



Tactile distance adaptation aftereffects do not transfer to perceptual hand maps

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ABSTRACT

Recent studies have demonstrated that mental representations of the hand dorsum are distorted even for healthy participants. Perceptual hand maps estimated by pointing to specific landmarks (e.g., knuckles and tips of fingers) is stretched and shrunk along the medio-lateral and the proximo-distal axes, respectively. Similarly, tactile distance perception between two touches is longer along the medio-lateral axis than the proximo-distal axis. The congruency of the two types of distortions suggests that common perceptual and neural representations may be involved in these processes. Prolonged stimulation by two simultaneous touches having a particular distance can bias subsequent perception of tactile distances (e.g., adaptation to a long distance induces shorter stimuli to be perceived even shorter). This tactile distance adaptation aftereffect has been suggested to occur based on the modulations of perceptual and neural responses at low somatosensory processing stages. The current study investigated whether tactile distance adaptation aftereffects affect also the pattern of distortions on the perceptual hand maps. Participants localized locations on the hand dorsum cued by tactile stimulations (Experiment 1) or visually presented landmarks on a hand silhouette (Experiment 2). Each trial was preceded by adaptation to either a small (2 cm) or large (4 cm) tactile distance. We found clear tactile distance aftereffects. However, no changes were observed for the distorted pattern of the perceptual hand maps following adaptation to a tactile distance. Our results showed that internal body representations involved in perceptual distortions may be distinct between tactile distance perception and the perceptual hand maps underlying position sense.

1. Introduction

We can effortlessly perceive the size and position of objects touching our body. If a spider lands on a hand, one can immediately perceive its size and location on the skin surface, even with eyes closed. Then, you could try to swat the spider with the opposite hand by estimating its spatial location in space. However, the estimation of tactile size on the body surface and the location of touch in external space are not simple processes. Longo, Azañón, and Haggard (2010) proposed a model of somatoperceptual information processing postulating that the location of touch is localized on the skin surface by referring touch to the superficial schema, which is a static mental representation mediating localization of somatic sensations on the body surface (Head & Holmes, 1911). This representation is assumed to be distinct from another form of body representation (the postural schema), which is a dynamic representation of the position of the body in space (Head &

Holmes, 1911). A third body representation (the model of size and shape) was introduced by Longo et al. (2010) to describe a static, stored mental representation of the body size and shape. Notably, according to this somatoperceptual processing model, the model of size and shape) is needed both to estimate the metric properties of touch (e.g., the size of the spider, or distance between its legs) and to locate touches or body parts in space (see Fig. 1).

Intriguingly, a large body of research has demonstrated similar patterns of perceptual distortions for tactile distance perception and perceived locations of body landmarks or touches in space (for reviews see Longo, 2015, 2017a). For example, in the case of tactile distance perception, Longo and Haggard (2011) reported that the perceived distance between two touches on the hairy skin surface of a hand (hand dorsum) is approximately 40% longer when the stimuli are aligned with the medio-lateral axis (*across* the hand) compared to the proximo-distal axis (*along* the hand).

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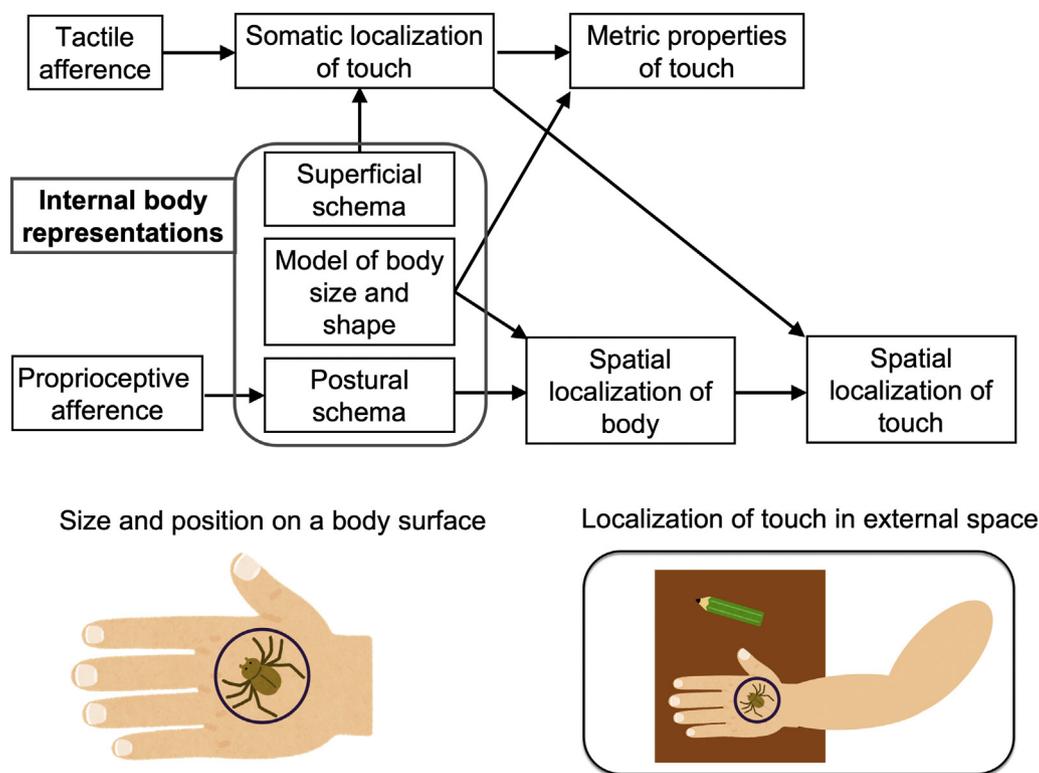


Fig. 1. Schematic illustration of the model of somatoperceptual processes proposed by Longo et al. (2010).

