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RESEARCH ARTICLE

Tactile localization biases are modulated by gaze direction

Sonia Medina[1] · **Luigi Tamè**[1] · **Matthew R. Longo**[1]

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Abstract Identifying the spatial location of touch on the skin surface is a fundamental function of our somatosensory system. Despite the fact that stimulation of even single mechanoreceptive afferent fibres is sufficient to produce clearly localised percepts, tactile localisation can be modulated also by higher level processes such as body posture. This suggests that tactile events are coded using multiple representations using different coordinate systems. Recent reports provide evidence for systematic biases on tactile localisation task, which are thought to result from a supramodal representation of the skin surface. While the influence of non-informative vision of the body and gaze direction on tactile discrimination tasks has been extensively studied, their effects on tactile localisation tasks remain largely unexplored. To address this question, participants performed a tactile localization task on their left hand under different visual conditions by means of a mirror box; in the mirror condition, a single stimulus was delivered on participants' hand, while the reflexion of the right hand was seen through the mirror; in the object condition, participants looked at a box through the mirror, and in the right hand condition, participants looked directly at their right hand. Participants reported the location of the tactile stimuli using a silhouette of a hand. Results showed a shift in the localization of the touches towards the tip of the fingers (distal bias) and the thumb (radial biases) across conditions. Critically, distal biases were reduced when participants looked towards the mirror compared to when they looked at their right hand suggesting that gaze direction reduces the typical proximodistal biases in tactile localization. Moreover, vision of the hand modulates the internal configuration of points' locations, by elongating it, in the radio-ulnar axis.

Keywords Tactile localization · Vision · Body representation · Gaze direction

Introduction

Identifying the spatial location of touch on the skin surface is among the most fundamental of tactile computations. Indeed, stimulation of even single mechanoreceptive afferent fibres is sufficient to produce clearly localised percepts (Schady et al. 1983). Tactile localisation is, however, also modulated by higher level processes (Azañón et al. 2016), such as the position of the body in external space (Azañón and Soto-Faraco 2008; Badde et al. 2014; Tamè et al. 2017c) and the internal postural configuration of the hand (Tamè et al. 2017b). These results are evidence that tactile localisation requires the involvement of multiple representations of the tactile event using different coordinate systems (Badde and Heed 2016). Other studies have reported systematic biases on localisation of touch onto the skin of the hand (Culver 1970; Mancini et al. 2011a; Margolis and Longo 2015), arm (Cholewiak and Collins 2003; Azañón et al. 2010; Steenbergen et al. 2012), and belly (Cholewiak et al. 2004). For example, Mancini et al. (2011a) delivered a single stimulus to several locations on the dorsum and fingers of the left hand. Participants localised each stimulus by clicking a mouse cursor on the corresponding location on a hand silhouette on a monitor. They found systematic distal and radial biases in localisation on the dorsal hand

✉ Luigi Tamè
luigi.tame@gmail.com

✉ Matthew R. Longo
m.longo@bbk.ac.uk

[1] Department of Psychological Sciences, Birkbeck, University of London, London WC1E 7HX, UK

surface. Distal and radial biases refer to a shift, in the tactile localization with respect to the position of the touches on the skin, in the proximal–distal and radio-ulnar hand axes, respectively. These biases were specific to the skin surface stimulated, and did not occur on the glabrous skin of the palmar hand surface. Critically, however, the biases occurred independently of the type of peripheral receptor stimulated (i.e., Aβ, Aδ, C), suggesting that they result from a central, supramodal representation of the skin surface (Mancini et al. 2011a).

Although tactile localization is accomplished by the somatosensory system, the way in which we experience the world through perception is using multiple systems in which information from different senses is combined together to construct our conscious perceptual experience. One factor that has been found to have widespread influences on somatosensory processing is vision of the body. Indeed, vision of the body, even when non-informative about stimulation, has been shown to speed reaction times to tactile stimuli (Tipper et al. 1998, 2001), improve tactile spatial acuity (Kennett et al. 2001; Longo et al. 2008; Konen and Haggard 2014), modulate somatosensory event-related potentials (Taylor-Clarke et al. 2002; Sambo et al. 2009; Gillmeister and Forster 2010; Longo et al. 2011), increase somatosensory intra-cortical inhibition (Cardini et al. 2011), reduce the intensity of acute pain (Longo et al. 2009, 2012a; Romano and Maravita 2014), as well as modulating processes including sensorimotor integration (Tamè et al. 2017a), tactile distance perception (Longo and Sadibolova 2013), and limb temperature (Sadibolova and Longo 2014). More generally, vision of the body has been shown to enhance tactile performance both in healthy individuals (Pavani et al. 2000; Tamè et al. 2013) and neurological patients with a deficit in tactile acuity (Serino et al. 2007). Despite several circumstances in which vision improve tactile performance, it is important to note that this is not always the case. Indeed, some studies showed that vision in some context may have no effect or impaired tactile performance (e.g., Press et al. 2004; Harris et al. 2007; Gillmeister et al. 2010). Moreover, individuals with visual impairment may perform better than healthy sighted subjects in certain tactile tasks (e.g., Röder et al. 2004; Azañón et al. 2017).

Despite the widespread effects of vision of the body on somatosensory processing, little research has investigated the effects of seeing the body on tactile localisation. Harrar and Harris (2009) manipulated vision of the body in a study that focused on the effects of eye-gaze. They found that non-informative vision of the stimulated forearm led to a spatial expansion of reported locations along the proximo-distal arm axis. Two subsequent studies, however, have found no effects of vision of the body on perceived size (Mancini et al. 2011b; Longo and Sadibolova 2013). Here, to further investigate this issue, we adapted the paradigm of Mancini et al. (2011a), described above, to investigate the effects of seeing the body on tactile localisation.

