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RESEARCH ARTICLE

Visual detail about the body modulates tactile localisation biases

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Abstract The localisation of tactile stimuli requires the integration of visual and somatosensory inputs within an internal representation of the body surface and is prone to consistent bias. Joints may play a role in segmenting such internal body representations, and may therefore influence tactile localisation biases, although the nature of this influence remains unclear. Here, we investigate the relationship between conceptual knowledge of joint locations and tactile localisation biases on the hand. In one task, participants localised tactile stimuli applied to the dorsum of their hand. A distal localisation bias was observed in all participants, consistent with previous results. We also manipulated the availability of visual information during this task, to determine whether the absence of this information could account for the distal bias observed here and by Mancini et al. (Neuropsychologia 49:1194–1201, 2011). The observed distal bias increased in magnitude when visual information was restricted, without a corresponding decrease in precision. In a separate task, the same participants indicated, from memory, knuckle locations on a silhouette image of their hand. Analogous distal biases were also seen in the knuckle localisation task. The accuracy of conceptual joint knowledge was not correlated with tactile localisation bias magnitude, although a similarity in observed bias direction suggests that both tasks may rely on a common, higher-order body representation. These results also suggest that distortions of conceptual body representation may be more common in healthy individuals than previously thought.

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Introduction

Localising tactile stimuli on the body surface typically relies on integrating somatosensory and visual information within a common frame of reference (Kennett et al. 2001). When access to visual information is restricted, and somatosensation relied upon to localise tactile stimuli, performance is both relatively imprecise (Harris et al. 2004; Moore and Schady 1995) and prone to systematic biases. For example, substantial constant errors of localisation have been reported on a variety of body parts, including the hand (Culver 1970; Mancini et al. 2011), forearm (Azañón et al. 2010; Cholewiak and Collins 2003), and abdomen (Cholewiak et al. 2004). These mislocalisation patterns emerge regardless of the class of peripheral receptor stimulated (e.g. Aβ, Aδ, C; Mancini et al. 2011; Steenbergen et al. 2012) or manner of response (Harrar et al. 2013; Mancini et al. 2011), suggesting that they may reflect distortions of a central, supramodal representation of the body surface.

The body surface, however, is not a homogenous field, but contains numerous anatomical landmarks and boundaries, such as joints, that may play an important role in segmenting such internal body representations (de Vignemont et al. 2009; Knight et al. 2014). There is evidence that these landmarks may serve as reference points in tactile localisation, with localisation accuracy highest in the region of joints (Cholewiak and Collins 2003), and mislocalisation errors often reported in the direction of the nearest joint (Boring 1942; see also Trojan et al. 2006). This influence of the joints may arise

partly because tactile localisation relies on reference to body representations which are themselves segmented by joints. It is therefore possible that explicit knowledge of joint locations could influence tactile localisation performance.

In a recent study, Mancini et al. (2011) reported large distal localisation biases on the dorsal hand surface. These biases cannot be straightforwardly interpreted as biases towards the nearest joint. Indeed, the closer stimuli were to the wrist, the larger the distal biases were, exactly the opposite of what would be predicted by an attraction towards joints. Mancini and colleagues asked participants to indicate the perceived location of touch by clicking a mouse cursor on a silhouetted image of their hand, partly in order to minimise the use of visual landmarks, such as knuckles, as reference points. Of course, the fact that visual detail about landmarks was not present in the silhouetted image does not imply that participants were not implicitly filling in such detail—possibly incorrectly—in ways which might have affected the obtained biases.

The present study therefore investigated how the presence of visual detail influences the reported location of tactile stimuli by directly comparing responses when participants localised touch on a full-colour photograph of their hand or on the same image converted into a silhouette. To further investigate how participants may have filled in missing detail in the silhouette condition, we administered a task in which participants judged on a silhouette of their hand where each of their knuckles was located. This knuckle localisation task allowed us to estimate conceptual misunderstanding of hand configuration. We predicted that the pattern of constant errors observed in the knuckle localisation task would predict differences in constant errors of tactile localisation when participants responded on a silhouette, compared to a full-detail photograph of their hand.