Similar distortions have been reported for perceived locations of body landmarks in space. For example, Longo and Haggard (2010) asked participants to judge the location of the knuckles and tips of their fingers by placing the tip of a long baton on a board on top of the occluded hand. Using the relative relationships among the judged landmarks, Longo and Haggard (2010) depicted an implicit geometric structure of the hand underlying position sense (hereafter, perceptual hand maps). They found that the shape of these maps were stretched toward the medio-lateral axis and shrunk along the proximo-distal axis, similar to the pattern of distortions found for perceived distances on the dorsum of the hand. Similar distorted patterns have been observed for perceptual hand maps estimated by localisation of locations cued by visual markers on a hand silhouette (Longo, Mancini, & Haggard, 2015), by touch (Longo, 2017b; Longo et al., 2015; Longo & Morcom, 2016; Mattioni & Longo, 2014), and by verbal estimates of the perceived distance between two sequential touches applied to the hand (Longo & Golubova, 2017). The similar patterns of perceptual distortions obtained for tactile distance perception and perceived locations of body landmarks or tactile localization on the hand, might imply the use of a common internal “distorted” body representation (a model of size and shape). However, Longo and Morcom (2016) found that magnitudes of the perceptual distortion toward the medio-lateral axis in tactile distance perception and localization permeances on the hand dorsum were not positively correlated. They proposed that the internal body representations underlying perceptual distortions might be distinct for tactile distance perception and perceptual hand maps. However, it is also possible that an internal body representation is shared but obscured, given that task demands and resulting response patterns are distinct for tactile distance perception and perceptual hand maps underlying position sense. Further investigation is therefore required to test whether there is a common internal body representation underlying distortions for tactile distance perception and perceptual hand maps by using a single measurement.

For this purpose, the current study focused on perceptual adaptation aftereffects. Adaptation has been extensively used to induce perceptual

changes, and in principle, modulate neural responses for particular attributes of a stimuli. For example, after prolonged exposure to a haptic object of a particular size (e.g., a large ball), subsequent smaller objects are perceived even smaller (Kappers and Bergmann Tiest, 2013; Maravita, 1997; Uznadze, 1966). Recently, Calzolari, Azañón, Danvers, Vallar, and Longo (2017) reported that adaptation to tactile distances produces corresponding aftereffects. They stimulated the participants' hand dorsum with long (4 cm) or short (2 cm) tactile distances with a two-points stimulus. Repeated stimulation of 60 s (each stimulation is around 1 s) was initially applied and 10 s top-up stimulations were introduced to maintain the effects. After adaptation, perceived tactile distance changed on the stimulated skin surface such that the long adaptation stimulus induced the perception of a subsequent distances to be perceived shorter than it is and vice versa for the shorter adaptation stimulus. It is also notable that the adaptation to the long distance on the medio-lateral axis cancelled the perceptual distortion of tactile distance (i.e., distances on the medio-lateral axis perceived larger than those on the proximo-distal axis) so that the distance perception across the medio-lateral and proximo-distal axes became more similar. Furthermore, tactile distance adaptation aftereffects did not transfer across different orientations or even across regions within the hand. Such selectivity suggests that tactile distance adaption aftereffects might induce changes in relatively early perceptual and neural somatosensory processing (Calzolari et al., 2017).

If a common internal representation (the model of size and shape) is involved in the emergence of distortions both for tactile distance perception and for perceptual hand maps underlying position sense and if adaptation could affect this internal representation, then adaptation to tactile distances might modulate both tactile distance perception and perceptual hand maps. To test this possibility, we repeatedly presented a long or short tactile stimulus to induce tactile distance adaptation on the participant's hand dorsum (Fig. 2A). In addition to the tactile distance judgment task used to measure adaptation aftereffects (Fig. 2B), we asked participants to localize either a tactile event on the hand (Experiment 1) or a proprioceptive location on the hand cued through