While few studies have investigated the effects of actual vision of the body on tactile localisation, several studies have shown that head orientation (Ho and Spence 2007; Pritchett et al. 2012) and direction of eye-gaze (Harrar and Harris 2009, 2010; Pritchett and Harris 2011; Pritchett et al. 2012; Harrar et al. 2013) produce shifts in the perceived location of touch. Such findings fit within a larger literature showing widespread influences of gaze-centred frames of reference across sensorimotor modalities (Andersen and Mountcastle 1983; Lewald and Ehrenstein 1996; Batista et al. 1999; Boussaoud and Bremmer 1999). Other studies have found that directing gaze towards the stimulated hand modulates neural processing of touch, distinct from effects of actually seeing the hand (Forster and Eimer 2005; Gherri and Forster 2014, 2015).

In this study, we investigated the effects of vision of the stimulated body part and of gaze direction towards that body part on tactile localisation on the skin surface. We used the localisation paradigm developed by Mancini and colleagues (Mancini et al. 2011a) in which the participant is touched at a location on their hand and indicates the perceived location of touch by clicking the mouse cursor on the corresponding location on a silhouette image of a hand. Participants made localisation judgments on their left hand in three visual conditions. We used the mirror-box illusion to manipulate the visual content that participants saw (Ramachandran et al. 1995). In the *View Stimulated Hand* condition, participants saw the reflection of their right hand in a mirror aligned with their body midline, which appeared to be a direct view of their stimulated left hand. In the *View Object* condition, they looked at the reflection of an object through the mirror. Note that in these two conditions, gaze direction was held constant. Finally, in the *View Other Hand* condition, they looked directly towards their non-stimulated hand (i.e., right hand). The purpose of this set of conditions was twofold: first, to test whether seeing or not seeing the hand affect tactile localization when gaze is kept constant (*View Stimulated Hand* vs. *View Object*) and second, to test whether gaze direction affects tactile localization when the visual input is kept constant (*View Stimulated Hand* vs. *View Other Hand*). Direction of eyes and head was always aligned across conditions. If vision of the body modulates tactile localization, we expect to find different localization judgments when participants are seeing the hand compared to when they are seeing an object. Moreover, if gaze direction modulates tactile localization, we expect to find a different performance when the gaze is directed towards the stimulated hand compared to when is directed in the opposite direction. Finally, if both visions of the body and gaze directions affect tactile localization, we expect different performances across the three experimental conditions.

Materials and methods

Participants

Thirty participants (mean ± SD, 31.3 ± 7.4 years; 19 female) took part in the study. Participants gave their informed consent prior to participation and reported normal or corrected to normal vision and normal touch. The study was approved by the local ethical review committee at Department of Psychological Sciences, Birkbeck, University of London and was carried out according to the principles of the 1964 Declaration of Helsinki. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971; $M = 87$, range 54–100).

Fig. 1 Picture of a participant's hand prior to start with the experiment. The knuckles of the index and the little fingers were marked with a cross and the nine landmarks were positioned on the dorsum of the hand. The landmarks were enumerated from the upper-left corner of the grid (landmark 1) to the lower right corner (landmark 9)

Stimuli

The tactile stimuli consisted in a calibrated nylon filament (von Frey hair, 40 mm long, 60 g bending weight). Each stimulus was administered manually by the experimenter in a pre-marked location on the participant's unseen hand. Before the start of the experiment, a 3 × 3 grid was made with blank ink centred on the dorsum of the participant's left hand using a plastic template (Fig. 1). The distance between adjacent locations in the grid was 2 cm.

Procedure

Participants sat with their hands on a table on either side of a mirror (47 cm width, 35 cm high) aligned with their body midline. Velcro disks on the table indicated where the participant should place the tip of the index finger of each hand, 20 cm on either side of the mirror. There were three visual contexts, as shown in Fig. 2. First, in the *View Stimulated Hand* condition, the participant placed their right hand in front of the mirror. When they looked into the mirror, they saw the reflection of their right hand, which appeared to be a direct view of their left hand. Second, in the *View Object* condition, a rectangular box of approximately similar size to a hand (14.5 × 9.0 × 8.0 cm) was placed in front of the mirror. When participants looked into the mirror, they saw the reflection of the box, which appeared to be in the location, where their left hand was located. During this condition, participants were asked to place their right hand on their right knee. Third, in the *View Other Hand* condition, the participant placed their right hand in front of the mirror. Instead of looking into the mirror, however, they looked directly at their right hand.

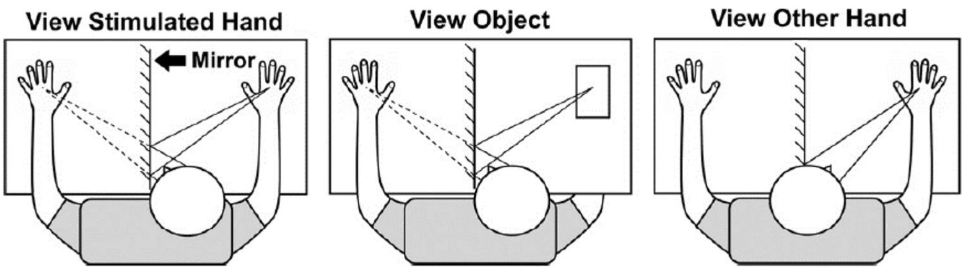

Fig. 2 Schematic representation of the experimental conditions. The first picture on the left represents the view stimulated hand condition, the central picture as view object condition and the one on the right for the view right hand condition. The mirror box throughout the experiment permanently covered participant's left hand

