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Stability of tactile hand space representation following sensory loss

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A B S T R A C T

Several studies have shown the presence of significant distortions in tactile perception across different body parts in healthy individuals. These distortions are flexible and perceptual, as revealed by studies that have temporarily altered the visual experience of the body leading to changes in perceived tactile distances. Further, evidence suggests that cortical areas help to mitigate these distortions by rescaling the distorted body representations into an object-centred frame and preserving tactile size constancy. This rescaling implies that the brain possesses a representation of the physical size of the stimulated body part. However, it remains unclear whether long-term visual deprivation could affect tactile size constancy and body distortions. To answer this question, we asked blind and sighted individuals to estimate tactile distances between pairs of touched points delivered on the dorsum of their hands and fingers. The results showed that, regardless of visual experience, both groups of participants showed typical hand distortions, suggesting that even a lack of visual information since birth does not influence the spatial representation of tactile stimulation. On a more theoretical level, these data reveal that tactile size constancy is a stable principle of the system and develops even in the absence of visual input.

1. Introduction

In our daily life, our hands play a crucial role in virtually everything: from the moment we wake up and pull the blankets off our body, wave "goodbye"' to our family before driving to work, to the evening in which we use our hands to cook and eat. All these manual gestures are commonly accompanied by vision, in that vision either guides reaching, grasping as well as communicative behaviours or helps adjust them (e.g., the trajectory of a reaching movement, Goodale & Keith Humphrey, 1998; Stone & Gonzalez, 2015; Ryan et al., 2024).

The extreme use we make of our hands and the tight relationship between hands and vision suggests that our knowledge about the size and shape of our hands should be highly accurate. However, there is converging evidence that

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this might *not* be the case, leaving the debate still open. As revealed by different studies, the perception of our body size and shape is highly distorted (Fuentes, Longo, & Haggard, 2013; Sadibolova, Ferrè, Linkenauger, & Longo, 2019; Longo, 2017; Di Vita, Boccia, Palermo, & Guariglia, 2016; for a review, see Longo, 2022), and the magnitude and direction of these distortions are dependent upon the most reliable source of sensory information available during the task. For example, when participants are asked to estimate the position of their fingers in external space (without visual feedback, thus relying on proprioceptive information), they perceive their hands to be wider and their fingers to be shorter than their actual size (Coelho, Zaninelli, & Gonzalez, 2017; Longo, Mattioni, & Ganea, 2015; Longo & Haggard, 2011). Moreover, changes in the spatial position of the fingers relative to one another affect body representations (Tamè, Bumpus, et al., 2017). Similarly, when participants are asked to judge the distance between two tactile points applied to their hand and fingers (thus relying on tactile information), the magnitude of their overestimation accords to the tactile distance anisotropy, by which stimuli applied in the transverse direction (i.e., along the width of the hand) are perceived as longer than the same physical distances applied along the longitudinal direction (i.e., length of the hand, Longo & Haggard, 2011).

Interestingly, when estimates have to be made visually, the performance appears more accurate. For example, participants are highly accurate when asked to match images of body parts to the size and shape of their own body (i.e., template matching task, Longo & Haggard, 2010; though see Giurgola, Bolognini, & Nava, 2020), as well as when asked to indicate specific locations on their hand (Longo, 2014). In particular, in the study by Longo (2014), the role of vision was assessed by asking participants to localise landmarks placed on their hand using a stick under visual or haptic (i.e., blindfolded) feedback. Using Procrustes alignment, real hand vs estimated hand landmarks configurations were compared, showing that, irrespective of visual feedback, participants displayed similar patterns of hand distortions, suggesting that distortions reflect stable features of body representation that do not depend upon vision, though may be affected by gaze direction (Medina, Tamè, & Longo, 2018). However, it should be noted that vision did not abolish the presence of distortions but nevertheless altered them in magnitude. Indeed, participants in the sighted condition perceived their fingers as shorter, which is in line with other studies showing a reduction in the perceived tactile distance on the hand when non-informative vision is present (Longo & Sadibolova, 2013). These findings are in line with the notion that vision could play a modulatory role in somatosensory processing, for instance, by enhancing tactile perception and acuity (Kennett, Taylor-Clarke, & Haggard, 2001; Merz, Meyerhoff, Frings, & Spence, 2020), improving inter-hemispheric integration (Tamè, Carr, et al., 2017), as well as influencing the perceived location of touch on the skin (i.e., this perception depends partly on the position of the eyes in the head, Harrar & Harris, 2010).