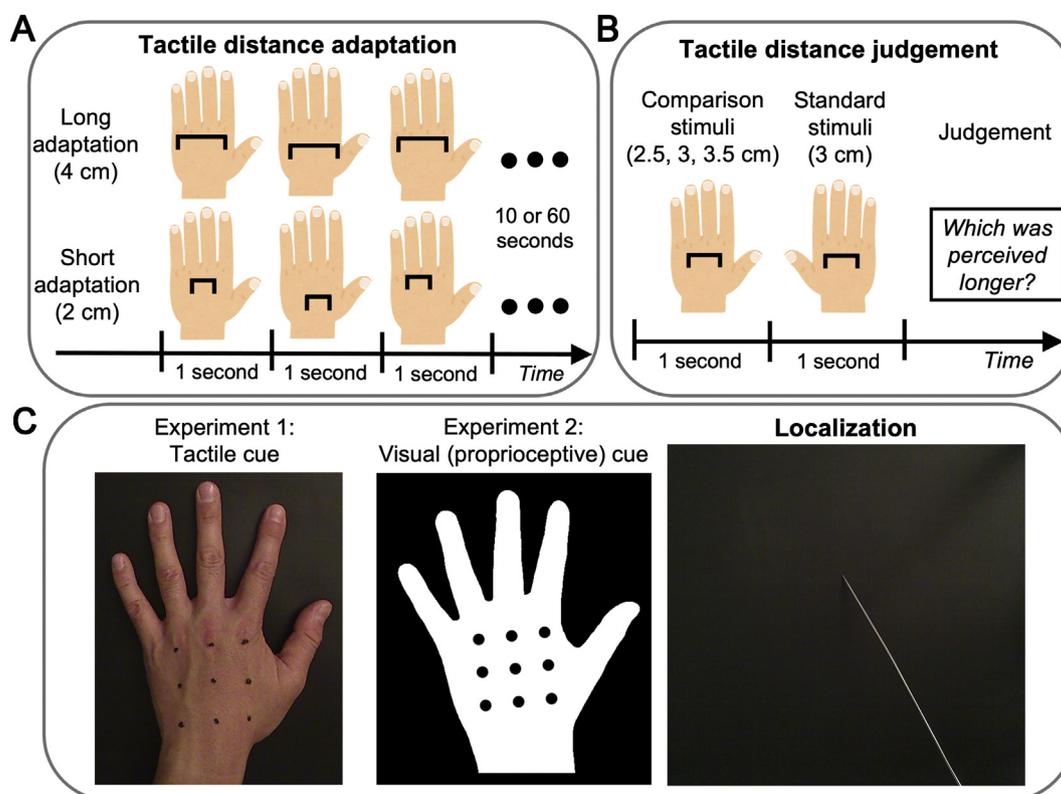


Fig. 2. Schematic illustrations of the experimental procedures. (A) Tactile distance adaptation. Pairs of touches separated by either a long (4 cm) or a short (2 cm) distance were repeatedly presented on random locations of participant's left hand dorsum. (B) Tactile distance judgment task. The comparison and one of the test stimuli were sequentially presented on the dorsum of the right and left hands, respectively. Participants were asked to judge which stimuli was perceived as longer. (C) Localization tasks. Each localized position on participant's left hand was cued by tactile stimulation (Experiment 1) on the predefined, marked location or by visual cue appearing on a hand silhouette (Experiment 2). Judgments were performed by pointing with a long baton to the perceived cued location on a black board, which covered the participant's left hand.

vision (Experiment 2; Fig. 2C) after adaptation (localization tasks). If a common internal body representation underlies both the distortions of tactile distance perception and the perceptual hand maps underlying position sense, we would predict that the long and short adaptation along the medio-lateral axis would result in smaller and larger magnitudes, respectively, of the perceptual distortion toward the medio-lateral axis of perceptual hand maps. However, we found no effects of the tactile distance adaptation on the patterns of perceptual distortions on the implicit geometric structure of the hand estimated by the localization tasks in both experiments, indicating that tactile distance adaptation aftereffects do not transfer to the perceptual hand maps underlying position sense.

2. Methods

2.1. Participants

Forty healthy participants took part in the study after giving informed consent, 20 in Experiment 1 (10 females; mean age: 32.7 years, SD: 13.9 years, mean handedness score according to the Edinburgh Inventory (Oldfield, 1971): 60.64, 17 right-handed (range: 33.3–100) and three left-handed (one was -4.8 , two were -17.6)) and 20 in Experiment 2 (12 females; mean age: 27.7 years, SD: 7.1 years, mean handedness score: 74.66, 19 right-handed (range: 25–100) and one left-handed (-73.9)). All participants reported no abnormalities in tactile perception, and were naïve to the purpose of the experiments. They were paid or given course credits for their participation, and gave written informed consent. One and two participants in Experiment 1 and 2, respectively, were excluded from analyses because of displacement of the hand from the initial position (movement exceeding 10% of

the distance between the metacarpophalangeal joints of the thumb and little fingers) in at least one of the localization task sessions, and were replaced by new recruited participants. One additional participant in each experiment was also excluded from analyses and replaced with a new one because of a computer problem (Experiment 1) and because around 25% of photo images were blurred preventing the coding of the pointing responses (Experiment 2). All procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London. The study was conducted in accordance with the principles of the Declaration of Helsinki.

2.2. Overview of experimental designs

In each experiment, a tactile distance adaptation phase of ten seconds preceded each individual trial in the distance judgment and localization tasks, which were included as separate blocks. In addition, adaptation was applied with either short (2 cm) or long (4 cm) length adaptor. Thus, each participant completed 4 blocks (e.g., the tactile distance and localization task blocks with adaptation to a short distance were introduced first, followed by the two blocks with adaptation to a long distance) The order of the adaptations was counterbalanced across participants. The order of the tasks (tactile distance judgment or localization task first) was fixed in each adaptation condition for each participant but counterbalanced across participants.

2.3. Experiment 1

2.3.1. Tactile distance adaptation

Procedures for inducing adaptation were adapted from those used in our previous study (Calzolari et al., 2017). Stimuli were pairs of pointed

wooden rods mounted on foam boards and separated by 2 (short) and 4 cm (long) similar to those used in several previous studies from our lab (Calzolari et al., 2017; Le Cornu Knight, Longo, & Bremner, 2014; Longo & Haggard, 2011). The tip of the rods was rounded off to form a blunt point (approximately 1 mm width). Stimuli were delivered manually by the experimenter who sat across from the participant. Participants sat on a chair, placing their palms on a table with the digits pointed toward the experimenter. Participants were asked to keep their hands still. The experimenter monitored the position of the hand during each session. In separate conditions, the short or long adapting stimulus was repeatedly applied to the left hand in the medio-lateral orientation (Fig. 2A). Tactile adaptation was applied for 10 s before each trial in the distance judgment and localization tasks. On each trial, we stimulated different random locations of the hand (i.e., the area ranged within the metacarpophalangeal joints, wrist, and lateral sides of the hand), so that the stimulations were never applied systematically to the exact same locations on the skin. The duration of each touch was around 1 s. Longer periods of adaptation (60 s, approximately) were delivered on the first and middle trials of each task, to induce and reinforce reliable adaptation effect and to diminish any possible residual adaptation from the previous adaptation condition.

2.3.2. Tactile distance judgment

To test the strength and direction of the adaptation, on each trial, immediately following the 10 s adaptation phase, two tactile stimuli were sequentially presented once for 1 s on the dorsum of each hand. In particular, a comparison stimulus (i.e., 3 cm distance) was applied to the right (non-adapted hand), and a test stimulus of varying distances (2.5, 3, and 3.5 cm), to the adapted left hand (Fig. 2B). Immediately after the second touch, participants were asked to report verbally, and without time pressure, whether the first or the second stimulus was perceived as longer. This two-alternative forced choice (2AFC) response mode, orthogonal to the tested dimension (i.e., right-left hand), reduced the possible involvement of response or decisional biases (Calzolari et al., 2017; Longo & Haggard, 2011). The task consisted of 30 trials (3 test stimuli \times 2 blocks \times 5 repetitions) in each adaptation condition. The size of the test stimuli was randomized across trials in each block. The order of which the comparison or the test stimulus was applied first was fixed in each block but changed across the blocks in each participant and counterbalanced among the participants. The participants were blindfolded with an eye mask during the task including the distance adaptation phase.