Methods

Participants

Fifteen healthy volunteers (8 females; 25 ± 4.1 years, range 19–57) participated. All were right-handed as assessed by the Edinburgh Hand Inventory (*M*: 94.02; SD: 11.15). Participants gave informed consent and were given either course credits or cash for taking part. Procedures were approved by the local ethics committee.

Materials and procedure

Tactile localisation task

Procedures were similar to those of Mancini et al. (2011). At the start of the experiment, a photograph of the participant's right hand against a plain background was captured using a digital camera. The resulting image (3,264 × 2,448 pixels) was one of two images presented to participants during the experiment. The second image was produced by editing the original image with the threshold tool in the GNU Image Manipulation Program (GIMP version 2.8.2), to generate a monochrome 'Silhouette' image. All textural and colour information was thus removed from the original photograph, leaving a black and white outline of the participant's hand. Figure 1 shows examples of 'silhouette' and 'photograph' stimuli. During the experiment, images were presented on a display monitor 75 cm from where participants were seated, subtending a visual angle of approximately 18.3° horizontally and 13.7° vertically. When presented in this way, images were of approximately equal size to participants' actual hands.

Participants sat with both arms lying flat on a table, uncrossed and perpendicular to the shoulders, with the dorsum of the hand facing up. Both hands were occluded

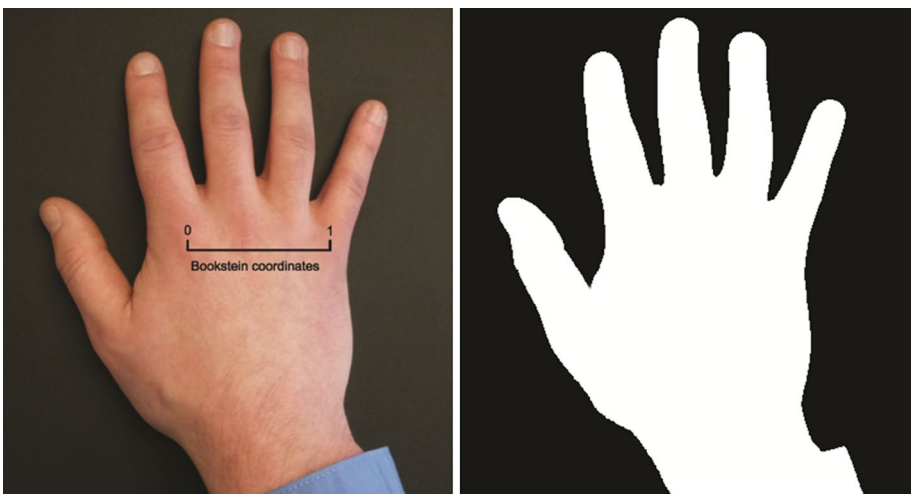

Fig. 1 An example of 'photograph' (*left*) and 'silhouette' stimuli similar to those used in the experiment

from the participant's view by a piece of plain black card. During each trial, participants were stimulated at one of twelve locations (landmarks) on the dorsal surface of their right hand. Landmarks were arranged in a 4 × 3 grid, and marked in advance by drawing dots with a non-permanent marker through a plastic stencil. One edge of the stencil was aligned with the participant's wrist, so that the three columns of landmarks lay longitudinally on the hand. Participants' hands were out of view while landmarks were being applied, and participants did not see the landmark locations until the experiment was complete. Figure 2 shows a schematic overview of the experimental setup. Landmarks were stimulated once per trial with a von Frey hair (255 mN). This force is strong enough to be easily felt, but painless, and was demonstrated to participants prior to the start of the experiment.

Each trial began with participants fixating a cross in the centre of the display screen; this fixation point was therefore presented in the vertical plane, while the stimulated hand lay horizontally on the table. A single landmark was then stimulated for approximately 2 s, after which either the 'photograph' or 'silhouette' image appeared on the display monitor. Participants then indicated, by using their left hand to move a crosshair cursor and click on the displayed image of their hand, where they judged the location of the stimulation to be. This ended the trial and restored the fixation cross. Participants were instructed to be as accurate as possible and avoid ballistic points when responding. Participants were also instructed to report all accidental responses, which were removed from subsequent analyses. The mouse cursor started at a random location on the screen on each trial, to make responses on successive trials as independent as possible.

