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**Journal Article**



**Citation:**

Mancini, F.; Longo, M.R.; Iannetti, G.T.; Haggard, P. (2011)
A supramodal representation of the body surface –
*Neuropsychologia* v.49(5), pp. 1194-1201

# A Supramodal Representation of the Body Surface

**Flavia Mancini[1, 2], Matthew R. Longo[1,4], Gian Domenico Iannetti[3], Patrick Haggard[1]**

[1]Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, United Kingdom

[2]Department of Psychology, University of Milano-Bicocca, Milano 20126, Italy

[3]Department of Neuroscience, Physiology, and Pharmacology, University College London, London WC1E 6BT, United Kingdom

[4]Department of Psychological Sciences, Birkbeck, University of London, London WC1E 7HX, United Kingdom

*Correspondence to:*
Patrick Haggard
Institute of Cognitive Neuroscience, University College London
17 Queen Square, London WC1N 3AR, United Kingdom
p.haggard@ucl.ac.uk

Number of figures and tables: 5 figures, 1 table
Supplemental material: 1 figure, 1 table
Number of pages: 23
Number of words: 5706

## Abstract

The ability to accurately localize both tactile and painful sensations on the body is one of the most important functions of the somatosensory system. Most accounts of localization refer to the systematic spatial relation between skin receptors and cortical neurons. The topographic organization of somatosensory neurons in the brain provides a map of the sensory surface. However, systematic distortions in perceptual localization tasks suggest that localizing a somatosensory stimulus involves more than simply identifying specific active neural populations within a somatotopic map. Thus, perceptual localization may depend on both afferent inputs and other unknown factors. In four experiments, we investigated whether localization biases vary according to the specific skin regions and subset of afferent fibers stimulated. We represented localization errors as a 'perceptual map' of skin locations. We compared the perceptual maps of stimuli that activate Aβ (innocuous touch), Aδ (pinprick pain), and C fibers (non-painful heat) on both the hairy and glabrous skin of the left hand. Perceptual maps exhibited systematic distortions that strongly depended on the skin region stimulated. We found systematic distal and radial (i.e, toward the thumb) biases in localization of touch, pain, and heat on the hand dorsum. A less consistent proximal bias was found on the palm. These distortions were independent of the population of afferent fibers stimulated, and also independent of the response modality used to report localization. We argue that these biases are likely to have a central origin, and result from a supramodal representation of the body surface.

**Keywords**: somatosensory perception, pain, touch, body representation, multisensory integration, parietal cortex

## Introduction

When an insect lands on the back of our hand, we need to localize it precisely in order to swat it away. Localization becomes even more important if the insect represents a threat to our bodies, e.g. it painfully bites us. Thus, the localization of cutaneous stimuli on the body surface (*topognosis* or *locognosis*) is fundamental for effective use of somatosensory processing. The representations used to achieve localization, however, are only poorly understood.

Many studies have emphasized that the systematic spatial relation between skin receptors and cortical neurons (i.e., somatotopy) allows precise perceptual localization (for a review, see J. L. Ochoa, 2010), at least in densely-innervated skin regions. Since Weber's (1834/1996) studies of the 'error of localization', the majority of psychophysical studies of touch and pain localization have focused instead on the *precision* of localization (e.g., Harris, Karlov, & Clifford, 2006; Harris, Thein, & Clifford, 2004; Moore & Schady, 1995; Ylioja, Carlson, Raij, & Pertovaara, 2006). Fewer studies have investigated *biases* in perceptual localization, though there have been sporadic reports of various systematic biases (e.g., Boring, 1942; Culver, 1970; Parrish, 1897). These biases can be thought of as reflecting a distorted 'perceptual map' of the skin surface (Rapp, Hendel, & Medina, 2002; Trojan et al., 2006). Importantly, biases (i.e. constant error) in localization are logically independent of the precision of localization (i.e. variable error). The nature and origin of these distortions are unclear, but their existence suggests that perceptual localization involves more than simply identifying specific active neural populations within a somatotopic map. Particularly, it has been suggested that biases in perceptual localization might reflect the reference to some anatomical point, or local sign that could provide a perceptual anchor for identifying the site of stimulation (Culver, 1970; Weber, 1834/1996). Thus, localizing a somatosensory stimulus may depend on both afferent inputs and other unknown factors.

Consistent biases for tactile localization have been reported, including radial bias towards the thumb on the palm (Culver, 1970), and distal bias towards the wrist on the forearm (Azanon, Longo, Soto-Faraco, & Haggard, 2010; Parrish, 1897). Further, localization of thermal stimuli on the forearm elicited more idiosyncratic biases, which varied from person to person (Trojan et al., 2006, 2009). While these studies are suggestive, they provide only a fragmented view of the overall perceptual

map of the skin, so that its global organization remains unclear.