2.3.3. Localization task

Following the adaptation phase, on each trial, participants were required to locate with a pointer stick one of 9 possible equidistant locations on the adapted left hand (Longo, 2017b; Longo et al., 2015; Longo & Haggard, 2010; Longo & Morcom, 2016; Mattioni & Longo, 2014). Each location was distributed equally on a 3×3 grid on the middle of the hand dorsum. The three rows ran along the medio-lateral hand axis, while the three columns ran along the proximo-distal axis (Fig. 2C). The position of the upmost row was set such that the center of the row was corresponding with the metacarpophalangeal joint of the middle finger. The orientation of the upmost row was consistent with that of the metacarpophalangeal joints of the index and ring fingers along the medio-lateral axis. To prevent the hand from moving, a Velcro tape was used to attach the bottom of the index and ring fingers to the table. A board (40 \times 40 cm) was placed over the hand, resting on four pillars (7 cm high) to occlude the hand from view during the task including the distance adaptation phase. The judged locations were cued by tactile stimulation. The 3×3 grid of possible locations was marked on the hand dorsum using a plastic template (5 cm on a side, an equidistant separation of 2.5 cm between each location; Fig. 2C). On each trial, the experimenter lifted the occluding board (turning it toward the participant so that it still blocked their view of their hand). After the tactile distance adaptation was applied, the experimenter

touched one of the 9 points with a von Frey hair (255 milliNewtons) for approximately 1 s, and then placed the occluding board back down to allow the participant to point. The participant's task was to place the tip of a long baton (34 cm length, 2 mm diameter) on the occluding board directly above the location where the touch had occurred. They were instructed to be precise in their judgments and avoid ballistic pointing or strategies such as referring the outline of the hand. To ensure that they judged each landmark individually, the experimenter asked the participant to move the baton to the edge of the table before the start of each trial. When the participants indicated their response, a photograph was taken and saved for offline coding with a web camera (Logitech Webcam Pro 9000 HD suspended on a tripod at 41.5 cm above the occluding board, 1600 \times 1200 pixels) and a custom MATLAB (MathWorks, Natick, MA) script with a laptop computer (Dell Latitude E7440). At the beginning and end of each session, a photograph of the participant's hand was taken to check that the hand had not moved during the task. There were 27 trials (9 locations \times 3 blocks) in each adaptation condition. In each block, the order of the locations was randomized.

2.4. Experiment 2

The procedures of Experiment 2 were identical to Experiment 1, except that, in the localization task, the judged locations were cued by a white dot appearing on a silhouette of a hand image, rather than by touch. The hand image was presented in front of the participant (Fig. 2C) on a PC display (Dell, 33.9 \times 27.1 cm, 1280 \times 1024 pixels) using Psychtoolbox (Brainard, 1997; Pelli, 1997) in MATLAB. A photo image of one of the experimenter's hand was used as a template for the silhouette. One of the 3×3 grid of possible locations with an equidistant separation of 1.5 cm between dots was visually cued on each trial. The position and orientation of the upmost row of the grid in the image was determined before the hand image was converted to a silhouette.

2.5. Data analysis

For the tactile distance judgment task, the proportion of responses for each test stimuli that were judged as longer was calculated for each participant. This variable was then submitted to a two-way repeated measures analysis of variance (ANOVA) with factors adaptation conditions (2 levels: long adapter and short adapter) and test stimuli (3 levels: 2.5, 3, 3.5 cm) in each experiment. We also performed a three-way mixed design ANOVA with a between-subject factor (experiments) and within-subject factors (adaptation conditions and test stimuli). These analyses were performed as the manipulation check to ensure that the tactile distance adaptation reliably occurred in each experiment. Note that because we used the 2AFC task in which participants judged which of two tactile distances was larger, we can only draw conclusions about relative, and not absolute, tactile distance perception.

For the localization tasks, data coding and analyses were conducted as in Longo and Morcom (2016) using a custom MATLAB script with Psychtoolbox (Brainard, 1997; Pelli, 1997). Mean x-y pixel coordinates were calculated for each landmark location for each adaptation condition. Distances between mean x-y pixel coordinates of each adjacent cued location were then calculated along the medio-lateral and proximo-distal axes. These values were converted into cm based on the x-y pixel coordinates of a ruler attached to the table. Distance values between each adjacent cued location were averaged in each axis as representing medio-lateral and proximo-distal distances. In each experiment, a two-way repeated measures ANOVA with the factors of adaptation conditions (2 levels: long adapter and short adapter) and axes (2 levels: medio-lateral and proximo-distal) was performed. We also performed a three-way mixed design ANOVA with a between-subject factor (experiments) and within-subject factors (adaptation conditions and axes).

