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1 RUNNING HEAD: Visual Detail and Tactile Localisation

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6 Visual Detail about the Body Modulates Tactile Localisation Biases

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Abstract

1
2 The localisation of tactile stimuli requires the integration of visual and somatosensory inputs within
3 an internal representation of the body surface, and is prone to consistent bias. Joints may play a role
4 in segmenting such internal body representations, and may therefore influence tactile localisation
5 biases, although the nature of this influence remains unclear. Here, we investigate the relationship
6 between conceptual knowledge of joint locations and tactile localisation biases on the hand. In one
7 task, participants localised tactile stimuli applied to the dorsum of their hand. A distal localisation
8 bias was observed in all participants, consistent with previous results. We also manipulated the
9 availability of visual information during this task, to determine whether the absence of this
10 information could account for the distal bias observed here and by Mancini and colleagues (2011).
11 The observed distal bias increased in magnitude when visual information was restricted, without a
12 corresponding decrease in precision. In a separate task, the same participants indicated, from
13 memory, knuckle locations on a silhouette image of their hand. Analogous distal biases were also
14 seen in the knuckle localisation task. The accuracy of conceptual joint knowledge was not
15 correlated with tactile localisation bias magnitude, although a similarity in observed bias direction
16 suggests that both tasks may rely on a common, higher-order body representation. These results also
17 suggest that distortions of conceptual body representation may be more common in healthy
18 individuals than previously thought.

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20 Keywords: Touch, Tactile Localisation, Body Representation

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Introduction

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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., A β , A δ , 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 and colleagues (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

1 asked participants to indicate the perceived location of touch by clicking a mouse cursor on a
2 silhouetted image of their hand, partly in order to minimise the use of visual landmarks, such as
3 knuckles, as reference points. Of course, the fact that visual detail about landmarks was not present
4 in the silhouetted image does not imply that participants were not implicitly filling in such detail –
5 possibly incorrectly – in ways which might have affected the obtained biases.

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

16 Method

17 *Participants*

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

23 *Materials and procedure*

24 *Tactile localisation task.* Procedures were similar to those of Mancini and colleagues (2011).
25 At the start of the experiment, a photograph of the participant's right hand against a plain
26 background was captured using a digital camera. The resulting image (3264x2448 pixels) was one

1 of two images presented to participants during the experiment. The second image was produced by
2 editing the original image with the threshold tool in the GNU Image Manipulation Program (GIMP
3 version 2.8.2), to generate a monochrome 'Silhouette' image. All textural and colour information
4 was thus removed from the original photograph, leaving a black and white outline of the
5 participant's hand. Figure 1 shows examples of 'silhouette' and 'photo' stimuli. During the
6 experiment, images were presented on a display monitor 75cm from where participants were seated,
7 subtending a visual angle of approximately 18.3° horizontally and 13.7° vertically. When presented
8 in this way, images were of approximately equal size to participants' actual hands.

9 Participants sat with both arms lying flat on a table, uncrossed and perpendicular to the
10 shoulders, with the dorsum of the hand facing up. Both hands were occluded from the participant's
11 view by a piece of plain black card. During each trial, participants were stimulated at one of twelve
12 locations (landmarks) on the dorsal surface of their right hand. Landmarks were arranged in a 4 x 3
13 grid, and marked in advance by drawing dots with a non-permanent marker through a plastic
14 stencil. One edge of the stencil was aligned with the participant's wrist, so that the three columns of
15 landmarks lay longitudinally on the hand. Participants' hands were out of view while landmarks
16 were being applied, and participants did not see the landmark locations until the experiment was
17 complete. Figure 2 shows a schematic overview of the experimental setup. Landmarks were
18 stimulated once per trial with a von Frey hair (255 milliNewtons). This force is strong enough to be
19 easily felt, but painless, and was demonstrated to participants prior to the start of the experiment.