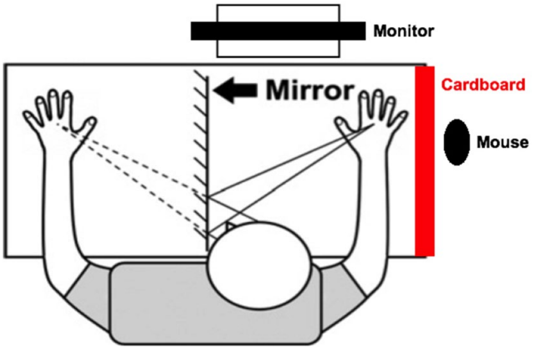

Fig. 3 Experimental setup. Image showing cardboard sheet (red colour) to cover the mouse. Once the stimulus was delivered on the left hand, participants were asked to close their eyes and move their right hand surrounding the cardboard sheet towards the mouse. Immediately after reaching the mouse, the silhouette of a hand appeared on the screen of the monitor and participants pointed with the mouse the exact location that they perceived that they were touched on. After answering, they were asked to close their eyes and move the hand back to the previous position as per figure above

To allow the participant to make localisation judgments, a Dell 15'' monitor was positioned in their right hemi-space aligned with their right shoulder (see Fig. 3). A black cardboard sheet of approximately the same size as the mirror was positioned about 20 cm to the right of participant's right hand to occlude the mouse, which was placed on the other side of the cardboard (Fig. 3). The participant used the mouse to give their response.

The participant's task was to judge the perceived location of each tactile stimulus on their left hand by positioning the mouse cursor (a thin crosshair) on the corresponding location on a silhouette of a left hand appearing on the monitor. On each trial, participants were asked to look at the reflexion in the mirror or at their right hand (depending on the condition). After approximately 3 s, a single stimulus of 1 s of duration was delivered at one of the nine marked locations on the dorsum of their left hand. Experimenter asked participant to close her/his eyes and to move their right hand towards the mouse immediately after the stimulation, and then, the mirror was covered and the participant opens the eyes to make the judgment on the silhouette that appeared on the monitor. The silhouette consisted of a white template of a hand (15 × 7.5 cm) over a black background, with no references about the position of the knuckles, nails, or wrist bones. The hand was presented vertically oriented with the palm facing down to match the position of the stimulated participants' hand (i.e., left hand). The participant was then asked to carefully localise the stimulus by clicking on the point on the silhouette that corresponded to the location they felt the touch on their left hand. Once the stimulus was localised, the participant moved their right hand back to the starting position (either in front of the mirror or in their knee).

Participants were not allowed to look at the marked locations on their left hand at any time until after the experiment was completed. Moreover, to make vision of the hand/object as consistent as possible, participants were asked to close their eyes every time their right hand was moving, both when they reached for the mouse and when they placed their hand back at the starting position. In addition, in the *View Stimulated Hand* and *View Object* conditions, the experimenter covered the mirror with a cloth curtain immediately after the stimulation was delivered and uncovered the mirror before the start of the next trial. In the *View Other Hand* condition, the mirror remained covered throughout the block.

The order of the locations that were stimulated within the blocks was randomized for each participant. The experiment consisted of a total of 360 trials divided into 6 blocks (two of each condition) of 45 trials each, separated by short breaks. Each block included five trials of each of the nine locations, presented in a randomized order. There were 40 repetitions of stimulation for each of the 9 locations for each participant and visual condition. The first three blocks included one block for each condition, counterbalanced according to a Latin square. The last three blocks were performed in the reverse order. Figure 4 shows a short questionnaire that was administered after each block to assess the participant's subjective experience, similar to the previous studies in our lab (Longo et al. 2009, 2012b; Longo and Sadibolova 2013). The experiment lasted approximately 75 min.

Analyses

Analysis procedures were similar to those used in our previous studies (Mancini et al. 2011a; Margolis and Longo 2015). The actual locations where the stimulation was delivered was recorded by taking a picture of the dorsum of participant's left hand from directly overhead once the grid was drawn. Subsequently, *x*- and *y*-coordinates of the knuckles and the nine stimulus locations were coded offline. To compare the locations of responses with actual stimulus locations, we used a two-point registration procedure (Bookstein 1991; Zelditch et al. 2004). The centre of the knuckle of the little finger was defined to be coordinate (0, 0) and the centre of the knuckle of the index finger as coordinate (1, 0), with all other points scaled accordingly. This results in a common, hand-centred frame of reference for expressing the locations of both actual stimulus locations and responses. Because Bookstein coordinates were expressed using the distance between the knuckles of the little and index fingers as the unit vector on the *x*-axis, the *x*-coordinate indicates location in the radio-ulnar hand axis, while the *y*-coordinate indicates location in the proximodistal hand axis.

Localisation performance was analysed both in terms of constant error (i.e., the vector connecting actual to judged

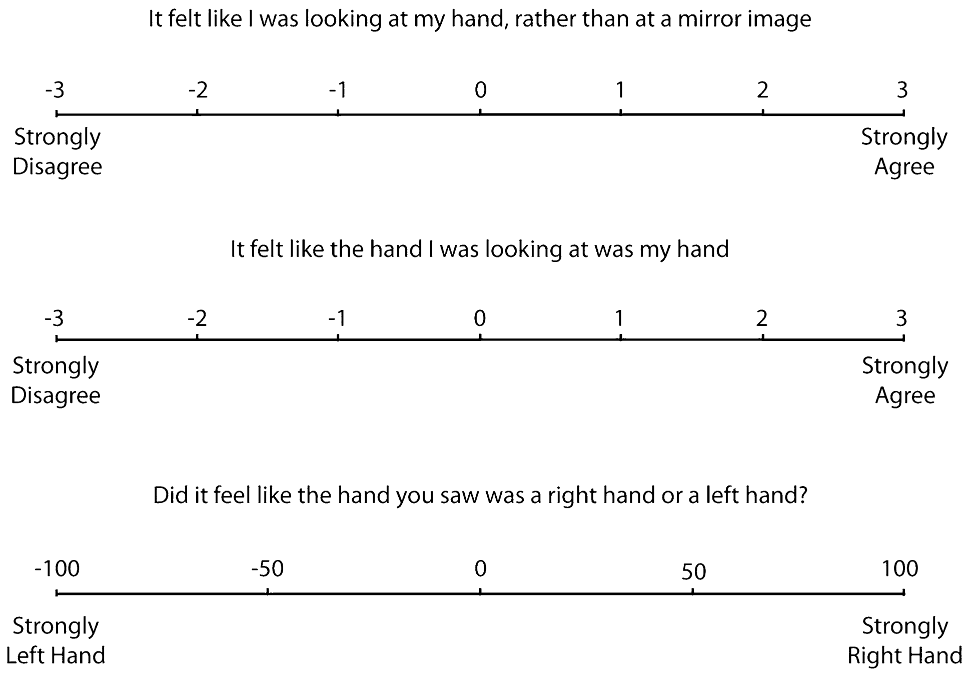

Fig. 4 Questionnaire administered to participants after each block. On each question, participants were allowed to give any number between minimum level and maximum level (Longo et al. 2009)