To assess the amount of overall distortion of the judged locations as a whole map, we used a method called Procrustes alignment (Bookstein, 1992; Rohlf & Slice, 1990). This allowed us to compare and estimate configurations of homologous landmarks by translating, rotating, and scaling them so as to minimize the distance between pairs of landmarks. First, we used generalized Procrustes analysis (Gower, 1975), implemented in the shape analysis MATLAB toolbox developed by Simon Preston (University of Nottingham, <https://www.maths.nottingham.ac.uk/plp/pmzsp/shape.php>), to superimpose the map obtained from each participant in each adaptation condition on an idealized square grid reflecting the location of the 9 equidistant points. We then estimated grand-average maps for each adaptation condition by averaging all participants' superimposed maps. Second, we used Procrustes alignment to quantify the overall level of distortion in perceptual maps (Longo & Golubova, 2017; Longo & Morcom, 2016). We used the Procrustes distance, i.e., the square root of the sum-of-squares of the residual distances between pairs of homologous landmarks, as a measure of the overall dissimilarity in shape between two maps. To determine the amount of distortion, we stretched a perfect square grid reflecting the location of the 9 points by different amounts to find the stretch that maximized the similarity with each participant's perceptual hand map. Stretches were defined by the multiplication of the x-coordinate (reflecting location in the medio-lateral hand axis) by a stretch parameter. Stretch parameter values between 0.33 and 3 were tested by exhaustive search with a resolution of 0.0005 units in natural logarithm space (i.e., 4415 steps). For each participant and each experimental condition, we determined the value of the stretch parameter that minimized the dissimilarity in shape (i.e., that minimized the Procrustes distance) between the stretched grid and the participant's perceptual hand map. A stretch value of 1 therefore indicates a perfectly square grid, stretch of < 1 indicates a tall thin grid, and stretch of > 1 indicates a squat fat grid. We predicted that, if the distance adaptation aftereffects could affect the patterns of perceptual distortions on the perceptual hand maps underlying position sense, the long and short adaptation along the medio-lateral axis should result in smaller and larger stretch values, respectively. We then used two-tailed *t*-tests with Bonferroni correction and paired two-tailed *t*-tests to compare the best-fitting stretch values against 1 and between adaptation conditions, respectively. We also performed a two-way mixed design ANOVA with a between-subject factor (experiments) and a within-subject factor (adaptation conditions).

All statistical tests and averaging were performed on log-transformed values which were converted back to ratios to report means. The data analyses were conducted using JASP (version 0.9; JASP Team, 2018).

3. Results

3.1. Tactile distance judgment

We calculated the proportion of responses that each level of the test stimulus was judged as longer than the comparison stimulus in each adaptation condition (Fig. 3A and B, left). In both experiments, the proportions in the short adaptation condition were larger than those in the long adaptation condition. This indicates that the short adaptation condition induced longer tactile distance perception as compared to the long adaptation condition. A two-way repeated measures ANOVA with factors adaptation conditions and test stimuli showed a significant main effect of adaptation condition in both experiments ($F(1, 19) = 20.96, 18.18, ps < 0.001, \eta_p^2 = 0.52, 0.49$ in Experiments 1 and 2, respectively). The significant main effect of the test stimuli simply showed that the longer test stimuli were judged as longer and vice versa ($F(2, 38) = 27.33, 46.28, ps < 0.001, \eta_p^2 = 0.59, 0.71$ in Experiments 1 and 2, respectively). In Experiment 1, the ANOVA also found a significant interaction ($F(2, 38) = 3.25, p < .05, \eta_p^2 = 0.15$). A simple main effect of the adaptation conditions showed the longer tactile

distance perception in the short adaptation condition in the 3 and 3.5 cm of the test stimuli ($Fs(1, 57) > 11.73, ps < 0.002$) but not in the 2.5 cm of the test stimulus ($F(1, 57) = 1.01, p = .32$). In contrast, no significant interaction was observed in Experiment 2 ($F(2, 38) = 0.98, p = .39, \eta_p^2 = 0.05$). These differences between experiments may simply be based on individual differences in tactile perception and/or sensitivities among the individuals of each group. In fact, a three-way mixed design ANOVA with factors experiments, adaptation conditions, and test stimuli showed neither significant main effect of experiments ($F(1, 38) = 0.11, p = .74, \eta_p^2 = 0.003$) nor interaction effects related to the factor experiments ($Fs(1, 38; 2, 76) < 2.02, ps > 0.14, \eta_{ps}^2 < 0.05$). These results show that our experimental manipulation is effective and sufficient to induce perceptual aftereffects on perceived tactile distance.

3.2. Perceived distance in localization tasks

A central question of this study is whether tactile distance adaptation aftereffects will affect the patterns of perceptual distortions on the perceptual hand maps estimated by the localization tasks. Perceived distances between each adjacent cued location were calculated and averaged along the medio-lateral and proximo-distal axes (Fig. 3A and B, right). The results of both experiments showed that the distances between judged locations were similar across the two adaptation conditions in each axis. Two-way repeated measures ANOVAs with the factors adaptation conditions and axes for each experiment revealed a clear main effect of axis showing that the distance between the judged locations was longer for the medio-lateral axis than the proximo-distal axis ($F(1, 19) = 19.34, 65.75, ps < 0.001, \eta_p^2 = 0.50, 0.78$ in Experiments 1 and 2, respectively). Critically, however, there were no significant effects of adaptation condition in both experiments ($F(1, 19) = 0.22, 1.83, p = .65, 0.19, \eta_p^2 = 0.01, 0.09$ in Experiments 1 and 2, respectively). No significant interactions were observed for either experiment ($Fs(1, 19) < 0.98, ps > 0.36, \eta_{sp}^2 < 0.05$). A three-way mixed design ANOVA with factors experiments, adaptation conditions, and test stimuli showed a main effect of experiments (Experiment 1: 3.76 cm; Experiment 2: 3.26 cm; $F(1, 38) = 5.86, p = .02, \eta_p^2 = 0.13$) but no significant interaction effects related to the factor experiments were found ($Fs(1, 38) < 3.36, ps > 0.08, \eta_{ps}^2 < 0.08$).