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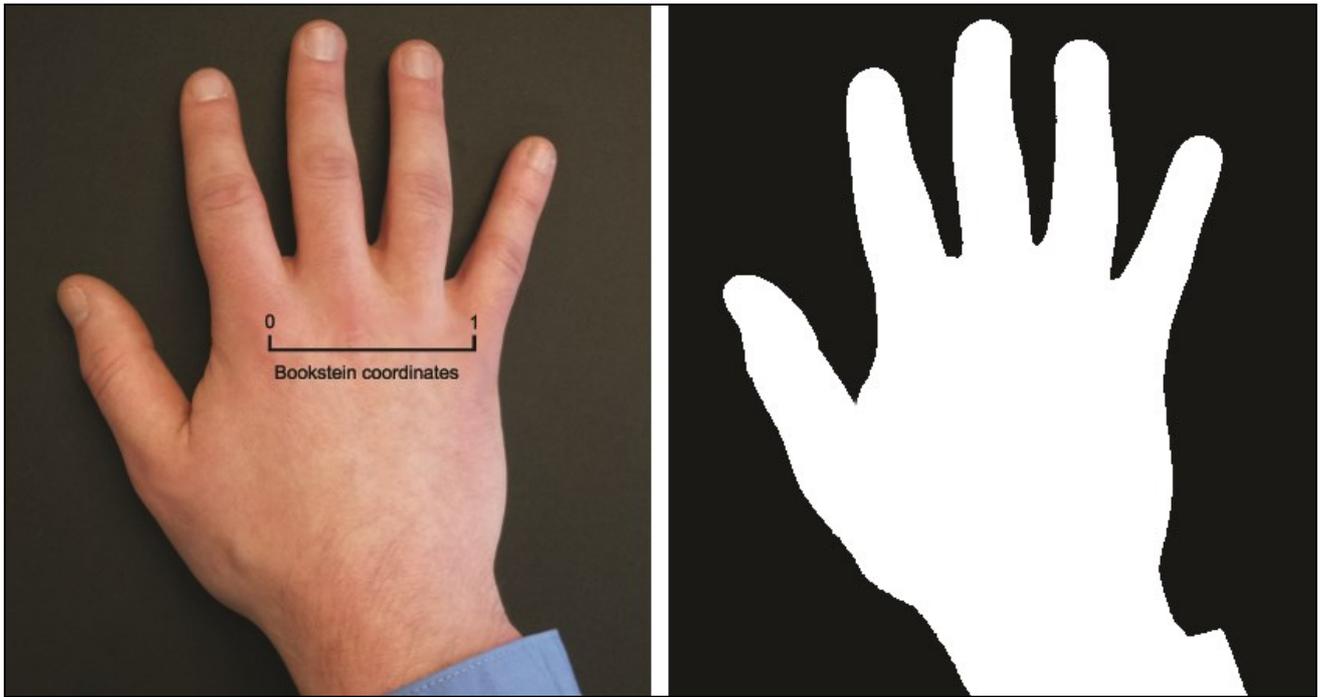


Fig. 1 An example of 'photo' (left) and 'silhouette' stimuli similar to those used in the experiment

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 2s, after which either the 'photo' 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 'photo' 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 minutes.

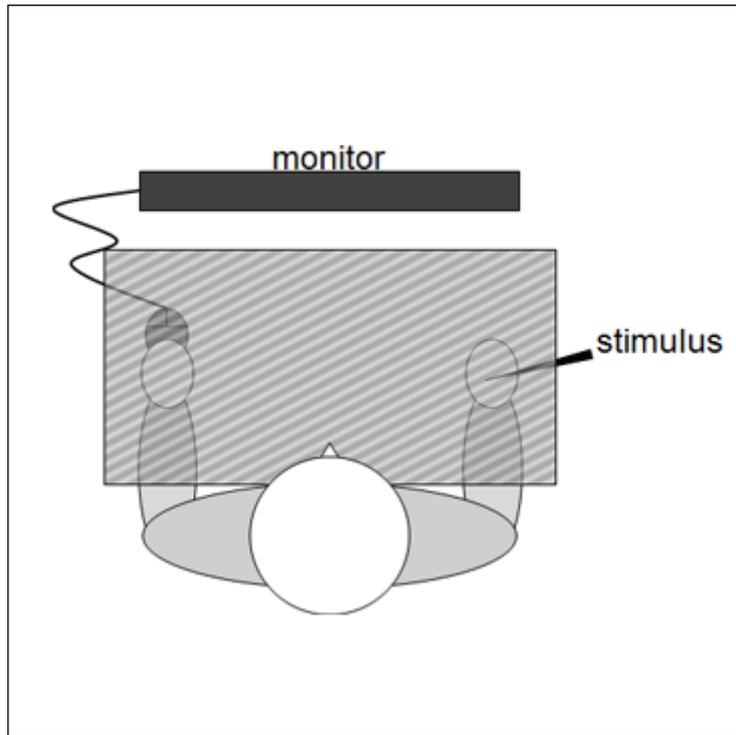


Fig. 2 Schematic overview of the experimental setup. The striped area represents an opaque cover that hid participants' hands from view for the duration of both experiments

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 three minutes to complete. At the end of the experiment a second photograph

1 was taken of the participant's right hand, with the landmark dots visible, for use in analysis.