stimulus location) and in terms of variable error (i.e., the spread of responses around the mean response). Distal (i.e., towards the fingertips) constant error biases were quantified as the difference between the *y*-coordinates of each response and the actual location of the stimulus. Radial (i.e., towards the thumb) constant error biases were quantified as the difference of the *x*-coordinates of responses and actual stimulus location. Variable errors in the radio-ulnar and in the proximo-distal axes were quantified as the standard deviation of responses in the *x*-coordinate and the *y*-coordinate, respectively.

Results

Questionnaire

Participants' ratings for the agreement for each sentence were first compared against "0" using a *t* tests, namely, neutral response. As shown in Fig. 5a, participants agreed that 'It felt like I was looking at my hand and not at the mirror image' in the *View Stimulated Hand* condition ($M \pm \mathrm{SE} = 1.14 \pm 0.27$), $t(29) = 4.17$, $p < 0.001$, $d = 0.76$, and in the *View Other Hand*

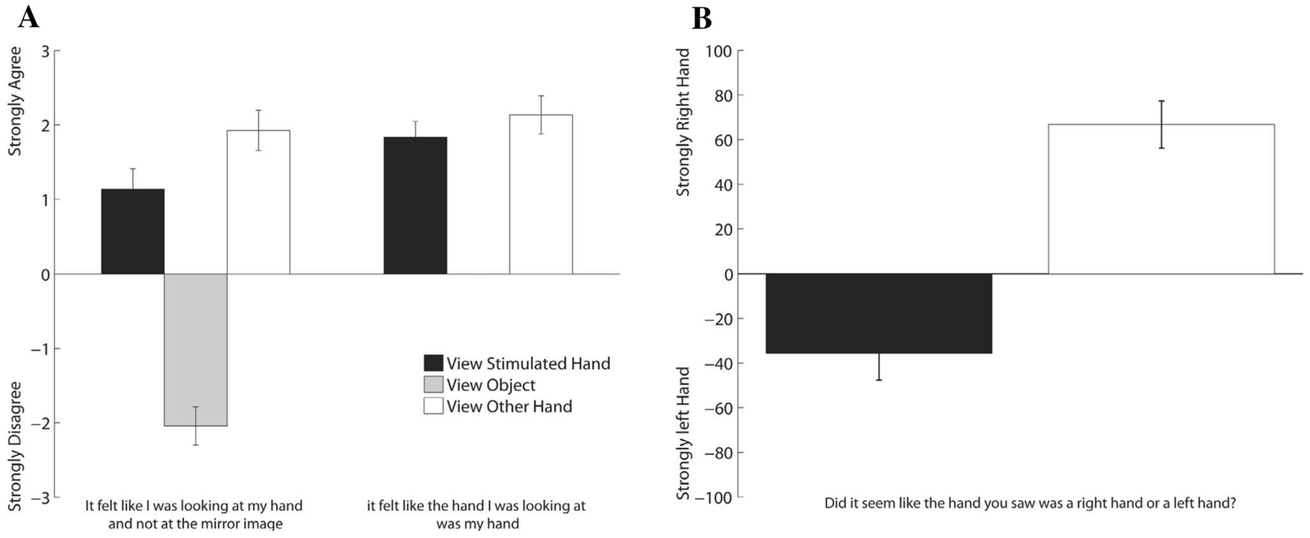

Fig. 5 Participants' ratings for the agreement (**a**) and left–right questions (**b**). Error bars represent the standard error of the mean (± SEM)

condition ($M \pm \mathrm{SE} = 1.93 \pm 0.27$), $t(29) = 7.10$, $p < 0.001$, $d = 1.30$, but disagreed in the *View Object* condition ($M \pm \mathrm{SE} = -2.04 \pm 0.26$), $t(29) = -7.92$, $p < 0.001$, $d = 1.45$. These results confirm that participants did have the illusion of seeing their real hand in the mirror and not a mere reflection.

Moreover, participants agreed with the statement ‘it felt like the hand I was looking at was my hand’ both in the *View Stimulated Hand* condition ($M \pm \mathrm{SE} = 1.83 \pm 0.21$), $t(29) = 8.64$, $p < 0.001$, $d = 1.58$, and in the *View Other Hand* condition ($M \pm \mathrm{SE} = 2.13 \pm 0.26$), $t(29) = 8.30$, $p < 0.001$, $d = 1.52$. They reported that the hand they saw seemed like a left hand after *View Stimulated Hand* condition ($M \pm \mathrm{SE} = -35.6 \pm 12.0$), $t(29) = -2.96$, $p < 0.007$, $d = 0.54$), but seemed like a right hand in *View Other Hand* condition ($M \pm \mathrm{SE} = 66.8 \pm 10.6$), $t(29) = 6.31$, $p < 0.001$, $d = 1.15$ (see Fig. 5b). Thus, the mirror box successfully generated the feeling of seeing a real left hand.