There were 8 blocks, with 12 trials in each, making a total of 96 trials. Each landmark was stimulated once per block, in random order. Either the 'photograph' or 'silhouette' image was presented for the duration of each block, with the image presented alternating between blocks. The starting image was counterbalanced across participants. Participants were allowed to take breaks, but were reminded not to look at their hands at any point. This task lasted approximately 30 min.

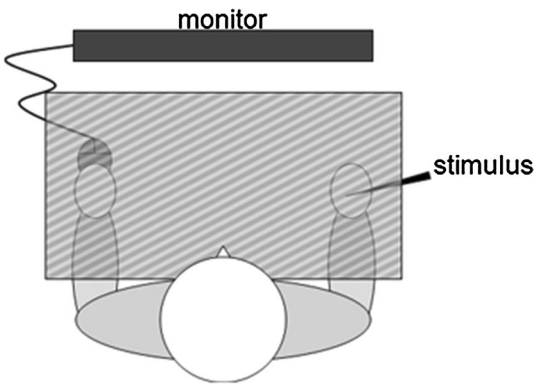

Fig. 2 Schematic overview of the experimental setup. The *striped area* represents an opaque cover that hid participants' hands from view for the duration of both experiments

Knuckle localisation task

Participants remained seated as before, and the 'silhouette' image was displayed on the monitor throughout. Individual trials proceeded largely as before; however, rather than attempting to localise stimulation on their hand, participants were required to attempt to localise the centre of their knuckles on each finger from memory. The centre of each knuckle was marked in advance with the same non-permanent marker: participants were asked to make a fist, and marks were made at the approximate apex of each knuckle. As with the hand landmarks above, participants were unable to view their knuckles while these marks were being applied. The experimenter verbally instructed the fingers (thumb, index, middle, ring, and little finger) in random order, and participants clicked a location on the image to indicate the perceived the location of the knuckle. Participants were instructed to avoid moving their stimulated right hand while carrying out the task, to minimise the use of proprioceptive information to inform task performance. However, the unstimulated left hand was free to move in order to register responses. Five blocks of five trials took approximately 3 min to complete. At the end of the experiment, a second photograph was taken of the participant's right hand, with the landmark dots visible, for use in analysis.

Analysis

In order to compare participants' responses and stimulus/knuckle locations, all were encoded into a common frame of reference using so-called Bookstein coordinates (Bookstein 1991), as in the study of Mancini et al. (2011). The centre of the index finger knuckle was defined as Bookstein coordinate (0,0), and the centre of the little finger knuckle as (1,0). Stimulus locations, knuckle locations, and responses were recorded within their relevant images as (x, y) coordinates relative to the axis formed by these loci and then combined within a common coordinate system for analysis.

Performance was analysed in terms of bias direction and magnitude (constant error, or CE, vector), and the spread of responses around the mean response location (variable error—a measure of precision). The CE vector is the vector between the actual and perceived locations and can be decomposed into proximo-distal and medio-lateral components. Because Bookstein coordinates are defined using the distance between the knuckles of the index and little fingers

as the unit vector along the *x*-axis, the medio-lateral component of the CE vector can be calculated as the difference in *x*-coordinates, while the proximo-distal component can be calculated as the difference in *y*-coordinates. Variable error was calculated as the standard deviation of responses, separately for the medio-lateral (i.e. standard deviation of *x*-coordinates) and proximo-distal (i.e. standard deviation of *y*-coordinates) axes.

Comparisons between the direction of constant errors across conditions were performed using the Watson-Williams test, a generalisation of a one-way ANOVA for circular data (such as angles) to test the null hypothesis that mean vector direction is equal across conditions (Batschelet 1981). The Watson-Williams test was performed using the CircStat toolbox for MATLAB (Berens 2009).

Participants were asked to report any unintentional responses, which were noted and removed from subsequent analysis (0.76 % of trials). Outliers were defined as responses that fell at a distance of three or more standard deviations from a participant's mean response for a particular landmark (the average judged location, collapsed across all other trials) and were removed from analysis (1.11 % of trials).