We therefore performed several experiments measuring constant errors in localization to provide a detailed description of perceptual maps for a single body part, the hand. We specifically investigated: (1) whether there are systematic constant errors in perceptual localization on different skin regions (e.g., hairy vs. glabrous skin), and (2) whether such biases are specific to certain classes of afferent inputs (e.g., innocuous vs. nociceptive), or alternately are supramodal. Thus, we studied localization biases on the hairy and the glabrous skin of the left hand in response to somatosensory stimuli which selectively activate afferents mediating tactile (Aβ), pinprick pain (Aδ), or non-painful heat (C) sensations.

The study of the organization of the perceptual map of the body may clarify its neural bases. For example, there is evidence for differential organization of early somatosensory processing of touch and pain (e.g., Chen, Friedman, & Roe, 2009; Kenshalo, Iwata, Sholas, & Thomas, 2000; Ploner, Schmitz, Freund, & Schnitzler, 2000; Tseng, Tseng, Chao, Lin, & Hsieh, 2010; Whitsel, Favorov, Li, Quibrera, & Tommerdahl, 2009). In particular, nociceptive processing may not share the complex, hierarchical organization of tactile processing (Ploner et al., 2000). Further, intraneural recording studies report a very precise match between the activated afferent unit, and perceptual localization (for a review, see Ochoa, 2010), suggesting that localizing a somatosensory stimulus within a somatotopic map is an important component of localizing it on the body. Therefore, if localization biases arise from the organization of early, modality-specific, cortical areas, different patterns of bias would be expected for localization of innocuous and nociceptive inputs, indicating that perceptual maps mainly depend on somatotopic maps. Alternatively, localization biases may arise from a higher-level, supramodal representation of the body surface, in which case a common perceptual map would be expected across different sensory inputs.

## Materials and Methods

Four experiments were conducted, investigating localization on the left hand (see Table 1). *Experiment 1* investigated the localization of touch on the hairy skin of the back of the hand (fingers and dorsum). Participants localized an innocuous tactile

stimulus (Aβ fibers) applied to their hand by using a mouse to position a cursor on a picture of the silhouette of their own hand, presented on a computer monitor. *Experiment 2* compared perceptual maps of different sets of fibers on the hairy and glabrous skin of the hand; specifically, we investigated whether the possible localization biases on the palm and on the dorsum were depending on the sensory class of afferent fibers stimulated, by comparing localization of stimuli activating (a) touch (Aβ fibers), (b) first pain (Aδ fibers), or (c) second pain (C fibers). *Experiment 3* ensured that the biases we observed were actually defined on the skin surface, rather than in a retina- or torso-centered frame of reference, by varying the postural orientation of the stimulated hand relative to the rest of the body. Finally, *Experiment 4* served to control for the possibility that biases were a product of the response modality (i.e., pointing with a mouse cursor), rather than localization as such, by having participants localize stimuli haptically on a prosthetic hand.

(Table 1 about here)

**Participants**

Thirty-three healthy volunteers (17 females) between 18 and 46 years old (mean ± SD, 24.8 ± 5.3 years) participated ($n$ = 10 for Exp. 1; $n$ = 9 for Exp. 2, $n$ = 9 for Exp. 3, and $n$ = 5 for Exp. 4) for payment. All the participants were right-handed (Edinburgh Inventory; mean ± SD, 90.8 ± 19.3). Procedures were approved by the UCL ethics committee.

**Stimuli**

*Mechanical stimulation*

In Exps. 1-4, the tactile stimuli consisted in a calibrated nylon filament attached to a wooden stick (von Frey hair, 2.41gf bending weight, diameter 0.50 mm). Each stimulus was administered manually by the experimenter in a pre-marked location on the participant's unseen hand.

*Thermal stimulation*

In Exp. 2, pain and heat sensations were evoked delivering pulses of radiant heat that were generated by an infrared neodymium:yttrium-aluminum-perovskite (Nd:YAP) laser with a wavelength of 1.34 μm (ElEn, Florence, Italy). At this short

wavelength, the skin is highly transparent to the laser radiation, and consequently, the laser pulses directly and selectively activate Aδ- and C-fiber nociceptive terminals located in the superficial layers of hairy and glabrous skin (Iannetti, Zambreanu, & Tracey, 2006). The laser pulse was transmitted via an optic fiber and focused by lenses to a spot diameter of approximately 7 mm. A visible He-Ne laser spot was used to point the Nd:YAP laser at the target location. The duration of each laser pulse was 4 ms. The skin temperature of the area stimulated was monitored at the beginning of each block with an infrared thermometer, and kept at the temperature of approximately 32º C (mean ± SD, 32.2 ± 0.53) (see Iannetti et al., 2004, for the effect of baseline skin temperature on laser-evoked pain ratings and brain responses). To avoid increases of baseline temperature, as well as nociceptor fatigue or sensitization, at least 1 min was allowed to elapse between successive stimulations of the same location.