Constant error biases

Figure 6 shows the locations of stimulations and of localisation judgments in each condition, while Fig. 7 shows the magnitude of distal and radial biases. The distal and radial biases, in each condition, were first separately compared against “0” using *t* tests. Large distal biases were apparent in all three conditions: in the *View Stimulated Hand* condition (0.35 Bookstein units), $t(29) = 16.28$, $p < 0.001$, $d = 2.97$; In the *View Object* condition (0.35 Bookstein units), $t(29) = 15.01$, $p < 0.001$, $d = 2.74$; and in the *View Other Hand* condition (0.39 Bookstein units), $t(29) = 16.66$, $p < 0.001$, $d = 3.04$). These results replicate the large distal biases reported in several recent studies (Mancini et al. 2011a; Margolis and Longo 2015; Longo et al. 2015).

The critical question here was whether the magnitude of these biases was modulated by the visual condition. A one-way analysis of variance (ANOVA) revealed that the magnitude of distal bias did, indeed, differ significantly across conditions, $F(2,58) = 16.76$, $p < 0.001$, $\eta_p^2 = 0.37$. In comparison with the *View Other Hand* condition, distal biases were reduced in both the *View Stimulated Hand* condition,

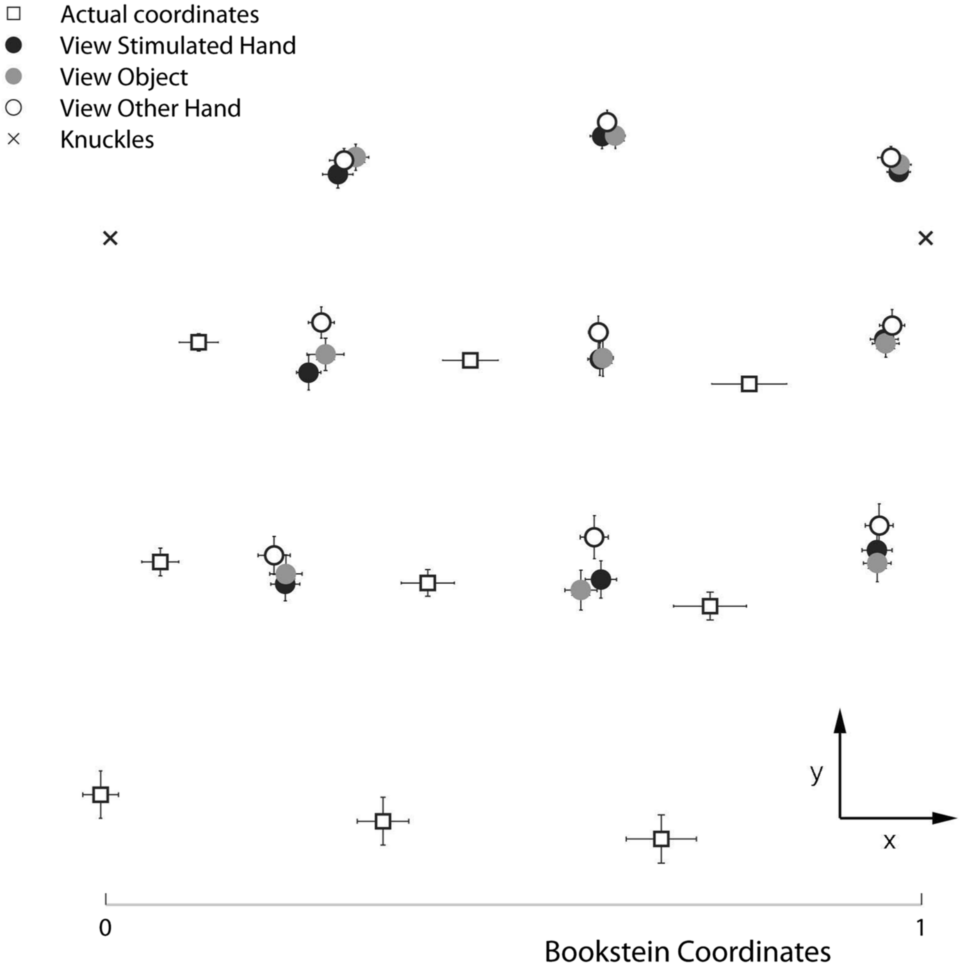

Fig. 6 Average actual (squares) and judged (circles) location of the tactile stimuli in the different visual condition are plotted in Bookstein shape coordinates, centred on the knuckle of the little finger (0, 0) and of the index finger (1, 0). Horizontal and vertical lines represent the standard error of the mean (± SEM). Note that horizontal and vertical lines for the actual grid configuration reflect participant’s individual differences of their hand for the same grid points

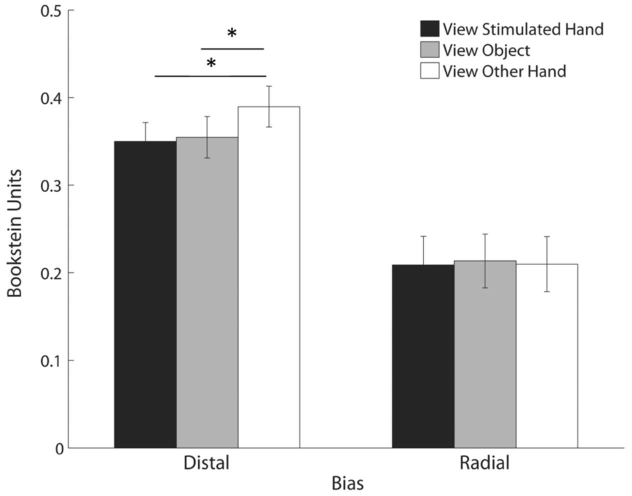

Fig. 7 Distal and radial bias in the three experimental conditions. Error bars indicate the standard errors of the mean (± SEM). * denotes $p < 0.05$

