difficult to interpret their data. They claimed to find shifts correlated with eye position for visual, auditory, proprioceptive, and imaginary stimuli suggesting that they are all coded and updated in a visual reference frame. However, since they used eccentric pointing in order to determine where subjects' perception of the stimuli were, they conceded in their discussion that all their effects might have been due to proprioceptive shifts of perceived limb

position. While proprioceptive shifts are also interesting, as they demonstrate that limb position is coded not only in a body-based reference frame but also in a visual reference frame, they are not the aim of the current study. It appears that humans need visual feedback in order to correctly estimate retinal eccentricity and accurately point to a target (Henriques et al. 1998). Presumably, repeatedly pointing, reaching, and grasping behaviours have calibrated the proprioceptive system so that there are no localization errors when looking at the object, but since we rarely perform these tasks under eccentric viewing, that system is not completely calibrated. Since deviated gaze causes errors in pointing, in order to remove this source of error, subjects were instructed to view their pointing arm as they would under normal circumstances.

Effect of eye position at body sites that cannot be viewed directly

We suggest (although it has not yet been tested) that partially coding the location of touches in a visual reference frame may not necessarily require previous visual experience of the stimulated body part, since visual enhancement of touch does not require previous visual experience of the skin. Tactile performance is improved when vision of the stimulated body part (normally the arm) is available when compared to tactile performance on body parts when they are held out of view (for improved acuity, see acuity Kennett et al. 2001; for improved reaction times, see Press et al. 2004). Tipper et al. (2001) demonstrated that non-informative vision of the body improves tactile perception even for body parts that are not directly visible (such as the face and the back of the neck). Their results suggest that direct viewing is not necessary in order for vision to modulate the tactile response. As such, we predict that tactile localization on body parts that are not directly visible (such as the face) would also be affected by eye position. If such an effect of eye position were found for tactile localization on the face, it would suggest a coding partially relative to the eyes that is generated by a cognitive image of the body (a conglomerate of images, including those seen in mirrors) as opposed to the image of the body seen directly.

Pattern of errors smaller for action than for perception?

Both perceptual tasks (Harrar and Harris 2009) and the action task reported here show the same pattern of localization errors in the direction of eye position. However, larger errors appear to be associated with perceptual-type tasks than with action-type tasks. Harrar and Harris (2009) report shifts in tactile localization between 0.02 and 0.1 cm/deg for a perceptual task, while here we measured 0.016 cm/deg for the action-type task.

A similar difference in the size of eye-position-related errors was found for proprioceptive stimuli (limb position) measured by both active and perceptual methods. Gross et al. (1974) had their participants either point to or report verbally the position of their unseen arms and hands. They reported significantly smaller errors when participants reached to their unseen hand, as opposed to reporting its location verbally. Similarly, Kammers et al. (2006), measuring knowledge of arm position through joint awareness had smaller errors when measured actively compared to perceptually. We have identified two possible reasons that the effects might be smaller in action tasks.

Firstly, the different degrees of effect could indicate different coding systems employed for the stimuli depending on what they were going to be used for. While both mechanisms would be partially in visual coordinates, since both perception and action show errors related to gaze, there could be different eye-position gains associated with the mechanism that codes for perception versus the mechanism that codes for action. Under this dual-system model, the smaller effect of eye position on an action-type task might be due to such localizations being better calibrated. Every time a touch is reached for, feedback is received, which could be used to calibrate the tactile representation and correct for eye-position-related errors in that system.

A second, more parsimonious explanation is that the decreased error associated with action compared to perception might be an artefact effect of different measurement methods used. When determining the location of a touch or the position of a limb, body-based response methods (such as pointing) might be associated with smaller errors since they do not require comparisons be made cross-modally. Perceptual tasks in many of the studies described above required the position of the target stimulus to be determined relative to a visual stimulus, which itself might be affected by the same factors that displaced the target stimulus. In order to compare the sizes of the effects associated with perceptual and active tasks, both need to be assessed within the same modality as the stimulus being measured. We suggest that the methodology used is a more likely explanation for the difference in the amount of tactile shift due to eye position found in the perception and action tasks than potential difference in cortical mechanisms.

Conclusion

When participants point to the location of a touch, they make systematic errors in localizing the touch in the direction in which their eyes are pointing. We conclude that this indicates that eye position is used in the coding of touch and that tactile stimuli are coded in both body-based and eye-based coordinates both when touch is used to guide

actions and for perception. Whether the location of touch is updated in this intermediate coordinates system to guide action is a matter for future research.

Acknowledgments We would like to thank Richard Dyde for constructing the touch screen apparatus. The Natural Sciences and Engineering Research Council (NSERC) of Canada sponsored these experiments. Vanessa Harrar holds an NSERC scholarship.

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