Results

Tactile localisation task

Figure 3 shows the mean positions of actual stimulus locations in the tactile localisation task (white circles) as well as judged locations in both the silhouette (shaded circles) and photograph (black circles) conditions. Consistent with the results of Mancini et al. (2011), large distal biases were found, both in the 'silhouette' (*M*: 0.28 Bookstein units, $t_{(14)} = 11.96$, $p < 0.001$) and 'photograph' (*M*: 0.20 Bookstein units, $t_{(14)} = 12.31$, $p < 0.001$) conditions. However, there was no significant overall radial bias, regardless of whether 'silhouette' (*M*: 0.02 Bookstein units, $t_{(14)} = 0.72$, $p > 0.1$) or 'photograph' (*M*: −0.03 Bookstein units, $t_{(14)} = -1.22$, $p > 0.1$) images were presented.

Separate 4 × 3 × 2 factorial ANOVAs were carried out on the distal and radial components of the CE vector for each stimulus location, with levels corresponding to the four rows and three columns of the stimulus grid, as well as condition ('silhouette' or 'photograph'). Both distal ($F_{(1,23)} = 73.72$, $p < 0.0001$) and radial ($F_{(1,23)} = 37.03$, $p < 0.001$) components varied as a function of condition, with biases of larger magnitude present in the 'silhouette' relative to the 'photograph' condition. Distal components varied with proximo-distal ($F_{(3,21)} = 21.00$, $p < 0.0001$), but not radio-ulnar ($F_{(2,22)} = 0.80$, $p > 0.5$), grid position, while radial components varied with radio-ulnar ($F_{(2,22)} = 26.62$, $p < 0.01$), but not proximo-distal ($F_{(3,21)} = 2.23$, $p > 0.1$), grid position. Distal biases became progressively larger towards the proximal end of the stimulus location grid, while radial biases increased progressively towards the thumb.

Variable errors were separated into radio-ulnar and proximo-distal components prior to analysis. A 2 × 2 ANOVA was carried out on these components, with levels