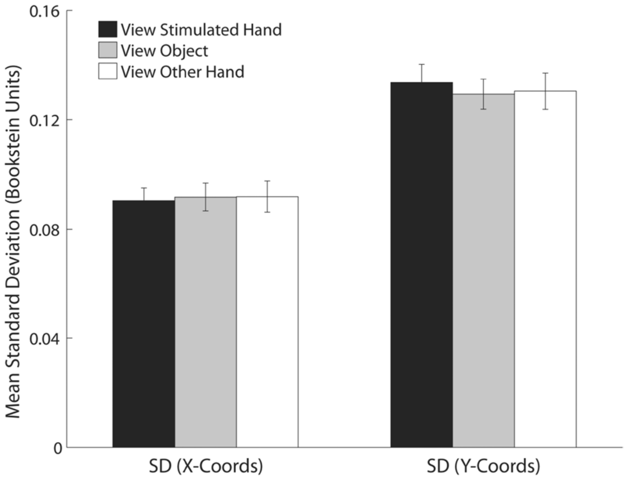

Fig. 8 Variable errors in the three experimental conditions. Error bars indicate the standard errors of the mean (± SEM)

$t(29) = -4.57$, $p < 0.001$, $d_z = 0.83$, and in the *View Object* condition, $t(29) = -5.55$, $p < 0.001$, $d_z = 1.01$. There was no difference between the *View Stimulated Hand* and *View Object* conditions, $t(29) = -0.64$, $p = 0.528$, $d_z = 0.12$. Thus, the effects seem to be driven not by the visual content of what is seen, but by whether or not gaze is directed towards the body. This pattern suggests that distal localisation biases are modulated by the direction of gaze, rather than by the visual content of seeing the body.

There were also clear radial biases in all three conditions: in the *View Stimulated Hand* condition (0.21 Bookstein units), $t(29) = 6.42$, $p < 0.001$, $d = 1.17$; the *View Object* condition (0.21 Bookstein units), $t(29) = 6.97$, $p < 0.001$, $d = 1.27$; and in the *View Other Hand* condition (0.21 Bookstein units), $t(29) = 6.67$, $p < 0.001$, $d = 1.22$. An ANOVA on the radial biases did not reveal any significant effect of condition, $F(2,58) = 0.39$, $p = 0.678$, $\eta_p^2 = 0.01$. The presence of medial localisation biases, such as distal biases, is consistent with the previous reports (Mancini et al. 2011a; Longo et al. 2015), though no such biases were apparent in the study of Margolis and Longo (2015).

Variable errors

As described above, variable errors in the radio-ulnar and proximo-distal axes were quantified by the standard deviation of x and y components of the Bookstein coordinates, respectively. These data are shown in Fig. 8. We conducted a 3 × 2 ANOVA on this data with factors 'condition' (*View Stimulated Hand*, *View Object*, *View Other Hand*) and 'orientation' (radio-ulnar, proximo-distal). There was a clear main effect of orientation, $F(1,29) = 72.85$, $p < 0.001$, $\eta_p^2 = 0.72$, with larger variability in the proximo-distal axis (i.e., the Bookstein y-coordinates) than in the radial-ulnar axis (i.e., the Bookstein x-coordinates). This result directly replicates the pattern reported by Margolis and Longo (2015) that the precision of localisation is higher across the width of the hand dorsum than along its length. It is also consistent with other data showing that the spatial acuity of touch on the hairy skin is higher in the radio-ulnar than in the proximo-distal limb axis (Boring 1930; Weber 1834/1996; Cody et al. 2008).

There was, however, no significant difference between the three conditions in terms of variable error, $F(2,58) = 0.08$, $p > 0.921$, $\eta_p^2 = 0.00$, nor an interaction between orientation and condition, $F(2,58) = 0.49$, $p > 0.612$, $\eta_p^2 = 0.02$. Thus, while the direction of gaze modulates the magnitude of constant error biases in tactile localisation, this does not appear to result in any changes in the precision of responses.

Internal configuration of responses

Harrar and Harris (2009) found that non-informative vision of the stimulated arm led to an expansion of localisation responses on the forearm. When the arm was visible, stimuli near the wrist were localised closer to the wrist and stimuli near the elbow were localised closer to the elbow, compared to a condition in which the arm was not visible. Given that we also compared tactile localisation judgments in conditions, where the participant either could or could not see the stimulated body part, we investigated whether similar spatial distortions were apparent. We did this in two ways. First, given that the effect observed by Harrar and Harris (2009) appeared to be an overall expansion of the range of responses, we investigated whether the overall configuration of the nine stimulus locations was expanded in size. We quantified size of each configuration by calculating the centroid size, the root mean square of the distance from each of the nine points from their centre of mass (or centroid) (Bookstein 1991; Zelditch et al. 2004). For each participant, we calculated the centroid size (in Bookstein units) for the actual configuration of points on the hand and for responses in each of the three experimental conditions. These data are shown in Fig. 9a. An ANOVA comparing centroid size across the three conditions revealed no significant effect of condition on the size of configurations, $F(2, 58) = 1.96$, $p = 0.150$, $\eta_p^2 = 0.06$. Moreover, none of the conditions differed significantly from the actual size of the configurations on participants' hands (all p's > 0.50).

The second way we investigated spatial distortion was by assessing changes in the overall aspect ratio of the configuration; using a method, we have recently used to investigate distortions in position sense (Longo and Morcom 2016; Longo 2017) and tactile distance perception (Longo and Golubova 2017). We took a perfectly square 3 × 3 grid of points and stretched it in various ways by multiplying the x-coordinates by a stretch parameter. When the stretch parameter is less then 1, the grid is elongated along the proximo-distal axis, whereas when it is greater than 1, the grid is elongated across the radio-ulnar axis. For each map in each participant, we found the value of the stretch parameter than minimised the dissimilarity in shape between the stretched grid and the participant's data. Dissimilarity in shape was quantified by the Procrustes distance, and the root mean square of distances between pairs of homologous landmarks after the configurations has been translated, scaled, and rotated to be in best-fitting alignment (Rohlf and Slice 1990; Goodall 1991). Note that because Procrustes alignment normalises the overall size of configurations, stretch of the radio-ulnar axis is equivalent to compression of the proximo-distal axis and vice versa. Values of the stretch parameter between 0.33 and 3.0 were tested by exhaustive search with a resolution of 0.0005 units in natural logarithm space.