Importantly, though, the studies conducted to investigate the role of vision in hand distortions have only temporarily visually deprived participants, leaving open the question as to whether the effects observed could be due to the consequences of short-term deprivation, which commonly leads to rapid plastic changes in somatosensory representations and to a functional enhancement of tactile processing (Facchini & Aglioti, 2003; Weisser, Stilla, Peltier, Hu, & Sathian, 2005). If this were the case, one would expect that once participants regain their typical visual experience, the alterations in hand representation would gradually revert to their original state, reflecting the dynamic nature of sensorimotor plasticity. Nevertheless, evidence that simply blindfolding participants drives immediate changes in hand distortions is suggestive of the flexibility of bodily representations and that vision strongly contributes to triggering such plastic responses.

A way to assess the genuine relationship between vision and bodily distortions, without the confound of the effects of short-term deprivation, is to test blind individuals. In particular, the assessment of distortions in congenitally blind individuals (i.e., individuals who have never experienced any patterned vision since birth) can be the key to understanding the contribution of visual experience in the construction of the human body representations and its perceptual distortions. In particular, the assessment of hand distortions in blind individuals can aid in providing clues to important aspects/features of the complexity of bodily distortions phenomenon, namely their origin, mechanisms and functional role.

For instance, certain body parts engage in more precise and complex actions than others, such as the hands with respect to the trunk, legs, and feet. This, in turn, requires these body parts to have higher tactile sensitivity, which translates into having smaller receptive fields on the skin and larger representations at a cortical level. In agreement with the common view of cortical reorganisation, studies have shown that the brain of blind individuals seems to be subjected to massive cortical reorganisations (Singh, Phillips, Merabet, & Sinha, 2018; Siuda-Krzywicka et al., 2016), which includes, for example, the expansion of the somatosensory cortex, particularly finger representations (Burton, Sinclair, & McLaren, 2004), and the reorganization of the somatosensory thalamic regions and their functional connectivity with visual cortical regions in order to process high-level tactile language information (Lin et al., 2022). Nevertheless, the debate about the concept of cortical reorganisation is still contentious. Recent studies (e.g., Fine & Park, 2018; Makin & Krakauer, 2023; Muret & Makin, 2021) propose the term ‘remapping’ (instead of reorganisation) as more appropriate, as it conceptualises the change as a consequence of potentiation of pre-existing architecture that already has the appropriate representational and computational capability prior to damage or sensory loss. Importantly, this perspective speaks against cortical reorganisation, and in favour of fixed and pre-existing inputs, which get ‘unmasked’ due to sensory deprivation. Thus, the assignment of brain function to a specific cortical structure is defined and hardwired at birth, with little plasticity preserved in extremely short periods of time in early development.

On a perceptual level, behavioural studies have revealed the presence of body distortions, a general bias to overestimate body width compared to length/height (Longo, 2022). In typical development, the distribution of tactile sensitivity comes at a cost of tactile size constancy (Tamè, Limbu, Harlow, Parikh, & Longo, 2022), so that objects feel larger if the body part touching them has large receptive fields and feel smaller if touched by body parts with low-density receptive fields. Studies conducted in the past twenty years have suggested that if individuals had to gather information about tactile size solely from tactile receptive fields, their actions would be highly inaccurate (i.e., reaching towards an object). Indeed, individuals experience tactile size quite accurately, and their perception of change in tactile size is only a fraction (around 30%) of what would be expected if estimates had to be made according to tactile receptive fields (Taylor-Clarke, Jacobsen, & Haggard, 2004). Thus, it has been suggested that the perceptual system must use a compensatory mechanism in order to decrease tactile size discrepancies across body parts to achieve tactile size constancy. In particular, vision seems to play an important role in maintaining such constancy, by which it rescales tactile information on the object(s) placed in external space and ensures that the representation of the object (the body in this case) retains its actual (visual) size.