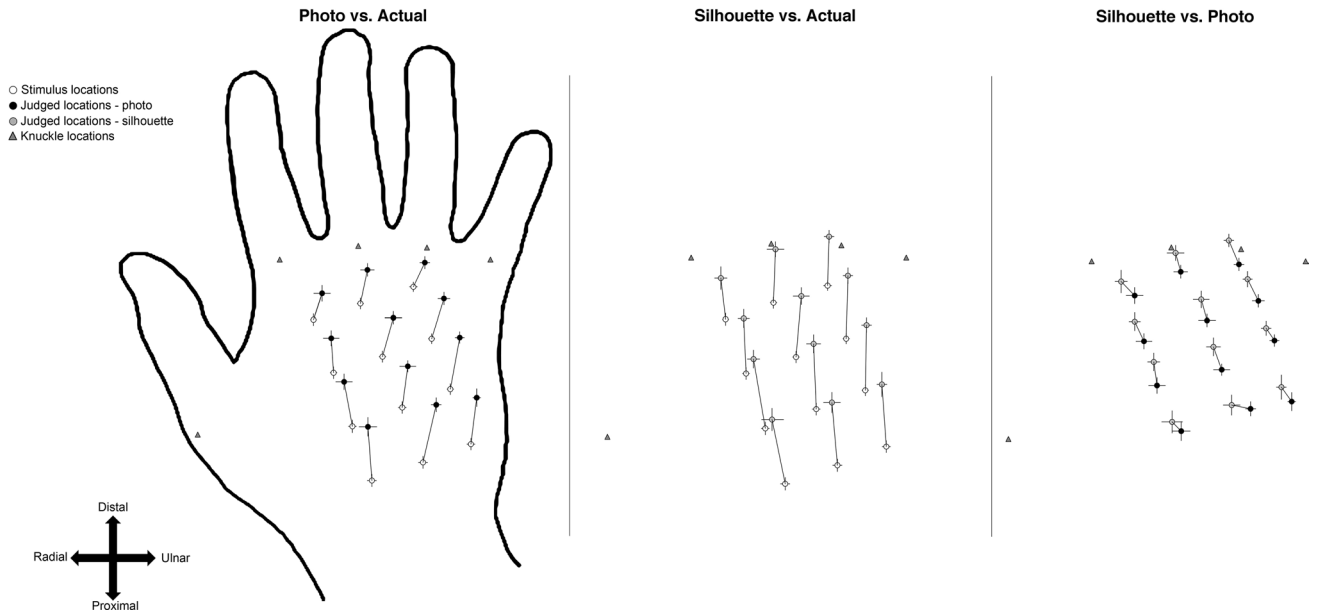

Fig. 3 A comparison of average actual stimulus locations (*unfilled circles*) with average judged locations in the silhouette (*grey filled circles*) and photograph (*black filled circles*) conditions of the tactile localisation task. *Filled triangles* represent true knuckle locations

corresponding to the condition ('photograph' or 'silhouette') and direction (radio-ulnar or proximo-distal) of error. In contrast to the clear effect of condition on bias magnitude, there was no difference between the two conditions in terms of variable error ($F_{(1,44)} = 0.02$, $p > 0.1$). Despite an increase in bias magnitude in the silhouette relative to the photograph condition, there was no corresponding increase in variable error. Thus, while the presence of visual detail about landmarks leads to a clear shift in the judged location of touch, there is no change in the *precision* of responses.

Intriguingly, there was a significant effect of direction on variable error, with larger errors in the proximo-distal, relative to the radio-ulnar, direction ($F_{(1,44)} = 12.83$, $p < 0.01$), consistent with previous findings that the spatial acuity of touch is higher across than along the limbs (e.g. Cody et al. 2008; Weber 1834/1996). There was no interaction between direction and condition ($F_{(1,44)} = 0.85$, $p > 0.1$).

The Watson-Williams test was used to compare the mean direction of constant error vectors in the two conditions, which did not differ significantly ($F_{(1,22)} = 2.36$). Thus, while the *magnitude* of biases was influenced by the presence of visual detail about landmarks, the *direction* of biases was not.

Knuckle localisation task

Figure 4 shows the mean positions of actual (white circles) and judged (black circles) knuckle locations. Across all fingers, there were significant distal (*M*: 0.17 Bookstein units, $t_{(14)} = 6.37$, $p < 0.0001$) and radial (*M*: 0.02 Bookstein units, $t_{(14)} = 2.56$, $p < 0.05$) biases. There were no significant differences between each knuckle in terms of distal bias ($F_{(4,70)} = 2.06$, $p > 0.05$); however, differences between knuckles in terms of radial bias did emerge ($F_{(4,70)} = 9.05$, $p < 0.0001$). Bonferroni-corrected post hoc multiple comparisons indicated that the thumb knuckle differed significantly from the index, middle, and ring fingers; the fifth and middle fingers also differed in their radial bias (all *p*s < 0.05). An ulnar localisation bias was apparent for the thumb and fifth finger knuckles, with the remaining knuckles showing a radial localisation bias.

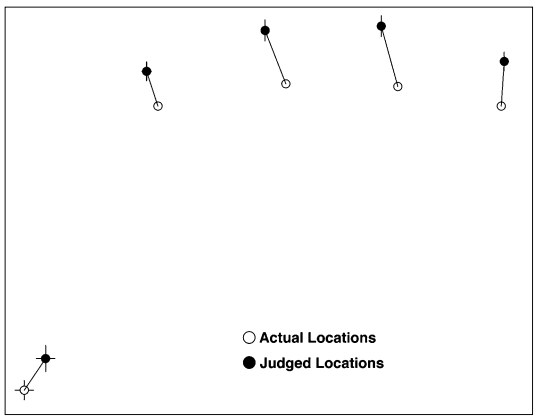

Fig. 4 A comparison of average actual (*unfilled circles*) and judged (*filled circles*) locations in the knuckle localisation task

There was no difference in CE vector direction between the hand and knuckle tasks (Watson-Williams test: $F_{(1,22)} = 1.35$). This indicates a consistency in bias direction across all tasks; mean angle from the Bookstein *x*-axis was 94.01° (*SD* ± 3.03). However, the mean spread of responses was larger in the hand task than in the knuckles task ($t_{(14)} = -15.13$, $p < 0.001$).