The best-fitting stretch parameters are shown in Fig. 9b. An ANOVA comparing the three conditions found that vision produced significant differences, $F(2, 58) = 7.39$, $p < 0.002$, $\eta_p^2 = 0.20$. Compared to the *View Object* condition, stretch parameters were significantly increased in both the *View Stimulated Hand* condition, $t(29) = 2.20$, $p < 0.036$, $d_z = 0.40$, and the *View Other Hand* condition, $t(29) = 4.03$, $p < 0.001$, $d_z = 0.74$. There was no significant difference between the two hand conditions, $t(29) = 1.55$, $p = 0.133$, $d_z = 0.28$. The best-fitting stretch parameters were significantly greater than 1 in both the *View Stimulated Hand* condition, $t(29) = 2.87$, $p < 0.008$, $d = 0.52$, and the *View Other Hand* condition, $t(29) = 3.29$, $p < 0.003$, $d = 0.60$, indicating that the configurations were on average elongated in the radio-ulnar axis (or, equivalently, compressed in the proximal–distal axis). No such deviation from a perfectly square configuration, however, was apparent in the *View Object* condition, $t(29) = 1.21$, $p = 0.222$, $d = 0.22$.

It is important to note that these two types of analyses on the internal configuration differ on an important aspect. Indeed, the first type of analysis quantifies the size of the configuration, whereas the second type of analysis estimates the shape of the configuration which does not include any information about the size, position in space, and orientation of the points.

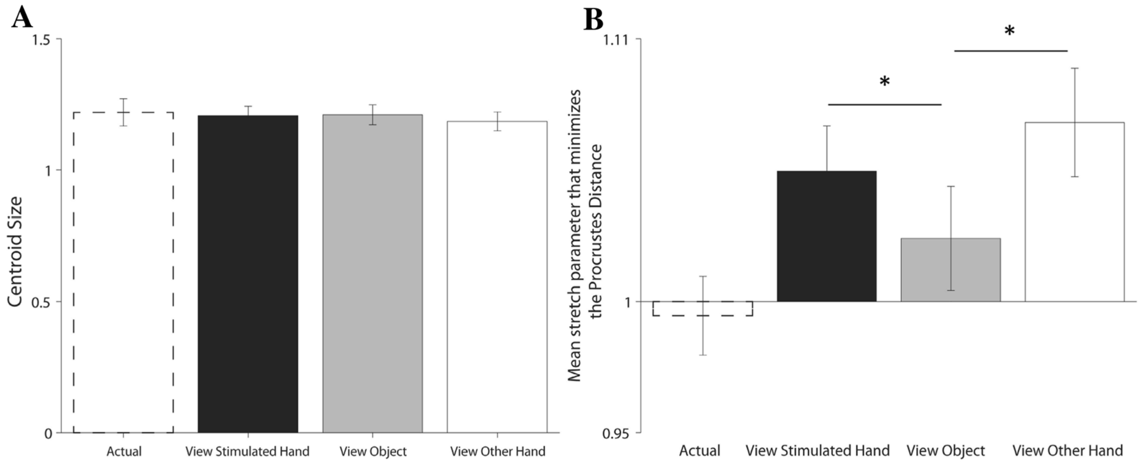

Fig. 9 Configuration analysis (**a**) and best fitting of the Procrustes Distance for the different visual conditions (**b**). Error bars indicate the standard errors of the mean (± SEM). * denotes $p < 0.05$

Discussion

These results demonstrate that looking towards the body, whether or not the body is actually seen, modulates the distal bias that is typically found in tactile localisation tasks. This is not the case when participants' gaze is directed towards the non-stimulated contralateral hand. Both distal and radial biases across participants are consistent with the results of the previous studies on tactile localisation on the dorsum of the hand (Mancini et al. 2011a; Longo et al. 2015). Critically, the distal bias (i.e., shift in the proximo-distal axis) was significantly modulated by vision of the body and gaze direction. Distal and radial biases refer to a shift, in the tactile localization with respect to the position of the touches on the skin, in the proximal–distal and radio-ulnar hand axes, respectively.

The fact that the distal bias was modulated in the same way, both regardless of the nature of the visual input (i.e., body or object) suggests that gaze direction is the most prominent factor that drives this effect in the present context. This result is compatible with several studies showing that head orientation (Ho and Spence 2007; Pritchett et al. 2012) and direction of eye-gaze (Harrar and Harris 2009, 2010; Pritchett and Harris 2011; Pritchett et al. 2012; Harrar et al. 2013) modulates the perceived location of touch. For instance, Ho and Spence (2007) showed that subjective judgements in localisation of touch are specially impaired when the direction of gaze is in the opposite direction with respect to the tactile stimulation. Previous reports have shown that proprioceptive orienting of the eyes or head can affect touch even in the absence of vision and vice versa (Tipper et al. 1998, 2001). For instance, Tipper et al. (1998) asked participants to detect, as quickly as possible, a tactile stimulus delivered either on the right or left hand. Across blocks, vision of the hands was occluded and participants looked at a monitor in front of them on which a real-time image of their hand was presented (visual-only). In another condition, participants oriented their gaze/head towards one hand, while direct vision was prevented (proprioceptive-only). Finally, in another condition, participants oriented their gaze/head towards one hand that was visible (vision proprioceptive). They found that both proprioceptive orienting and vision of the body alone facilitated detection of the tactile target (Tipper et al. 1998). This result demonstrates that proprioceptive orienting and vision of a body part can affect somatosensation independently. Interestingly, authors found that the combination of these two factors (i.e., proprioceptive orienting and vision) produces no further facilitation.