2

3 *Analysis*

4 In order to compare participants' responses and stimulus/knuckle locations, all were
5 encoded into a common frame of reference using so-called 'Bookstein coordinates' (Bookstein
6 1991), as in the study of Mancini and colleagues (2011). The centre of the index finger knuckle was
7 defined as Bookstein co-ordinate (0,0), and the centre of the little finger knuckle as (1,0). Stimulus
8 locations, knuckle locations, and responses were recorded within their relevant images as (x,y) co-
9 ordinates relative to the axis formed by these loci, and then combined within a common coordinate
10 system for analysis.

11 Performance was analysed in terms of bias direction and magnitude (constant error, or CE,
12 vector), and the spread of responses around the mean response location (variable error – a measure
13 of precision). The CE vector is the vector between the actual and perceived locations, and can be
14 decomposed into proximo-distal and medio-lateral components. Because Bookstein coordinates are
15 defined using the distance between the knuckles of the index and little fingers as the unit vector
16 along the x-axis, the medio-lateral component of the CE vector can be calculated as the difference
17 in x-coordinates, while the proximo-distal component can be calculated as the difference in y-
18 coordinates. Variable error was calculated as the standard deviation of responses, separately for the
19 medio-lateral (i.e., standard deviation of x-coordinates) and proximo-distal (i.e., standard deviation
20 of y-coordinates) axes.

21 Comparisons between the direction of constant errors across conditions were performed
22 using the Watson-Williams test, a generalisation of a one-way ANOVA for circular data (such as
23 angles) to test the null hypothesis that mean vector direction is equal across conditions (Batschelet
24 1981). The Watson-Williams test was performed using the CircStat toolbox for MATLAB (Berens
25 2009).

26 Participants were asked to report any unintentional responses, which were noted and

1 removed from subsequent analysis (0.76% of trials). Outliers were defined as responses that fell at a
 2 distance of three or more standard deviations from a participant's mean response for a particular
 3 landmark (the average judged location, collapsed across all other trials) and were removed from
 4 analysis (1.11% of trials).

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Results

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Tactile Localisation Task

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

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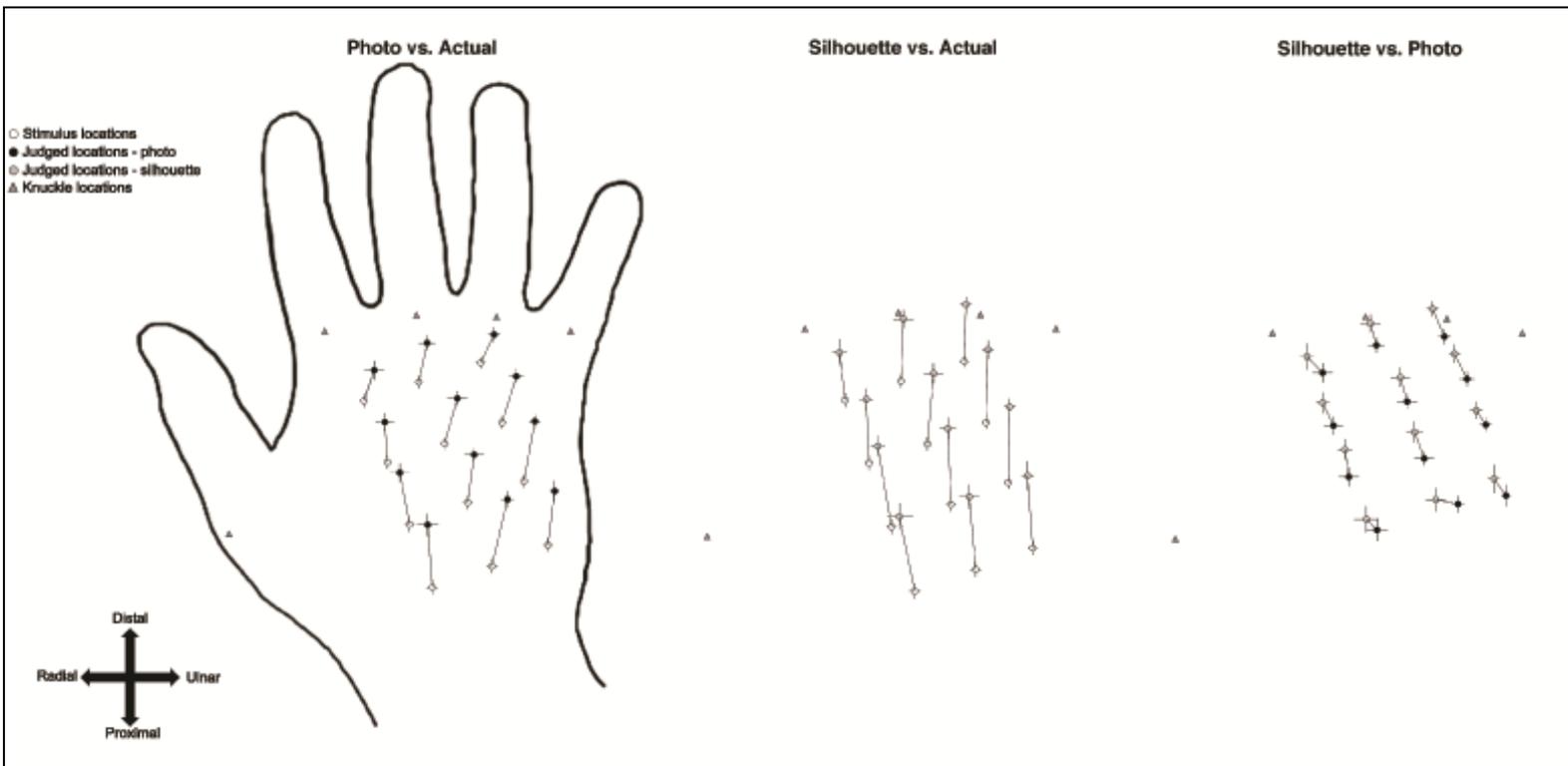
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Separate 4x3x2 factorial ANOVAs were carried out on the distal and radial components of
 the CE vector for each stimulus location, with levels corresponding to the four rows and three
 columns of the stimulus grid, as well as condition ('silhouette' or 'photo'). 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 'photo'
 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.