This specific account suggests that blind individuals—and especially congenitally blind who only had the possibility to know their own and other people's bodies through touch—might retain a more “homuncular” representation of their body, i.e., an overestimation of body size. In particular, this hypothesis applies to the hand, as blind individuals make large use of this specific body part in everyday life (Paterson, 2016); on the contrary, there appears to be no reason for “unseen” body parts (e.g., the back) to have different tactile receptive fields than sighted. Furthermore, blind individuals present enhanced tactile acuity, which has been found across blindness, irrespective of blindness onset (congenital or acquired later in development) and experience using Braille reading (Goldreich & Kanics, 2003). This superiority in tactile acuity could play a compensatory role, potentially leading the blind to present even larger distortions than the sighted (i.e., larger hand representation).

2. Aims and predictions

To observe the role of vision in the construction of hand representation and its distortions, here we tested congenitally and late blind, each age-matched with two groups of sighted controls, on a two-point tactile distance estimation task, in which participants were asked to report the perceived distance between two touches applied on their hand dorsum and fingers. We reasoned that if hand distortions are a fixed characteristic of body representations, then all participants, irrespective of visual experience, should display them in a similar fashion. On the contrary, if body distortions are the result of compensatory mechanisms, in which vision plays a role, then blind individuals should display larger distortions compared to sighted controls. In particular, studies have evidenced that some spatial abilities, such as the spatial remapping of touch, not only emerges in childhood (Pagel, Heed, & Röder, 2009), but depends upon visual input, so that even in the case of restoring of vision caused by cataract at the age of 2, the lack of automatic remapping of touch can be observed in adulthood (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013; Senna, Piller, Ben-Zion, et al., 2022; Senna, Piller, Gori, et al., 2022).

3. Methods and materials

3.1. *Participants*

Thirty-six Italian blind participants with varying experience with blindness onset participated in the study (20 males and 16 females, mean age ± SD = 47.3 ± 13.2). We recruited eighteen late individuals (8 males and 10 females; mean age ± SD = 51 ± 14.4) and eighteen congenital blind individuals (12 males and 6 females; mean age ± SD = 44 ± 11.3). In addition, thirty-six sighted participants (21 males and 15 females; mean age ± SD = 47, ± 13) were chosen as a control group matched to participants by visual deprivation, age, gender and educational level (see Table 1). The sample size was chosen a priori and calculated for a matched pairs t-test (.5 effect size, α .05 and power .80, N = 34). The study was approved by the Ethical Committee of the University of Milano-Bicocca (Protocol Number: 558). All participants took part in the study voluntarily and gave their informed consent before participating.

3.2. *Stimuli & procedure*

Stimuli and procedure were similar to those used in previous studies using a similar paradigm (Longo & Golubova, 2017; Tamè, Tucciarelli, Sadibolova, Sereno, & Longo, 2021). The task aims to investigate the body's shape by measuring perceived tactile distance in different orientations on a single skin surface (e.g., the back of the hand and fingers). Participants sat with their left hands on a table, with the dorsum facing up, their hands flat, and their fingers completely straight. Sighted participants performed the task blindfolded.

We applied tactile stimulation—using a 60gr von Frey filament—on the dorsum and fingers of the participant's left hand. Using a von Frey hair ensures that the amount of pressure applied at each location is kept constant across stimulations. Tactile stimulation was delivered manually by the experimenter in a pre-marked location on the participants' left hand: using a felt-tip pen to facilitate coding, a 3x3 grid was centred and drawn on the dorsum using a plastic template and pairs of points drawn on the first and second phalanxes of the participants' fingers (excluding the thumb). The distance between adjacent locations in the grid was 2 cm, while the eight points drawn on the phalanges were 2.5 cm, equidistant from each other. To ensure that the landmarks were placed in the same position for all participants, the top central hole of the grid was positioned 2 cm below the knuckle of the middle finger in the direction of the wrist. The grid was aligned with the proximo-distal axis of the middle finger, following an imaginary line connecting the fingertip and the knuckle of the middle finger. The pairs of points on the fingers were drawn using a pre-formed shape positioned on each finger's first and second phalanges (excluding the thumb) using the centre of the knuckle as a reference point (see Fig. 1C).