Two laser energies were used: 2 J to elicit non-painful heat sensations resulting from C-fiber activation (second pain), and 3 J to elicit pinprick pain sensations resulting from activation of Aδ fibers (first pain). The appropriateness of these energies was verified at the beginning of the experiment, by asking each participant to rate verbally the intensity of the sensation elicited by each laser energy on a Likert scale ranging from 0 to 10. A score of 0 was defined as "no pricking sensation" and 10 was defined as "the most intense pricking sensation imaginable". The 2 J stimulus elicited a mean rating of 0.7 (SD = 0.7) and the 3 J stimulus a mean rating of 3.4 (SD = 0.9).

In 5 of the 9 participants reaction times (RTs) to the detection of laser pulses were also tested, to ensure that 2 J laser stimuli were above the activation threshold of C-fibers but below the activation threshold of Aδ fibers. Indeed, RTs to C-fiber stimulation were longer than 650 ms, i.e. the cutoff between Aδ and C-fiber RTs (Mouraux, Guerit, & Plaghki, 2003; Plaghki & Mouraux, 2003) (mean RT for 2 J stimuli: ± SD, 1110 ± 433 ms), whereas RTs to Aδ fiber stimulation were not (mean ± SD, 468 ± 184 ms). In one participant we increased the energies to 3.5 J and 2.5 J to achieve differential activation of Aδ and C-fibers, on the basis of RTs.

**Procedure**

*Experiment 1*

In Exp. 1, the participants sat centrally in front of a computer screen, with

their left hand lying flat on the table, palm down, with the wrist straight. Their left hand and forearm were occluded by a black curtain (Figure 1b). On each trial, participants looked at a black screen and received a single light touch on the hairy skin of their left hand. Each stimulus was delivered in one of the 45 pre-marked locations on the hairy skin of the hand shown in Figure 1a. Stimulus locations were formed by a 3 x 3 grid approximately centred on the dorsum, a 2 x 2 grid on the proximal and middle segment of each finger, and a single 2 x 2 grid covering both segments of the thumb. The locations were marked with a felt pen at the beginning of the study by placing a plastic stencil over each skin surface. Approximately 1 sec after the stimulus, a life-size silhouette outline of the participant's hand was presented on the screen. We silhouetted photographs of the hand (high contrast black & white picture rendering a white opaque shape of the hand on a dark background), to remove any visual information about specific features of the hand, such as knuckles that could be used as landmarks. The mouse cursor had the shape of a thin cross and its starting position on the screen was randomly varied for each trial. The participant moved and clicked the mouse cursor in the location on the silhouette corresponding to where they perceived their own hand to have been stimulated. Participants were asked to be deliberate and precise in their responses and to avoid ballistic points. The position of the mouse click was computed and recorded. Participants were never allowed to look at their stimulated hand throughout the experiment. Ten blocks of 45 trials were presented, interrupted by short rest breaks, for a total of 450 trials. Each block consisted of one judgment of each location in random order. The experiment lasted approximately 60 min.

(Figure 1 about here)

*Experiment 2*

In Exp. 2, three types of sensory stimulation were administered to nine locations on both the dorsum and the palm of the left hand, in different sessions: innocuous stimuli eliciting tactile sensations (mediated by Aβ fibers), high-intensity radiant heat eliciting pinprick sensations (mediated by Aδ fibers), and low intensity radiant heat eliciting hot sensations (mediated by C-fibers). The task was the same as in the previous two experiments. Within each session, three blocks of each type of sensory stimulation were presented in a randomised order. Four sessions of 81 trials

each were administered (two for each skin surface) in a counterbalanced ABBA order.

*Experiment 3*

Though we interpret biases in Exps. 1-2 as reflecting mislocalization on the skin surface, such biases could potentially result from biases in motor control of the manual response or unspecified biases in a retina-centred coordinate frame. To control for this possibility, we performed an additional experiment in which the hand was placed in two different postures: 'straight ahead' (as in Exps. 1-2) or 'rotated' 90° clockwise relative to the body with the fingers pointing to the right. In the latter case, the visual display of the hand was also rotated to have the same orientation as the participant's hand. Tactile localisation was tested on the hand dorsum in the two postures in separate sessions of 90 randomised trials each, in a counterbalanced order across participants.