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

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6 Variable errors were separated into radio-ulnar and proximo-distal components prior to
 7 analysis. A 2x2 ANOVA was carried out on these components, with levels corresponding to the
 8 condition ('photo' or 'silhouette') and direction (radio-ulnar or proximo-distal) of error. In contrast
 9 to the clear effect of condition on bias magnitude, there was no difference between the two
 10 conditions in terms of variable error ($F_{(1,44)} = 0.02, p > 0.1$). Despite an increase in bias magnitude
 11 in the silhouette relative to the photo condition, there was no corresponding increase in variable
 12 error. Thus, while the presence of visual detail about landmarks leads to a clear shift in the judged
 13 location of touch, there is no change in the *precision* of responses.

14

15 Intriguingly, there was a significant effect of direction on variable error, with larger errors in
 16 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

1 al. 2008; Weber 1834/1996). There was no interaction between direction and condition ($F_{(1,44)} =$
 2 0.85, $p > 0.1$).

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

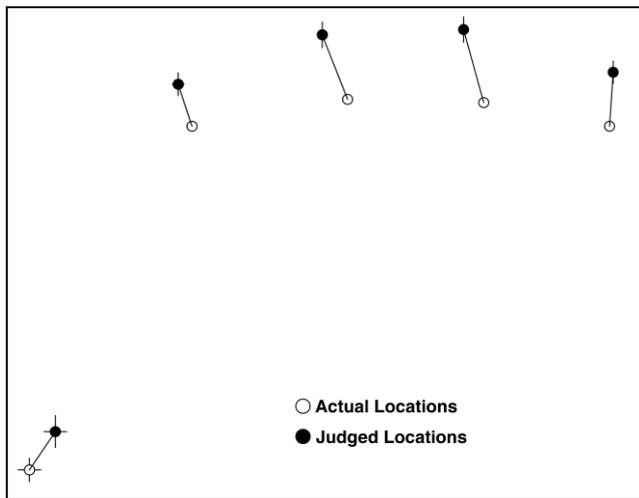
7 *Knuckle Localisation Task*

8 Figure 4 shows the mean positions of actual (white circles) and judged (black circles)
 9 knuckle locations. Across all fingers, there were significant distal ($M: 0.17$ Bookstein units, $t_{(14)} =$
 10 6.37, $p < 0.0001$) and radial ($M: 0.02$ Bookstein units, $t_{(14)} = 2.56$, $p < 0.05$) biases. There were no
 11 significant differences between each knuckle in terms of distal bias ($F_{(4,70)} = 2.06$, $p > 0.05$);
 12 however, differences between knuckles in terms of radial bias did emerge ($F_{(4,70)} = 9.05$, $p <$
 13 0.0001). Bonferroni-corrected post-hoc multiple comparisons indicated that the thumb knuckle
 14 differed significantly from the index, middle, and ring fingers; the fifth and middle fingers also
 15 differed in their radial bias (all $ps < .05$). An ulnar localisation bias was apparent for the thumb and
 16 fifth finger knuckles, with the remaining knuckles showing a radial localisation bias.