In this respect, a reduced shift of localisation along the proximo-distal axis can be described as an effect produced by the proprioceptive orienting of the gaze. Indeed, in our task, the direction of eyes and head was always aligned; therefore, we are seeing a more general effect of gaze, the sum of eye and head position (Pritchett and Harris 2011). A reasonable explanation is that depending on the direction of the gaze participants was changing the reference frame in which tactile stimuli were coded. Indeed, to locate a touch on our body, we need multiple spatial representations of the tactile event based on different reference frames. It is suggested that touch is initially encoded into a sensory space within the primary somatosensory map (Penfield and Boldrey 1937), but the location of the tactile event in further processing stages is then coded at other representational levels (Longo et al. 2010; Serino and Haggard 2010). Specifically, tactile sensation can be mapped in a mental body representation, enabling us to localise tactile events with respect to body parts and body sides (Schicke and Röder 2006; Tamè et al. 2011; Badde and Heed 2016), or in egocentric representations of external space, enabling the localization of tactile events in the outside world (Azañón et al. 2010; Tamè et al. 2017c). When participants were looking towards the mirror (i.e., view stimulated hand), stimuli were coded using hand-centred coordinates, whereas when the gaze was oriented towards the opposite hand (i.e., view other hand), away from the locus of stimulation, stimuli were coded using external reference frame coordinates. Indeed, when participants gaze is oriented towards the stimulated hand, there is no need to consider other parts of the external space to solve the present task. The significant reduction in the localization bias in the former case can be caused by the adoption of the hand-centred frame of reference which is intuitively smaller in terms of reference space compared to an external reference frame, making the localization less sensitive to the distortions in the proximo-distal axis.

Alternatively, it is possible that our effect is partly due to the allocation of attentive resources in the portion of the space, where the stimulation occurs (Driver and Grossenbacher 1988; Honoré et al. 1989). Indeed, the direction of the gaze is typically the localization in which the majority of attentional resources are allocated which is known to modulate tactile perception in several contexts (Michie et al. 1987; Làdavas et al. 2000; Sambo et al. 2009; Macaluso and Maravita 2010; Gillmeister and Forster 2010). Our data cannot disentangle between these two possibilities; however, a previous report by Harrar and Harris (2009) found by overtly orienting attention away from eye position that attention could account for only about 17% of the effect. Therefore, a pure attentional account seems to be less likely, though these two processes are not mutually exclusive.

Non-informative vision for the stimulated body part has been shown to increase tactile acuity (Kennett et al. 2001); therefore, we may have expected that the precision in localising touch on the hand dorsum increases when the hand was visible compared to when an object was seen as well as when the gaze was directed towards the stimulated hand. This was not the case, however, as there was no difference between the conditions in terms of variable error (i.e., the 'error of localisation', Weber 1834/1996). Vision of the body and gaze information has a specific influence on the size of distal biases, rather than affecting the precision of the responses consistent with previous reports that used a similar approach (Margolis and Longo 2015).

Internal configuration of responses

As described in the introduction section Harrar and Harris (2009) found that non-informative vision of the stimulated forearm led to a spatial expansion of judged locations along the proximo-distal arm axis. Given that in their study, judgments were made by indicating the corresponding location on a visually seen ruler, their pattern of results could arise either from visual modulation of the perceived location of touch or visual modulation of perceived arm length. In particular, when the arm was visible, stimuli near the wrist were localised closer to the wrist and stimuli near the elbow were localised closer to the elbow, compared to a condition in which the arm was not visible. In this respect, our results seem to support the notion of a modulation effect of tactile localisation on the skin (Mancini et al. 2011b; Longo and Sadibolova 2013), rather than changes in the perceived size of the body. Indeed, our analysis on the overall spatial configuration of the nine stimulus locations did not show an overall expansion in size (Fig. 9a) across conditions and with respect to the actual configuration. However, assessment of changes in the overall aspect ratio of the configuration, showed that the best-fitting stretch parameters increased when vision of the hand was present (i.e., view of the stimulated hand and view of the other hand) compared to when an object was seen and with respect to the actual configuration (Fig. 9b). This indicates that when the body was visible, the nine point's configurations on the hand dorsum were on average elongated in the radio-ulnar axis or compressed in the proximal–distal axis. Therefore, the central point in our view is that even if there is a change in perceived hand width, it is not at all obvious that this should produce any change at all in how the participant judges the point-by-point correspondence between locations on their own hand and locations on the silhouette. However, we acknowledge the fact that there is the possibility that changes in perceived body size might, to some extent, contribute to our results.

While several studies show the positive effects of vision of the body and gaze orientation on tactile discrimination tasks, to our knowledge, this is the first piece of evidence of such effects on a tactile localisation task. Mancini et al. (2011a) suggested that distorted supramodal representations of the body structure could be the origin of systematic biases found on a tactile localisation task. Given the wide evidence that states the central nature of changes in tactile perception via non-informative vision of the body and gaze direction, we propose that these representations of the body surface are modulated by high-level representations affecting the frame of reference in which tactile stimuli are coded, resulting in better performance in the somatosensory localisation tasks when gaze is directed towards the locus of stimulation. Instead, vision of the body modulates the overall configuration of the perceived tactile pattern.

In conclusion, the present results show that seeing the body and gaze orientations affects different dimensions of tactile localization. Namely, distal biases are reduced when participants looked towards the mirror compared to when they looked at their right hand, suggesting that gaze direction reduces the typical proximo-distal biases in tactile localization. Moreover, vision of the hand modulates the internal configuration of points' locations, by elongating it, in the radio-ulnar axis. These results add to a growing body of research demonstrating widespread effects of vision of the body and gaze orientation on somatosensation, including tactile reaction time (Tipper et al. 1998), tactile spatial acuity (Kennett et al. 2001; Harris et al. 2007), receptive field size (Haggard et al. 2007), intra-cortical inhibition (Cardini et al. 2011), somatosensory event-related potentials (Taylor-Clarke et al. 2002; Longo et al. 2011), tactile size perception (Longo and Sadibolova 2013), tactile localization (Harrar and Harris 2009), and pain (Longo et al. 2009; Mancini et al. 2011b).

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Compliance with ethical standards

Conflict of interests The authors declare no competing financial interests.

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