*Experiment 4*

We performed an additional control experiment to ensure that biases found in Exps. 1-3 were not an artifact of the response modality (visual localization). We adapted the procedure used by Elithorn et al. (1953), having participants respond by pointing with their non-stimulated hand on a left rubber hand. Blindfolded participants explored the rubber hand haptically with their right hand, then placed their right index finger on the location on the rubber hand corresponding to where they perceived the tactile stimulus to have been on their left hand dorsum. When they indicated verbally that they had made their response, the experimenter triggered a webcam suspended directly above the rubber hand to capture a photograph (1600 by 1200 pixels) showing the participant's index finger (with the midline previously marked) indicating the perceived location.

**Analyses**

A picture of each participant's hand with the grid of stimulus locations marked on it was taken at the beginning of the experiment. The locations of the knuckles, fingertips, stimulation locations, and participant's estimates of stimulus location were computed in x and y pixel coordinates. In order to place the actual and judged locations of each landmark into a common coordinate frame, we used the two-point registration method developed by Bookstein (1991) (*Bookstein coordinates*): two

specified landmarks are defined as being points (0,0) and (1,0) with other landmarks positioned accordingly. We defined the knuckle of the little finger as point (0,0) and that of the index finger as point (1,0). This procedure has two important benefits. First, it places the locations of the stimuli (coded from a photograph of each participant's hand) and the locations of the responses (defined by mouse clicks in Exps. 1-4 and by a photograph of the rubber hand in Exp. 5) into a common body-scaled, reference frame for comparison. Second, it defines unit length relative to the size of each participant's hand, removing individual differences in overall hand size, allowing averaging across participants.

Two independent components of localization error can be calculated (Figure 1c). Constant Error (CE) is the average signed error of a set of localization attempts. It represents localization bias, and is our main interest here. Variable Error is the standard deviation of a set of responses from the average response location. It represents the precision (consistency) of localization. The full report of the variable errors is given in the Supplementary Material.

We focused our analyses on the CE, which was analysed in two distinct ways. First, the CE was considered as an error vector starting from the actual location of one stimulus and pointing to its perceived location (Figure 1d). The CE *direction* is given by the angle of this vector (where 0° represents the line connecting the knuckles of the index and little fingers), while the CE *size* is given by the length of this vector (Figure 1d). In addition, to represent localization biases in a hand-centred reference frame, we also decomposed the CE vector into two components, one aligned with the proximo-distal axis of the hand (perpendicular to the line connecting the knuckles of the index and little fingers) and the other aligned with the ulnar-radial axis (parallel to that line) (Figure 1e).

CE direction was analysed using Watson-Williams non-parametric circular statistics test (Batschelet, 1981; Berens, 2009; Watson & Williams, 1956). This is equivalent to a classical one-factor ANOVA, and assesses whether two or more samples share a common mean direction or not. The CE size was analysed by repeated measures ANOVA. The vector components in the proximo-distal axis and in the ulnar-radial axis were compared to zero (null bias) by t-tests.

## Results

### Experiment 1

*Hand dorsum*

Figure 2a shows the mean position of the actual (grey circles) and the judged (white circles) locations of the tactile stimuli on the back of the hand. On the dorsum, there were significant radial ($t_{(9)} = 4.62$, $p = 0.001$) and distal components of the CE vector ($t_{(9)} = 6.49$, $p < 0.0001$). These results demonstrate striking similarity of localization biases across participants.

Moreover, the CE vectors of the nine dorsum locations did not differ in mean direction (Watson-Williams test: $F < 1$), which was, on average, 67.72° (SE ± 1.57) (see Figure 2b, where each arrow corresponds to the mean direction of each location CE vector). They did, however, differ in their size. Proximo-distal, but not radio-ulnar, position within the grid had a significant effect on the CE sizes (vector lengths) ($F_{(2,18)} = 17.61$, $p = 0.001$). CE sizes were larger for proximal than for distal stimulus locations. Bonferroni post-hoc comparisons showed a significant difference between the most distal row and both the middle ($p < 0.001$) and the proximal ones ($p = 0.006$).

*Hairy skin of fingers*

In 3.02% of trials where the stimulus was delivered on the back of the fingers, participants indicated a different finger from that stimulated. These interdigit errors were discarded.

Localization judgments showed significantly smaller CE sizes ($t_{(9)} = 7.13$, $p < 0.0001$) on the fingers than on the hand dorsum, though no significant differences were found between the five fingers ($F_{(4,36)} = 2.25$, $p = 0.083$).