Despite a similarity in bias direction, the nature of the relationship between the two tasks remains equivocal. There was no correlation in bias size between the two tasks, in either distal ($r = .23$, $p > 0.1$) or radial ($r = -.35$, $p > 0.1$) components. Nor was there a correlation in precision between the two ($r = -.06$, $p > 0.1$). Each participant's performance in the knuckle localisation task was therefore unrelated to their performance in the tactile localisation task, in terms of either spread of responses or bias magnitude.

Discussion

The presence of visual detail in the response image increases the accuracy—but not the precision—of tactile localisation. Our results clearly replicate the large distal biases of tactile localisation on the hand dorsum reported by Mancini et al. (2011). This bias was reduced by about one-third when visual detail was present in the images. This pattern suggests that participants may implicitly 'fill in' landmarks in a distorted manner when presented with a featureless silhouette. Consistent with this interpretation, in the knuckle localisation, task participants showed large distal biases in judging the location of their knuckles, suggesting surprisingly distorted conceptual understanding of the structure of hands. The fact that directionally similar biases emerged across all tasks and conditions suggests that all are performed with reference to a common, higher-order body representation, from which these biases may originate. However, the lack of correlation across participants between the tactile localisation and knuckle localisation tasks makes the exact relation between these effects unclear. While tactile localisation of stimuli on the skin can be thought of as a purely somatosensory task, par excellence, these results converge with other recent findings to suggest important connections between tactile localisation and vision (e.g. Harrar and Harris 2009; Harrar et al. 2013; Pritchett and Harris 2011; Pritchett et al. 2012).

In the tactile localisation task, a distal bias was found in both conditions, but was of larger magnitude in the

silhouette condition. This suggests that, when tactile and visual input is integrated, veridical visual information may serve to constrain the biases inherent in tactile localisation. As vision of the stimulated body part has been shown to increase tactile acuity (Kennett et al. 2001), it might have been predicted that the precision of responses would be higher in the photograph condition. This was not the case, however, as there was no difference between the photograph and silhouette conditions in terms of variable error (i.e. the 'error of localisation', Weber 1834/1996). Visual information had a specific influence on the size of biases, rather than affecting the precision of responses. Precision in the tactile task may have been ultimately limited by low-level factors such as the spatial acuity of cutaneous mechanoreceptor fields. Neurons representing the hairy skin of the limbs generally have elliptical receptive fields, with the longer axis extending in the proximo-distal plane (e.g. Alloway et al. 1989; Brooks et al. 1961). This may account for the fact that responses were relatively less precise in the proximo-distal direction. Distal bias also varied with proximo-distal grid position, with larger biases at proximal grid locations—this concurs with the pattern observed by Mancini et al. (2011), and demonstrates non-uniformity in distortions of body representation.

Unlike Mancini et al. (2011), we did not find a radial bias on the dorsum of the hand, although there was a significant radial bias component in the knuckle localisation task. While the radial bias observed by Mancini et al. (2011) was much less consistent than the distal bias, appearing only in certain conditions, it remains unclear why it did not emerge in our results. One possibility is that this discrepancy could be due to the fact that the right hand was stimulated in the present study, while Mancini et al. (2011) stimulated the left. Culver (1970) explored tactile localisation on the palm of the hand and found larger radial biases on the left relative to the right hand; it is possible that this asymmetry applies also to the dorsum of the hand, which could account for the pattern of results here.

Significant radial biases did, however, emerge in the knuckle localisation task, in addition to large distal biases. While there were no significant differences between the five knuckles in terms of distal bias, an effect of knuckle on radial bias was apparent. Post hoc comparisons showed that this was due to the influence of the thumb and fifth finger, both of which showed an incongruent ulnar bias. A possible explanation for the ulnar bias on the thumb relates to the orientation of the thumb knuckle. When the hand is placed palm-down on a surface (the position of participants' hands when photographs were taken), the four finger knuckles are oriented 'face on', while the thumb knuckle is oriented 'side on'. Accurate localisation of the centre of the thumb knuckle would therefore require participants to indicate a location on the very edge of the silhouetted image; however, many seemed to be overextending the strategy used for the other fingers, and indicating a location near the centre of the base of the thumb, leading to an apparent ulnar bias.