A photograph showing the participant's actual hand, with the grid and pairs of dots drawn, was taken at the beginning of

Table 1 – Blind participants' characteristics. The participant ID code is divided into two groups of participants with different blindness onset: C stands for Congenital blind, and L stands for Late blind.

Participants	Gender	Age (years)	Cause of blindness (etiology)	Onset blindness in years	Handedness
C_01	F	56	Congenital Glaucoma	At birth	Right
C_02	M	55	Problems during pregnancy	At birth	Right
C_03	F	29	Traumatic event	At birth	Right
C_04	M	37	Retinitis pigmentosa	At birth	Right
C_05	M	41	Congenital Glaucoma	At birth	Left
C_06	M	64	Retinitis pigmentosa	At birth	Right
C_07	M	36	Retinitis pigmentosa	At birth	Left
C_08	F	34	Traumatic event	At birth	Right
C_09	M	23	Unknown	At birth	Right
C_10	M	61	Congenital Glaucoma	At birth	Right
C_11	M	40	Retinitis pigmentosa	At birth	Left
C_12	M	46	Retinitis pigmentosa	At birth	Right
C_13	F	37	Retinopathy of Premature (RoP)	At birth	Right
C_14	M	35	Traumatic event	At birth	Right
C_15	M	50	Microphthalmia	At birth	Right
C_16	F	49	Unknown	At birth	Right
C_17	F	41	Retinitis pigmentosa	At birth	Right
C_18	M	54	Congenital Glaucoma	At birth	Left
L_01	F	34	Bilateral Retinoblastoma	32	Right
L_02	M	38	Retinoblastoma	34	Right
L_03	F	34	Neurofibromatosis	18	Right
L_04	M	52	Unknown	38	Right
L_05	M	57	Rheumatoid arthritis	37	Right
L_06	F	44	Glaucoma	24	Right
L_07	F	53	Usher syndrome	42	Right
L_08	F	66	Optic nerve atrophy	50	Right
L_09	M	22	Neurofibromatosis	16	Right
L_10	M	67	Unknown	62	Right
L_11	M	57	Unknown	41	Right
L_12	F	27	Traumatic event	11	Right
L_13	M	65	Unknown	49	Right
L_14	M	58	Unknown	46	Right
L_15	F	62	Unknown	42	Right
L_16	F	70	Traumatic event	55	Right
L_17	F	54	Retinitis pigmentosa	48	Right
L_18	F	55	Retinitis pigmentosa	40	Ambidextrous

each test; this allowed measurement of true hand proportions (see Fig. 1A). Pixel coordinates of each landmark were coded offline using the ruler function on Photoshop (Adobe Inc. 2019). Before starting the task, participants familiarized themselves with actual distances by touching a raised surface with their hand that reproduced distances of 1, 2, 5, 10 and 15 cm (see Fig. 1B).

There were eight blocks counterbalanced (i.e., in ABBA sequence) throughout the Experiment: four blocks with 72 trials each, for a total of 288 trials for the dorsum, and four blocks with 56 trials each, for a total of 224 trials for the fingers. In each block there were 36 combinations of the 9 points for the dorsum and 28 possible combinations of the 8 points for the fingers, crossed with two orders of stimulation, presented randomly. These combinations represent the only possible pairs of the 9 and 8 stimulus positions (see Table 2).