3.3. Stretch value in localization tasks

To calculate a single measure of distortion on the perceptual hand maps estimated by the localization tasks, we stretched an idealized square grid by different amounts to find the stretch that minimized the dissimilarity in shape (i.e., the Procrustes distance) within each perceptual hand map. Consistent with the judged distance data, the perceptual hand maps consistently showed the stretched shape along the medio-lateral axis in both adaptation conditions in each experiment (Fig. 4A and B, left). We evaluated the magnitude of the stretch value (i.e., a ratio of stretch between the medio-lateral and proximo-distal axes) along the medio-lateral axis. The means of the stretch values were consistently larger than 1, indicating the stretch in the proximo-distal axis. However, no significant differences were found between adaptation conditions in both experiments (Fig. 4A and B, right). Two-tailed *t*-tests with Bonferroni correction showed that the mean values were significantly larger than 1 in Experiment 1 ($M = 1.27$ and $1.23, t(19) = 5.02, 3.31, p < .001, 0.005, \text{Cohen's } d_z = 1.12, 0.74$ in the long and short adaptation conditions, respectively) and Experiment 2 ($M = 1.51$ and $1.47, t(19) = 7.80, 6.65, ps < 0.001, \text{Cohen's } d_z = 1.74, 1.49$ in the long and short adaptation conditions, respectively). However, paired two-tailed *t*-tests with Bonferroni correction showed no significant differences between the adaptation condition in either experiment ($t(19) = -0.66, -0.67, p = .52, 0.51, \text{Cohen's } d_z = -0.146, -0.149$, in Experiments 1 and 2, respectively). A three-way mixed design ANOVA with factors experiments and adaptation

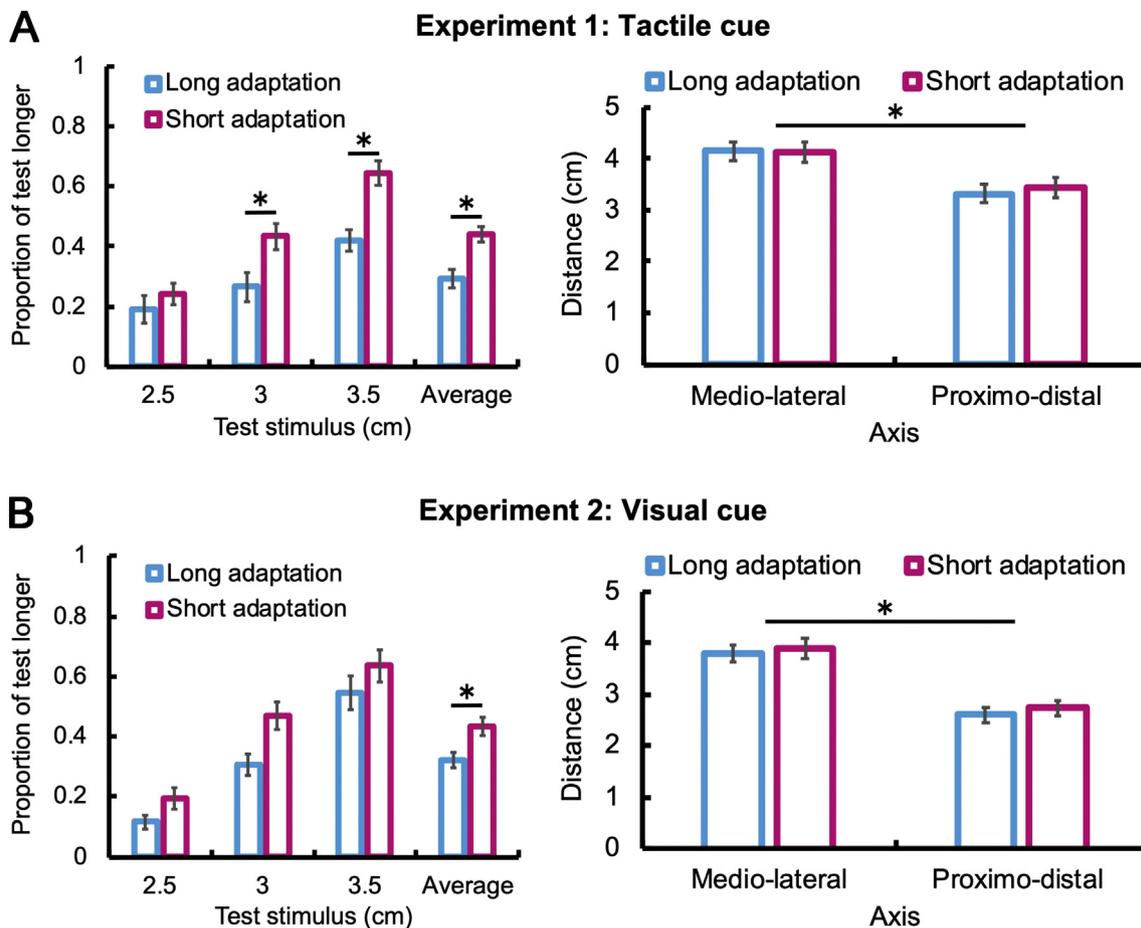


Fig. 3. Results of Experiments 1 (A) and 2 (B). The left panels show the results of the tactile distance judgment. The horizontal axis denotes the test stimuli and vertical axis denotes the proportion that the test stimulus was judged as longer. The comparison stimulus was always 3 cm. Clear tactile distance aftereffects were apparent in both experiments. The right panels show the results of the localization tasks. The horizontal axis denotes the axes along which the judged distances were calculated between the cued locations. The vertical axis denotes the averaged distance. The cyan and magenta plots indicate the longer and shorter adaptation conditions, respectively. Asterisks show significant differences ($p < .05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

conditions showed a main effect of experiments (Experiment 1: 1.10; Experiment 2: 1.19; $F(1, 38) = 6.00$, $p = .02$, $\eta_p^2 = 0.14$) but no significant interaction effect was found ($F(1, 38) = 0.00$, $p = .99$, $\eta_p^2 < 0.00$).

3.4. Bayesian statistical analyses

We found no differences between adaptation conditions for perceived distances and stretch values in either experiment. In order to evaluate the extent to which the obtained results provide positive support for a null hypothesis, we performed Bayes factor analyses comparing the two adaptation conditions. The Bayesian statistical analyses showed that the observed differences were more likely to have occurred under the null hypothesis than the alternative hypothesis. We calculated Bayes factors for null hypothesis (BF_{01}), and checked these values were larger than 1, which means support for null hypothesis. For the data of the distances between the judged locations, the Bayesian paired sample t -tests (default Cauchy prior width $r = 0.707$) supported the null hypothesis in Experiments 1 ($BF_{01} = 4.247$ and 2.660, for the medio-lateral and proximo-distal axes, respectively) and 2 ($BF_{01} = 3.110$ and 1.968 for the medio-lateral and proximo-distal axes, respectively). For the data of the stretch values, the Bayes paired sample t -tests showed the support of the null hypothesis in both the experiments ($BF_{01} = 3.552$ and 3.525 in Experiments 1 and 2, respectively).