The proximal segments of each finger except the thumb showed significant distal biases ($p$s < 0.05); the proximal segments of the little and ring finger exhibited also significant radial components of bias ($p$s < 0.05), and the thumb significant ulnar component ($t_{(9)} = -3.07$, $p < 0.001$).

Conversely, the middle segments did not show any significant distal component of bias ($p$s > 0.05). The proximal component was significant for the middle segment of the index finger only ($t_{(9)} = -5.83$, $p = 0.021$). Furthermore, the

middle segments of the little and ring fingers showed significant radial components of bias ($p$s < 0.05), whereas the index finger and the thumb exhibited a significant ulnar component ($p$s < 0.05).

Overall, a small proximal bias was found on the middle segments (mean ± SE, -0.01 ± 0.19), and a distal bias on the proximal segments (mean ± SE, 0.06 ± 0.01), leading to a significant difference in bias in the proximo-distal axis between these segments ($F_{(1,9)} = 11.87$, $p = 0.007$).

All analyses were repeated using Bookstein coordinates centred on each finger knuckle and tip, as opposed to knuckle of the little and index fingers: the pattern of results was not changed.

(Figure 2 about here)

**Experiment 2**

On the hand *dorsum*, analysis of the proximo-distal and ulnar-radial components of the CE vector (figure 4) again showed significant distal bias ($t_{(8)} = 5.24$, $p < 0.0001$), and also bias towards the thumb ($t_{(8)} = 8.54$, $p < 0.0001$). This replicates the results of Exps. 1-2. In contrast, a just-significant proximal shift ($t_{(8)} = -2.30$, $p = 0.049$) was found on the palm (Figure 3).

*Effects of sensory modality*

Mislocalizations of high and low-energy nociceptive stimuli (pain and heat) were similar to those of tactile stimuli, both on the hand dorsum and palm (Figure 3).

On the *dorsum*, analysis of the proximo-distal and ulnar-radial components of the CE vector again showed significant distal bias (pain: $t_{(8)} = 9.19$, $p < 0.0001$; heat: $t_{(8)} = 14.49$, $p < 0.0001$) and also radial bias towards the thumb (pain: $t_{(8)} = 3.84$, $p = 0.005$; heat: $t_{(8)} = 2.67$, $p = 0.028$). Inspection of the direction of the CE vector showed similar directions for touch (mean ± SE, 63.04° ± 1.49), pain (mean ± SE, 80.90° ± 4.08), and heat stimulation (mean ± SE, 86.21° ± 9.62) (Figure 4). We compared the directions of touch and pain vectors for each of the 9 locations, in a series of 9 Watson-Williams tests (Watson & Williams, 1956). The direction of CE vectors for touch and pain stimulation were statistically equivalent for 8 of the 9 locations tested. In the most proximal and ulnar location the difference was significant ($F_{(1,16)} = 6.22$, $p = 0.024$). However, one significant result might be expected in nine separate tests, under the binomial distribution ($p = 0.39$). Comparing the touch and heat conditions,

different CE directions were found for the three locations closest to the thumb, and for the one in the centre of the grid ($p < 0.05$): the estimated locations of low-energy nociceptive stimuli (heat) tended to be shifted distally and towards the centre of the grid. No significant differences emerged comparing the CE directions of each heat and pain stimuli. The size of CE vectors was greater in the heat (mean ± SE, 0.39 ± 0.01) than in the touch (mean ± SE, 0.28 ± 0.04) condition ($t_{(8)} = -2.69$, $p = 0.027$). Other pairwise comparisons showed comparable CE lengths.

On the *palm*, analysis of the proximo-distal and ulnar-radial components of the CE vector showed a significant proximal bias in each sensory condition (touch: $t_{(8)} = -2.30$, $p = 0.049$; pain: $t_{(8)} = -2.69$, $p = 0.025$; heat: $t_{(8)} = -3.20$, $p = 0.011$), and a significant radial bias only for pain ($t_{(8)} = -2.24$, $p = 0.052$). CE directions for thermal low (mean ± SE, 237.15° ± 15.94) and high-energy stimuli (mean ± SE, 233.65° ± 13.11) were equivalent ($p$s > 0.05) to those for touch (mean ± SE, 231.66° ± 20.32, Figure 4). A significant difference was found only for the most distal point closest to the thumb (touch vs. pain: $F_{(1,16)} = 6.80$, $p = 0.019$; touch vs. heat: $F_{(1,16)} = 8.24$, $p = 0.011$). The CE size was equivalent for touch, pain, and heat ($p$s > 0.05).

(Figure 3 about here)

Overall, Exp. 2 showed that the biases found for localizing touch were not dependent on the population of afferent fibres stimulated within that region, but were specific to particular skin regions.