In each trial, two pairs of touches defining different tactile distances were applied in sequence, either to two grid points drawn on the dorsum (i.e., dorsum block) or to two points drawn on the fingers (i.e., fingers block). Each location was stimulated for approximately 1 s with a 1-s inter-stimulus interval. Participants were instructed to verbally identify the perceived distances in centimetres between two pairs of tactilely stimulated locations, taking their time and trying to be as precise as possible but also avoiding spending too much time thinking about responses. They were told to indicate whatever distance felt most intuitive: they could respond to 0 cm if they felt that the same point was stimulated twice, even though, in reality, two different points were always stimulated in each trial. Short breaks were allowed between blocks.

In this kind of task, participants have generally been asked to base their responses on their subjective feelings of body size, body location, or stimulus size (i.e., apparent perspective). This raises the possibility of a dissociation between participants' subjective feelings and their actual beliefs (i.e., objective perspective) (Tamè, Linkenauger, & Longo, 2018). This type of instruction, focusing on the participant's subjective experience, is known as an 'apparent' instruction (Carlson, 1977). Apparent instructions are thought to direct the observers to base their judgments on more perceptual sources of spatial information (Predebon, 1992).

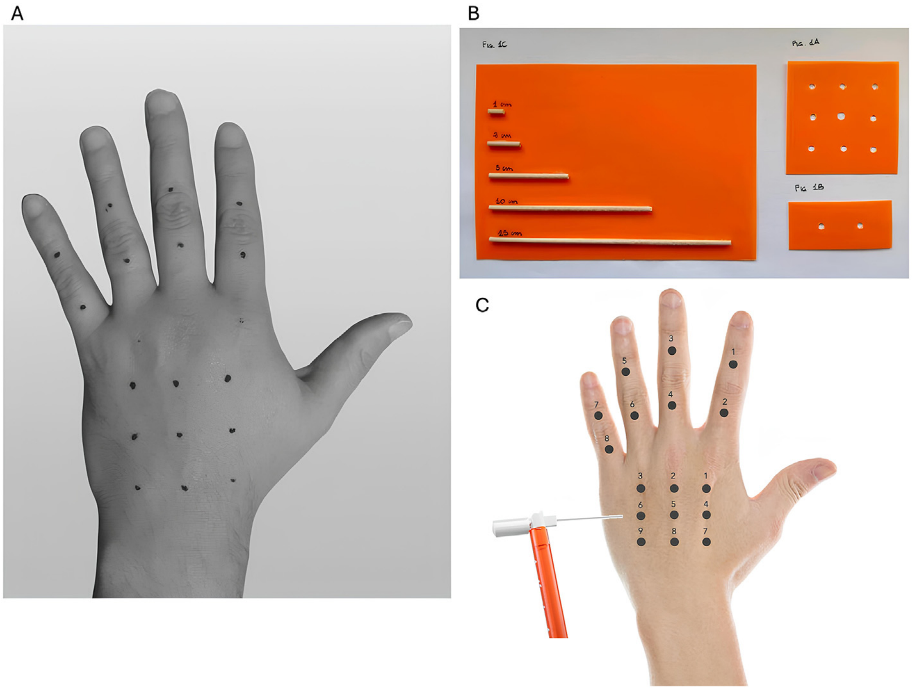

Fig. 1 – **A) Photo of the participant's left hand prior to the start of the Experiment. The grid, with nine landmarks, was positioned on the dorsum. The landmarks were enumerated from the upper-right corner of the grid (landmark 1) to the lower left corner (landmark 9). B) Plastic templates are used to draw the grid on the dorsum and the pairs of points on the phalanges, and plastic templates are used to familiarise participants with different lengths before starting the task. C) Example of tactile stimulation delivered with 60gr von Frey filaments.**

Table 2 – **Random block design: trials combination.**

Dorsum (A-B; B-A)	Fingers (A-B, B-A)
36 possible combinations of the 9 points = 72 trials per block 4 blocks = 288 trials in tot.	28 possible combinations of the 8 points = 56 trials per block 4 blocks = 224 trials in tot

3.3. *Statistical analysis*

Data analyses followed three-step procedures, including Multidimensional Scaling (MDS), Procrustes analysis and stretch analysis, which is described in turn below. Previous reports extensively described these procedures using a similar approach (Longo & Golubova, 2017; Tamè et al., 2021).