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

21 Despite a similarity in bias direction, the nature of the relationship between the two tasks
 22 remains equivocal. There was no correlation in bias size between the two tasks, in either distal ($r =$
 23 .23, $p > .01$) or radial ($r = -.35$, $p > .1$) components. Nor was there a correlation in precision
 24 between the two ($r = -.06$, $p > .01$). Each participant's performance in the knuckle localisation task
 25 was therefore unrelated to their performance in the tactile localisation task, in terms of either spread
 26 of responses or bias magnitude.

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

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Discussion

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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 and colleagues (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

1 (e.g., Harrar and Harris 2009; Harrar et al. 2013; Pritchett & Harris, 2011; Pritchett et al. 2012).

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

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

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

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

23 The biases in the knuckle localisation task also have interesting implications for
24 understanding the distortions of hand representation for position sense we have recently reported
25 (Longo and Haggard, 2010, 2012). Longo and Haggard asked participants to report the perceived
26 external spatial locations of the knuckles and tips of each finger and used the internal configuration

1 of these judgments to construct implicit perceptual maps of perceived hand shape. Intriguingly,
2 these maps showed several large and stereotyped biases, including an overall overestimation of
3 hand width and an overall underestimation of finger length. Longo and Haggard (2010) interpreted
4 these results as evidence for perceptual distortions of the metric properties of the body. The present
5 finding that participants explicitly judge their knuckles as being more distal on the hand than they
6 actually are suggests that the underestimation of finger length found in their localisation task may
7 reflect a *conceptual* misunderstanding of hand configuration, rather a perceptual distortion of finger
8 length. In contrast, no such explanation can be given for the overestimation of hand width, since the
9 distance between the judged locations of pairs of knuckles is similar to their actual distance. This
10 pattern suggests that the overall pattern of distortions observed by Longo and Haggard may reflect a
11 combination of perceptual and conceptual distortions, rather than a single, monolithic distortion.

12 The biases in both the tactile and knuckle localisation tasks were remarkably directionally
13 similar. This is despite the two tasks presumably utilising relatively dissimilar cognitive systems:
14 knuckle localisation requires the explicit recall of stored representations of the body, while tactile
15 localisation requires the coding of immediate somatosensory inputs within an internal body
16 representation. As somatosensory input was extremely limited in the knuckle localisation task, the
17 similarities in bias direction between the two tasks were likely to have arisen from one of their
18 shared characteristics: that both tasks required responses within an external, visual frame of
19 reference; or that both tasks involved reference to internal, supramodal body maps. Response
20 modality has not previously been found to affect tactile localisation biases (Harrar et al. 2013;
21 Mancini et al. 2011), so is arguably more likely that the observed similarities in bias direction arise
22 from properties of a shared, internal body representation, with its attendant biases, utilised by both
23 tasks.

24 Downstream of this common representation, however, the tasks appear to rely upon
25 sufficiently dissociated systems for no other correlation in performance to be found between them,
26 in either precision or bias magnitude. Accurate explicit knowledge of one's own joint locations

1 therefore appears to be unrelated to the magnitude of one's tactile localisation biases. This could be
2 interpreted as evidence against a role of joints in segmenting somatosensory body representation;
3 alternatively, the two tasks may simply harness sufficiently distinct cognitive systems for no
4 relationship to become apparent. While performance in the knuckle localisation task reflects the
5 accuracy of stored body information, performance in the tactile localisation task leans heavily on
6 somatosensory acuity, as evidenced by the fact that variable error was larger in the proximo-distal
7 than the medio-lateral hand axis, mirroring anisotropies of tactile acuity (Cody et al. 2008; Weber
8 1834/1996). For those tested in this study at least, there does not seem to be a close relationship
9 between these abilities. The spread of responses was larger in the tactile relative to the knuckle
10 localisation task, likely due to the fact that prior knowledge limits the number of possible response
11 locations in the knuckle localisation task to five. In the tactile localisation task, stimulus locations
12 could potentially be located anywhere on the hand, allowing for higher variability in responses.

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

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