**Experiment 3**

On the *dorsum*, analysis of the proximo-distal and ulnar-radial components of the CE vector again showed significant distal bias ($t_{(8)} = 5.03$, $p = 0.001$) when the participants' hand and the visual comparison hand were both rotated by 90 deg relative to the torso (Figure 4a).

Analysis of CE directions showed that the mean direction was 64.67° (SE ± 12.34) in the straight posture, and 82.78° (SE ± 18.12) in the rotated condition. For each of the nine locations, the direction of the CE vectors was not significantly different between the straight ahead and the rotated postures (all $p$s > 0.05). The CE size was equivalent for the two postures ($p$s > 0.05), except for the most distal and medial location ($t_{(8)} = 2.73$, $p = 0.026$). These results suggest that the bias is independent of hand posture.

**Experiment 4**

Using the rubber hand for localization judgments assumes that the participant's hand and the rubber hand have approximately the same shape. We validated this assumption by calculating an hand 'shape index' (SI, adapted from Napier, 1980) as [(hand width / hand length) * 100], where the hand width is the distance between the knuckles of the little and index finger, and the hand length is the distance between the knuckle of the middle finger and the wrist. The rubber hand had a similar shape (SI = 72.22) to the participant's real hands (mean ± SD, 83.94 ± 7.18). We then directly compared Bookstein coordinates for the actual locations from the participant's hand with those for responses on the rubber hand. Note that this transformation adjusts for differences in hand size.

The localization of tactile stimuli on a rubber hand showed a pattern of CEs analogous to those obtained when localizing the stimuli on the hand photograph. In particular, analysis of the proximo-distal and ulnar-radial components of the CE vector again showed significant distal bias using localization on the rubber hand (Figure 4b, $t_{(4)} = 12.62$, $p = 0.0002$).

The mean CE direction was 64.95° (SE ± 7.20) for visual localization on the picture, and 63.25° (SE ± 8.53) for tactile localization on the rubber hand. For each of the nine locations, the directions of the CE vectors were statistically equivalent between the straight ahead and the rotated postures (all *p*s > 0.05). The results of this experiment suggest that the pattern of error found in the present study is independent of response modality.

(Figure 4 about here)

## Discussion

In everyday language, to know something 'like the back of my hand' is to have intimate and expert knowledge. Our data suggest that this expression is misleading from a neuroscientific point of view. The brain appears to use a highly distorted perceptual map of the hand to localize somatic stimuli delivered to the body surface. This study yielded four main findings: (1) There are systematic biases in localizing stimuli on the hand dorsum. These consist in a distal and radial shift of the estimated spatial locations (Exps. 1-4). A less consistent proximal bias was found on

the hand palm (Exp. 2). (2) Even within the back of the hand, these biases are specific to particular skin regions, as they occur on the dorsum and on the proximal segments of the fingers, but not on the middle segments of the fingers (Exp. 1). (3) These biases are largely independent of the sensory submodality and population of receptors stimulated, since they are similar for selective stimulation of Aβ, Aδ and C primary afferents (Exp. 2). (4) These biases do not depend on either the posture of the hand (Exp. 3), or on the method used for providing localization responses (Exp. 4). To summarise, perceptual maps of the hand are strikingly consistent across individuals and across sensory modalities. Further, they are highly stereotyped and dramatically distorted. Together, these results may suggest that a supramodal representation of body structure contributes to somatosensory localization.

To our knowledge, this is the first quantitative comparison of perceptual maps of tactile and thermal sensations on the hand. The consistent pattern of biases observed on the hand dorsum contrasts with the idiosyncratic biases previously reported for the forearm (Trojan et al., 2006). Interestingly, Nathan and Rice (1966) reported that localization errors of tactile and heat stimuli on the hand dorsum are more common in the distal vs. proximal direction. Similarly, spatial discrimination thresholds for touch and pain on the hand dorsum are worse in the proximo-distal than in the radial-ulnar direction (Schlereth, Magerl, & Treede, 2001). This asymmetry may reflect the elongated shape of receptive fields on the hand dorsum (e.g., Alloway, Rosenthal, & Burton, 1989; Brown, Fuchs, & Tapper, 1975; Powell & Mountcastle, 1959). The finding of radial biases for localization of touch on the palm also replicates a previous report (Culver, 1970).

These systematic distortions in the perceptual maps contrast strikingly with intraneural recording studies (for a review, see Ochoa, 2010). These studies report a very precise match between (1) the identified receptive field of an afferent unit, and (2) the perceptual localization during stimulation from that intraneural site (Ochoa & Torebjork, 1983). However, these studies focussed on high-resolution skin regions, such as fingers and palm. In these regions we found smaller, and less consistent biases than in lower-resolution regions, like the hand dorsum.