3.3.1. *MDS*

MDS is a method for reconstructing the latent spatial structure underlying a set of items given a matrix of pairwise distances, or dissimilarities, between items (Cox & Cox, 2008; Longo & Golubova, 2017; Saporta, 1999; Shepard, 1980). It allows us to obtain bidimensional maps (dorsum and fingers) that describe the internal geometry of the tactile space. Using participants' judgments of the perceived distance between pairs of touched landmarks, we applied MDS to the resulting matrix to construct perceptual maps of the representation of the dorsum and fingers of the hand, separately. This approach produces an overall map of the geometry of tactile space for the hand dorsum and another for the fingers' dorsum (Fig. 2A), that can be compared with the actual configuration of the hand and fingers skin's surface. Multidimensional scaling was applied to the distance matrices for each participant using the ‘cmdscale’ command in MATLAB (Mathworks, Natick, MA). The output of MDS is a set of eigenvalues for each dimension and coordinates for each landmark in each dimension. As there are 9 for the hand and 8 for the finger's landmarks, MDS attempts to position the landmarks in 9 or 8-dimensional space, respectively, such that the distances between them are as proportional as possible to the perceived distances.

3.3.2. *Procrustes analysis*

Procrustes alignment superimposes two spatial configurations of homologous landmarks by translating, scaling, and rotating them to be as closely aligned as possible (Goodall, 1991; Rohlf & Slice, 1990). We used Procrustes alignment in two ways: at first, to quantify dissimilarity in shape and as a visualisation tool. If two configurations have exactly the same structure, they will be placed on top of each other, applying Procrustes alignment, resulting in a Procrustes distance of zero. On the other hand, two configurations with no shared spatial structure will have a Procrustes distance of one, assuming that size normalisation yields a total sum of squared variance of one inside each configuration. Then, we used Procrustes alignment to display the different configurations. Considering that we had to compare several hand and