4. Discussion

The current study investigated whether tactile adaptation aftereffects transfer to the perceptual hand maps estimated by localizations of landmarks on the hand with the tactile (Experiment 1) and visual (proprioceptive) cues (Experiment 2). We found clear evidence for tactile distance adaptation aftereffects, indicating that our experimental manipulation was effective. However, we found no evidence for transfer of such aftereffects to the pattern of perceptual distortions on the perceptual hand maps underlying position sense.

4.1. Tactile distance adaptation aftereffects

Our results provide a clear replication of the tactile distance adaptation aftereffects reported recently (Calzolari et al., 2017). The results of Experiments 1 and 2 showed that the test stimuli were judged as longer in the short adaptation condition relative to the long adaptation condition (Fig. 3A and B, left). Perceptual adaptation effect has been one of the reliable methods for psychophysical studies introducing perceptual and neural changes underlying the sensory process being adapted (Solomon & Kohn, 2014). Further, tactile distance aftereffect has been reported to have sharp selectivity, suggesting the involvement of relatively early perceptual and neural somatosensory processing stages (Calzolari et al., 2017). Moreover, as in the previous study (Calzolari et al., 2017), we adopted an interval forced choice method to

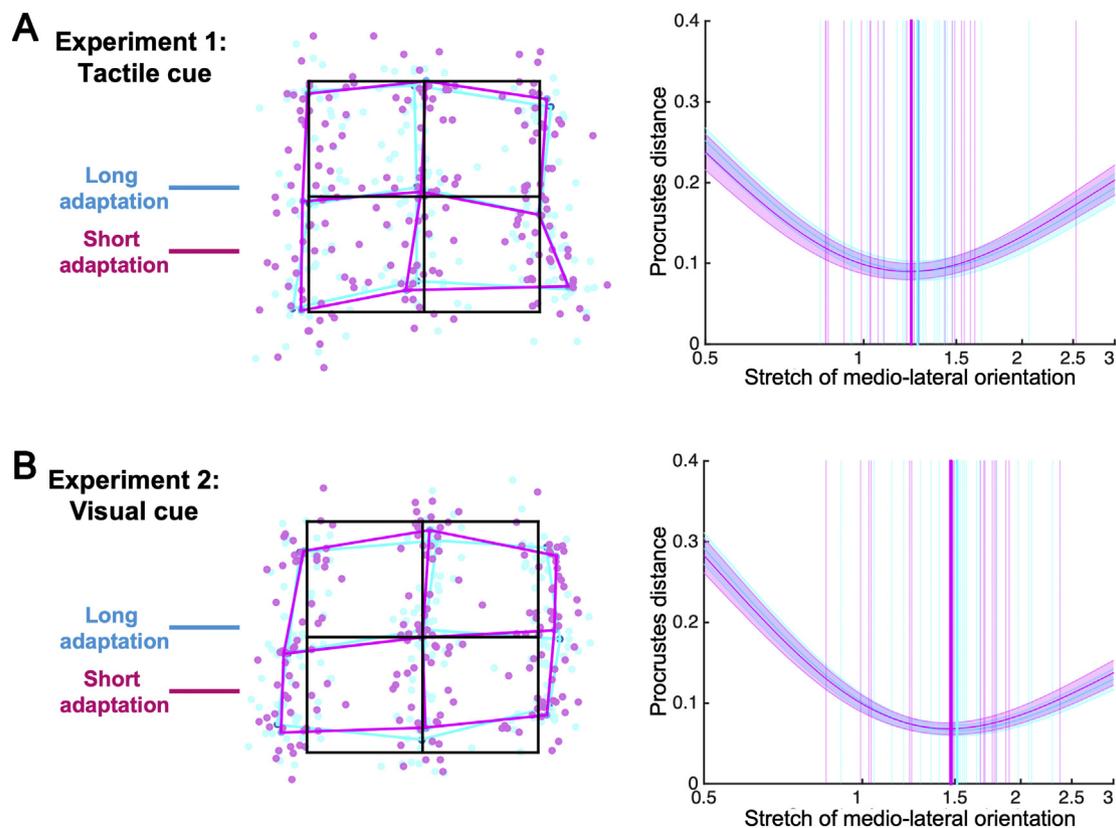


Fig. 4. Results of the localization tasks based on the Procrustes analysis in Experiments 1 (A) and 2 (B). The cyan and magenta plots indicate the long and short adaptation conditions, respectively. The plots with light colours show the individual data. The left panels show the whole maps representing the judged locations against an idealized square grid (black line). The right panels show the estimated minimum Procrustes distances. The horizontal axis denotes the stretch values. The larger values indicate the stretch toward the medio-lateral axis and shrunk with along the proximo-distal axis. The vertical axis denotes Procrustes distances. The bold line shows the mean stretch values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduce the possible involvement of response or decisional biases. We thus expect that tactile distance adaptation induced perceptual aftereffects based on putative changes in neural responses in the somatosensory cortices (Calzolari et al., 2017).