*Origin of the localization biases*

Two key findings of this study shed light on the origin of these localization

biases. First, biases are supramodal, being largely independent of the group of afferent fibers stimulated. This makes it unlikely that these biases have a peripheral origin, due, for example, to the functional properties of primary afferents. Given the segregation of modalities in early somatosensory cortices (e.g., Friedman, Chen, & Roe, 2004; Mountcastle, 1957), our finding of similar distortions for all tested afferent pathways rather suggests a role of regions *beyond SI*. Indeed, the role of SI in pain localization is controversial (Apkarian, Bushnell, Treede, & Zubieta, 2005; Bushnell et al., 1999; Seyal, Siddiqui, & Hundal, 1997). Moreover, there is evidence that localization of touch and pain involves also operculoinsular and posterior parietal regions. A positron emission tomography (PET) study reported enhanced activity in contralateral SI and inferior parietal cortices in a task that required selective attention to the location of laser stimuli (Kulkarni et al., 2005). Laser-evoked potential (LEP) studies suggest a specific involvement of operculoinsular regions, including the secondary somatosensory cortex, SII, when either a spatial discrimination (Schlereth, Baumgartner, Magerl, Stoeter, & Treede, 2003) or localization task (Bentley et al., 2004; Kanda et al., 1999; Valeriani et al., 2000) is performed. Attending to which finger was stimulated selectively activated the right temporo-parietal junction in a functional magnetic resonance (fMRI) study (Van Boven, Ingeholm, Beauchamp, Bikle, & Ungerleider, 2005). Finally, neuropsychological and transcranial magnetic stimulation (TMS) studies found that damage or disruption to the parietal cortex impairs the localization of both tactile and noxious stimuli (Paillard, Michel, & Stelmach, 1983; Porro et al., 2007; Rapp et al., 2002).

Second, biases are specific to each skin region. We also found, unsurprisingly, that localization is less biased on more densely-innervated skin surfaces. This indicates that low-level factors are also likely to play a role in the generation of the bias. Whereas variations across skin regions in *receptive field (RF) shape* and *density* can not explain the *direction* of the observed biases, they could rather explain the extent of these distortions. RFs of primary tactile neurons innervating the hairy skin are anisotropic and oval-shaped, with the long axis running proximo-distally (Alloway et al., 1989; Powell & Mountcastle, 1959). While RF anisotropy has obvious consequences for variable error (precision), it is unclear how it could produce systematic patterns of constant error (bias). In addition, differences in receptor density seem unable to explain the specific bias directions in our study, for two main reasons. First, when stimuli are delivered to the hairy skin of the middle finger segments, there

is a localization bias *away* from the densely-innervated fingertips (i.e., with an opposite direction than the bias observed on the hand dorsum). Second, on the glabrous skin, the perceptual maps did not reveal any attraction towards the densely-innervated fingertips. Conversely, RF characteristics and distribution might rather explain our finding of lower bias on the fingers and on the palm in comparison to the hand dorsum.

Taken together, these results suggest that perceptual localization relies both on the afferent input and on high-level structural representations of the body surface. Here we propose a simple model of the cortical mechanisms underlying touch and pain localization (Figure 5). Sensory inputs from each class of receptors are transmitted to primary somatosensory regions, where they are represented topographically, in distinct maps for each receptor population (e.g., Friedman et al., 2004; Mountcastle, 1957). However, localizing a stimulus within a somatotopic map is not sufficient to localize it on the skin surface. There is no fixed association between firing of a specific neuron and a specific skin location, because the plasticity of sensory cortices means that the receptive field of a specific neuron can change (Longo, Azanon, & Haggard, 2010; Medina & Coslett, 2010; Merzenich et al., 1984; Pons et al., 1991). Therefore, localization on the skin surface requires first learning, and then applying, an additional mapping between neural codes and skin locations. Moreover, the high plasticity of somatotopic maps means that these associations require constant updating.

In fact, the finding of stereotyped distortions in perceptual maps (particularly of poorly innervated skin regions) may suggest that locognosis involves not only localization on the skin, but also an additional referencing to actual *body structure*. This second step is not logically necessary, but it appears to occur automatically and particularly when the information provided by the lower level representations is poor due to the low resolution of the afferent input (e.g., on the hand dorsum). The less the somatosensory system knows about the location of one stimulus, the more it will revert to higher structural representations. Thus, localization judgements might be the product of two successive processing stages: localization of the stimulus on the skin surface, and registration of the skin surface with a structural model of the body. The first stage involves modality specific maps in early somatosensory cortices, while the second might be a supramodal body representation housed in non-primary somatosensory areas, possibly the posterior parietal cortex (G. Spitoni, G. Galati, G.