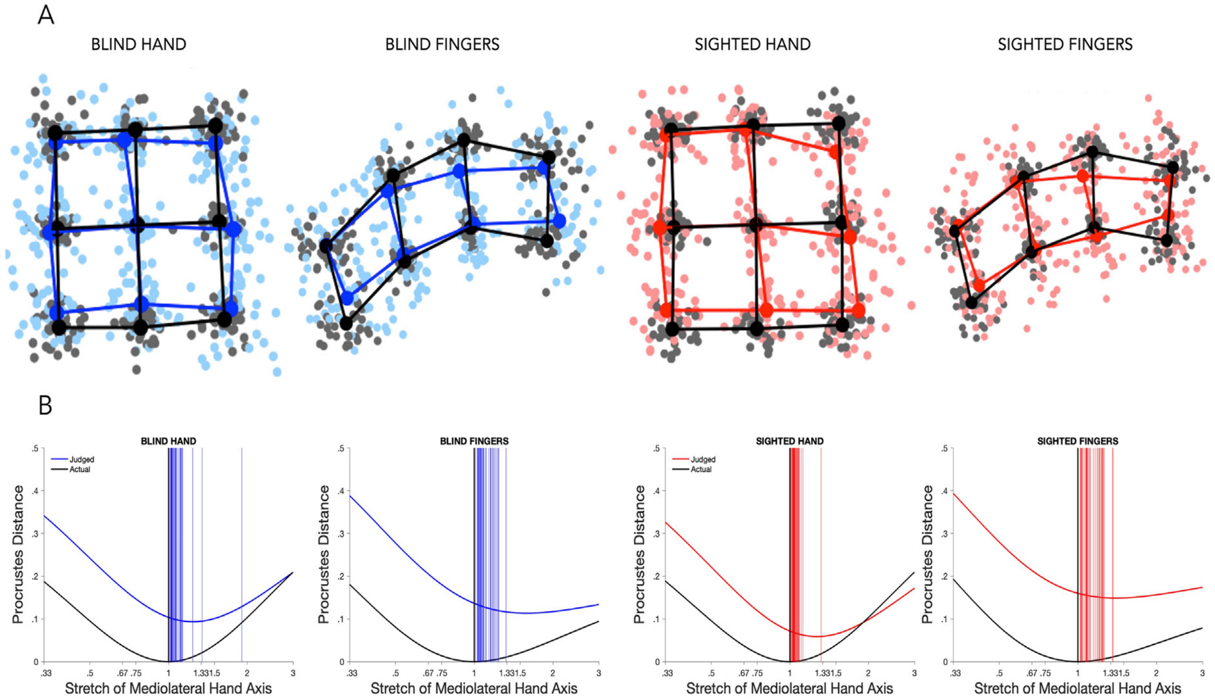

Fig. 2 — Perceptual hand representation of the spatial configuration of the skin surface. A) Generalised Procrustes alignment of the actual configuration of points on the hand (black dots and lines) and perceptual configurations (blue dots and lines for blind participants and red dots and lines for sighted participants). The light dots are data from individual participants, while the dark dots represent the average shape; B) Mean Procrustes distance of the perceptual configurations for each participant and idealised grid stretched by different amounts. A stretch of 1 indicates a square grid; stretches greater than 1 indicate a stretch in the mediolateral axis, while stretches less than 1 indicate a stretch in the proximo-distal axis. Blue and red lines, depending on the group, represent values for each participant.

finger maps, we used generalized Procrustes analysis (GPA) using Shape (a MATLAB toolbox from Dr Simon Preston, freely available for download [https://www.maths.nottingham.ac.uk/personal/spp/shape.php] based on an algorithm originating from Gower, 1975; Ten Berge, 1977). Indeed, GPA is designed to align and compare multiple shapes by removing differences in translation, rotation, and scaling. This makes it well-suited for group-level shape analysis across multiple subjects. Specifically, in the Shape MATLAB toolbox, it can input shape data from multiple subjects, from which toolbox will compute an average shape while minimizing individual differences due to position, orientation, and size.

3.3.3. *Stretch estimation*

Moreover, we estimated the overall stretch difference between the actual and estimated configurations in the medio-lateral axis for the hand and fingers (Tamè et al., 2021). The procedure was the same one used in a previous study (Longo & Golubova, 2017) as we multiplied the x-coordinates of a 3x3 square grid (for the hand) and a 2x4 grid (for the fingers) by a stretch parameter to generate grids of varying levels of stretch. When the stretch parameter was equal to 1, the grid was perfectly square. When it was greater than 1, the grid was stretched in the medio-lateral axis. When it was less than 1, the grid was stretched in the proximo-distal axis. For each participant and configuration (i.e., hand and fingers), 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 configuration. Values between .33 and 3 were tested by exhaustive search with a resolution of .0005 units in natural logarithm space. Note that for this and other tests involving ratios, the calculation of means and all statistical tests were conducted on log-transformed values, which were converted back to ratios to report mean values.

Finally, the participant distances provided by the subjects for each stimulated landmark were compared with the actual distances obtained through the pre-formed grid on the back, where each point was 2 cm apart, and the pairs of points drawn on the phalanges, which were 2.5 cm apart. We calculated the overestimation values of the fingers, and two-tailed t-tests were used for all planned comparisons.

4. Results

As shown in Fig. 2A, we were able to reconstruct the two-dimensional perceptual maps that show a good fit to the participants' actual skin shape for the dorsum of the hand and the fingers. The reconstructed configurations were similar across groups.