4.2. Distortions on perceptual hand maps

We also replicated the previous findings that the perceptual hand maps, estimated through the relative relationship between reported localizations of touches or landmarks on the hand, are stretched along the medio-lateral axis on the hand dorsum (Longo et al., 2015; Longo & Morcom, 2016). The results of both experiments demonstrated that the average distances between the judged positions of the landmarks on the hand dorsum was longer along the medio-lateral axis compared to the proximo-distal axis (Fig. 3A and B, right), consistent with other recent results (Longo, 2017b; Longo et al., 2015; Longo & Haggard, 2010; Longo & Morcom, 2016; Mattioli & Longo, 2014). The distortion of the implicit geometric structure of the hand was also demonstrated for the stretch values of the perceptual hand maps constructed by the overall patterns of the judged landmarks using Procrustes analyses (Fig. 4). These biases were highly consistent across experiments, indicating that similar perceptual distortions were observed irrespective of the sensory modality used as localization cue. Tactile localization in external space requires proprioceptive information about current postures (e.g., Azañón, Stenner, Cardini, & Haggard, 2015; Tamè, Azañón, & Longo, 2019). Thus, it is not surprising that similar patterns of perceptual distortions are found for the perceptual hand maps estimated through proprioceptive (cued through visual landmarks) or tactile cues.

4.3. No transfer of tactile distance adaptation aftereffects to perceptual hand maps

The main finding of the current study is that the tactile distance adaptation aftereffects had no apparent effect on the patterns of perceptual distortions on the implicit geometric structure of the hand underlying position sense. In both experiments, we found no significant differences of the adaptation conditions for the judged positions of the landmarks on the hand dorsum in terms of distance (Fig. 3A and B, right), shape of the perceptual hand maps, and stretch values (Fig. 4). Green (1982) suggested that tactile distance and localization judgments for tactile stimulation might interact to each other because the similar patterns of perceptual distortions were observed between the tasks. However, no effects of the adaptation were observed for the patterns of the perceptual distortion on the implicit geometric structure of the hand underlying position sense for the tactile localization cue (Experiment 1) as well as the visual cue (Experiment 2). One may note that the difference in the tactile stimuli between the adaptation (blunt sticks) and the localization task (thin Von-Frey hair) may affect the results in Experiment 1. The results of Experiment 2, where no tactile stimulation was applied for the localization task, were highly consistent with those in Experiment 1. This suggests that the exact nature of the stimulus cue for the localization tasks has little or no effect on the structure of the perceptual hand maps underlying position sense. We thus conclude that the difference in the tactile stimuli between the adaptation and localization may have little or no effect.

It has been shown that the patterns of distortions between tactile distance perception on a hand (e.g., Longo & Haggard, 2011) and the perceptual hand maps underlying position sense are very similar (e.g., Longo et al., 2015). By considering the somatoperceptual information

processing model (Fig. 1; Longo et al., 2010), we assumed that the model of body size and shape is commonly involved in both the distortions of tactile distance perception and the perceptual hand maps underlying position sense. Furthermore, the tactile distance adaptation aftereffects are assumed to induce changes in relatively early perceptual and neural somatosensory processing (Calzolari et al., 2017). Thus, we hypothesised that tactile distance adaptation aftereffects might modulate the internal body representations regarding body size and shape (the model of body size and shape), and this effect could transfer to the perceptual hand maps underlying position sense. However, our results showed that the tactile distance adaptation aftereffects did not have any effect on the pattern of distortions on the perceptual hand maps estimated by proprioceptive and tactile localization.

Longo and Morcom (2016) reported no correlations between the magnitude of the distortions toward the medio-lateral axis in tactile distance perception on the hand and the perceptual hand maps underlying position sense. They proposed that different body representations underlying these processes, although common low-level somatosensory processes are involved in shaping each body representation. Since the measurements were different between the tactile distance judgments and the localization performances, Longo and Morcom (2016) also suggested that the internal body representation could be shared but task demands and resulting patterns of perceptual distortions are distinct for tactile distance perception and the perceptual hand maps underlying position sense. Different from Longo and Morcom (2016), the current study used and compared a single measurement, i.e., the magnitude of the distortions on the perceptual maps, after applying the tactile distance adaptation. Thus, our results could not be explained in terms of the differences in task demands. Our current findings provide further evidence that the internal body representations regarding body size and shape may be distinct between tactile distance perception and the perceptual hand maps underlying position sense, although these processes would be based on common low-level somatosensory processing and have similar phenomenal characteristics (distortion).

In the current study, we replicated the tactile distance adaptation and found that the adaptation clearly affected tactile distance perception. However, it might be that the amount of tactile distance adaptation was not enough to induce changes in the internal body representation of body size and shape. Also, if internal body representations involved in perceptual distortions are distinct for tactile distance perception and the perceptual hand maps underlying position sense, we should expect some differences in brain responses. Specifically, neural activation patterns may be different for these distortions, especially in areas related to somatosensory processing. These possibilities should be addressed in future studies.

5. Conclusions

The very similar patterns of perceptual distortions toward the medio-lateral axis of the hand has been reported both for tactile distance perception (e.g., Longo & Haggard, 2011) and perceptual hand maps underlying position sense (e.g., Longo et al., 2015; Longo & Morcom, 2016). The distortions on perceptual hand maps were also observed when the hand image was constructed based on tactile distance perception (Longo & Golubova, 2017). However, the present results revealed that the tactile distance adaptation, which induce perceptual changes in tactile distance perception based on the modulations of neural responses at low somatosensory processing stages (Calzolari et al., 2017), does not have any effects on the pattern and magnitude of the distortion on the perceptual hand maps estimated by external spatial localization performances with different localization cues (tactile and visual cues). Similar to the previous finding showing no correlations in the magnitudes of distortions between tactile distance perception and perceptual hand maps (Longo & Morcom, 2016), our findings indicate that different internal body representations may underlie the

distortions of tactile distance perception and perceptual hand maps, although the similarities in distorted patterns imply the existence of common neural encoding processes for the representations of these tactile processes.

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Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

CRediT authorship contribution statement

Souta Hidaka: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Visualization. **Raffaele Tucciarelli:** Conceptualization, Methodology, Software, Validation, Formal analysis, Writing - review & editing. **Elena Azañón:** Conceptualization, Methodology, Validation, Writing - review & editing. **Matthew R. Longo:** Conceptualization, Validation, Resources, Writing - review & editing, Funding acquisition.

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