Antonucci, P. Haggard, and L. Pizzamiglio, unpublished observations). The second stage would also be the origin of the systematic directional biases found in the present study. Importantly, conscious perception of location arises only after the automatic operation of this second stage.

(Figure 5 about here)

Tactile localization biases reported in other studies might also depend on cortical representations of the body. For example, tactile localization on the forearm is more precise close to joints or even artificial landmarks (Cholewiak & Collins, 2003). Moreover, the distance between two tactile stimuli on two different body parts feels longer than an identical physical stimulus within a single body part, indicating that the metric representation of the body might be influenced by an internal representation of the body that contains information about body segments (de Vignemont, Majid, Jola, & Haggard, 2009). Future studies might test whether those results also reflect supramodal biases, or are specific for the tactile modality.

**Conclusions**

We used participants' attempts to localize somatosensory stimuli in order to measure perceptual maps of the hand. The perceptual maps varied systematically across stimulated skin regions. Within each skin region, however, the perceptual maps for touch, pain, and heat stimuli were largely similar. The localization of somatosensory stimuli was systematically shifted distally and radially on the hand dorsum, whereas a less consistent proximal bias was found on the hand palm. These findings provide evidence that localization biases have a common, central origin, and may reflect a supramodal representation of body structure.

## Acknowledgements

FM was supported by a PhD programme of the University of Milano-Bicocca, ML was supported by BBSRC project grant BB/D009529/1 to PH. PH was additionally supported by EU FP7 project VERE, and a Leverhulme Trust Major Research Fellowship. GDI is University Research Fellow of The Royal Society and acknowledges the support of the BBSRC.

## Figure captions

**Figure 1.** *(a) Stimulus locations.* The black circles represent the approximate locations of the stimuli on the glabrous and hairy skin of the left hand. *(b) Apparatus.* Participants localized the stimuli delivered to their unseen left hand on a silhouetted picture of their own hand. *(c) Calculation of the constant error (CE)*. The white squares represent four estimates (E1…E4) of the actual stimulus location (grey circle). The constant error (bias) was defined as the deviation of the average of the estimated locations (white circle) from its actual location. *(d) CE direction and size.* The CE direction was the angle of the CE vector, and the size was given by its vector length. *(e) CE axes.* The CE vector was also analysed in its two components, aligned with the proximal-distal and with the ulnar-radial axes.

**Figure 2.** *Exp. 1: Perceptual map of touch on the hairy skin of the left hand (N=10)*. The average actual (grey circles) and estimated (white circles) locations of the 45 stimuli, and the average position of the knuckles and the fingertips are plotted in Bookstein shape coordinates, centred on the knuckle of the little finger (0,0) and of the index finger (1,0). Bars represent ± 1 SE.

**Figure 3.** *Exp. 2: Perceptual maps of touch, pain, and heat on the left hand dorsum and palm (N=9)*. The average actual (grey circles) and estimated (white circles) locations of the 9 stimuli, and the average position of the knuckles are plotted in Bookstein coordinates, centred on the knuckle of the little finger (0,0) and of the index finger (1,0). Bars represent ± 1 SE.

**Figure 4.** *(a) Exp. 3: Control for pointing error.* Perceptual maps of touch on the left hand dorsum, in the straight ahead and rotated (90°) postures (N=9). *(b) Exp. 4: Control for response modality.* Perceptual maps of touch on the left hand dorsum. Localisation was reported on visually (picture of the hand, left panel) or haptically (by pointing to the corresponding location on a rubber hand) (N=5). The average actual (grey circles) and estimated (white circles) locations of the 9 stimuli, and the average position of the knuckles are plotted in Bookstein coordinates, centred on the knuckle of the little finger (0,0) and of the index finger (1,0). Bars represent ± 1 SE.

**Figure 5.** *A model for localization for touch, pain, and heat.*

**Table 1. Summary of experimental designs**

| | Sensation | Body part | Skin surface | Afferent Fibers Targeted | Response Modality |
|---|---|---|---|---|---|
| Experiment 1 | touch | dorsum, fingers | hairy | Aβ | visual |
| Experiment 2 | touch, pain, heat | dorsum, palm | hairy, glabrous | Aβ<br>Aδ<br>C | visual |
| Experiment 3 | touch | dorsum | hairy | Aβ | visual |
| Experiment 4 | touch | dorsum | hairy | Aβ | visual, tactile |

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