The large biases found in the knuckle localisation task may inform our understanding of body representation more generally. To know something 'like the back of one's hand' is used to indicate intimate familiarity with something. Remarkably, however, participants are strikingly biased in so basic a task as judging where on their own hand their knuckles are located. There is a longstanding literature on the clinical implications of both body image distortions (e.g. Cash and Deagle 1997; Critchley 1953) and impaired conceptual knowledge about bodies (e.g. Buxbaum and Coslett 2001; Kemmerer and Tranel 2008; Sirigu et al. 1991). Interestingly, recent results have provided clear evidence of both body image distortions (Fuentes et al. 2013) and impaired conceptual knowledge about bodies (this study) in healthy individuals. This pattern suggests that the disruptions of body representation in disease may not differ as qualitatively from healthy cognition as has sometimes been supposed.

The biases in the knuckle localisation task also have interesting implications for understanding the distortions of hand representation for position sense we have recently reported (Longo and Haggard 2010, 2012). Longo and Haggard asked participants to report the perceived external spatial locations of the knuckles and tips of each finger and used the internal configuration of these judgments to construct implicit perceptual maps of perceived hand shape. Intriguingly, these maps showed several large and stereotyped biases, including an overall overestimation of hand width and an overall underestimation of finger length. Longo and Haggard (2010) interpreted these results as evidence for perceptual distortions of the metric properties of the body. The present finding that participants explicitly judge their knuckles as being more distal on the hand than they actually are suggests that the underestimation of finger length found in their localisation task may reflect a *conceptual* misunderstanding of hand configuration, rather a perceptual distortion of finger length. In contrast, no such explanation can be given for the overestimation of hand width, since the distance between the judged locations of pairs of knuckles is similar to their actual distance. This pattern suggests that the overall pattern of distortions observed by Longo and Haggard may reflect a combination of perceptual and conceptual distortions, rather than a single, monolithic distortion.

The biases in both the tactile and knuckle localisation tasks were remarkably directionally similar. This is despite the two tasks presumably utilising relatively dissimilar cognitive systems: knuckle localisation requires the explicit recall of stored representations of the body, while

tactile localisation requires the coding of immediate somatosensory inputs within an internal body representation. As somatosensory input was extremely limited in the knuckle localisation task, the similarities in bias direction between the two tasks were likely to have arisen from one of their shared characteristics: that both tasks required responses within an external, visual frame of reference; or that both tasks involved reference to internal, supramodal body maps. Response modality has not previously been found to affect tactile localisation biases (Harrar et al. 2013; Mancini et al. 2011), so is arguably more likely that the observed similarities in bias direction arise from properties of a shared, internal body representation, with its attendant biases, utilised by both tasks.

Downstream of this common representation, however, the tasks appear to rely upon sufficiently dissociated systems for no other correlation in performance to be found between them, in either precision or bias magnitude. Accurate explicit knowledge of one's own joint locations therefore appears to be unrelated to the magnitude of one's tactile localisation biases. This could be interpreted as evidence against a role of joints in segmenting somatosensory body representation; alternatively, the two tasks may simply harness sufficiently distinct cognitive systems for no relationship to become apparent. While performance in the knuckle localisation task reflects the accuracy of stored body information, performance in the tactile localisation task leans heavily on somatosensory acuity, as evidenced by the fact that variable error was larger in the proximo-distal than in the medio-lateral hand axis, mirroring anisotropies of tactile acuity (Cody et al. 2008; Weber 1834/1996). For those tested in this study at least, there does not seem to be a close relationship between these abilities. The spread of responses was larger in the tactile relative to the knuckle localisation task, likely due to the fact that prior knowledge limits the number of possible response locations in the knuckle localisation task to five. In the tactile localisation task, stimulus locations could potentially be located anywhere on the hand, allowing for higher variability in responses.

To conclude, the present study provides further evidence for consistent distortions in conceptual body representations in healthy individuals. These distortions are attenuated, but not eliminated, when detailed visual information about the hand is made available. Intriguingly, directionally similar biases emerged in a knuckle localisation task that relies exclusively on conceptual knowledge of the body. It therefore seems likely that such biases originate from distorted body representations, rather than from purely perceptual factors.

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