Fig. 2B shows the mean Procrustes distance for values of the stretch parameter between .33 and 3. The best-fitting stretch parameters were significantly greater than 1 for the dorsum and fingers regardless of the visual experiences [Blind-dorsum: $M = 1.26$, $t\ (35) = 4.14$, $p < .0001$, $dz = .7$; Sighted-dorsum: $M = 1.32$, $t(35) = 6.9$, $p<.0001$, $dz = 1.15$; Blind-fingers: $M = 1.73$, $t(35) = 8.53$, $p < .0001$, $dz = 1.42$; Sighted-fingers: $M = 1.7$, $t(35) = 4.78$, $p < .0001$, $dz = .8$], indicating a substantial bias to overestimate distances in the medio-lateral compared to the proximo-distal hand axis. A direct comparison between sighted and blind participants did not reveal any differences across groups [Dorsum: Sighted vs. Blind, $t(35) = .98$, $p = .33$, $dz = .2$; Fingers: Sighted vs. Blind, $t(35) = -.86$, $p=.39$, $dz = .05$].

Our results for the blind group are in accordance with previous studies on sighted individuals (Longo et al., 2015; Longo & Golubova, 2017; Longo & Haggard, 2010; Tamè, Bumpus, et al., 2017; Tamè et al., 2022), as we found the same amount of overall underestimation of fingers' length. As shown in Fig. 3, averaging across the four fingers, a clear underestimation of the participants' estimated finger length compared to the actual length emerged for both the blind ($M \pm SE = 1.79 \pm .138$, $t(35) = 5.16$, $p < .0001$, $dz = .86$) and the sighted ($M \pm SE = 1.95 \pm .142$, $t(35) = 3.91$, $p < .0001$, $dz = .65$) individuals. However, we did not find any difference between the two groups across all four fingers' length ($t(35) = .776$, $p=.44$). Fig. 2A shows maps that are clearly distorted following the typical pattern reported by previous literature (Longo & Golubova, 2017; Longo & Haggard, 2011; Tamè, Bumpus, et al., 2017), regardless of visual experiences. Indeed, all participants showed similar anisotropies, i.e., a bias to overestimate the distance between touches oriented with the mediolateral hand axis compared to the proximo-distal axis.

Similarly, blind and sighted participants showed a related underestimation of finger length for each tactually stimulated landmark during the task compared to the actual length (2.5 cm), i.e., overall, the perceived distance between pairs of points on the participants' fingers was judged to be shorter than the actual distance by both groups (all comparisons $p < .0001$). Moreover, this underestimation did not differ between sighted and blind individuals, showing that both groups of participants have a similar pattern in perceiving finger lengths (see Fig. 3). A repeated measures ANOVA showed a main effect of Fingers ($F(3,210) = 7.63$, $p<.0001$, $\eta^2 = .006$), due to higher underestimation of the *little finger* compared to the *ring finger* [Little: $M = -27.77$, $SE = 4.2$; Ring: $M = -21.63$, $SE = 4.24$; $t(70) = -3.67$, $p=.002$, $dz = 1.5$], as well as higher underestimation of the *index* compared to the *ring finger* [Index: -28.21, $SE = 3.9$; Ring: $M = -21.63$, $SE = 4.24$; $t(70) = 3.96$, $p=.001$, $dz = 1.62$[. Finally, the *index finger* also showed higher underestimation than the *middle finger* [Index: -28.21, $SE = 3.9$; Middle: -23.63, $SE = 3.9$; $t(70) = 3.01$, $p=.02$, $dz = 1.2$]. No interaction effect [$F(3,210) = 1.32$, $p=.27$, $\eta^2 = .001$]. No differences between groups were found [$F(1,70) = .62$, $p=.43$, $\eta^2 = .008$].

Finally, we found no differences in the overestimation of spacing across pairs of knuckles between blind and sighted participants, suggesting that the degree of visual experiences does not affect the perceived finger space between groups (see Fig. 4). A repeated measure ANOVA showed a main effect of Pairs of knuckles [$F(2,140) = 10.43$, $p<.0001$, $\eta^2 = .02$], due to higher overestimation of the space across *index/middle* compared to *ring/little* [index/middle: $M = 60.16$, $SE = 8.13$; ring/little: $M = 41.75$, $SE = 6.4$; $t(70) = 3.5$, $p=.002$, $dz = 2.61$] irrespectively of distal and proximal distance, as well as higher overestimation of space across *middle/ring* compared to *ring/little* [middle/ring: $M = 64$, $SE = 9$; ring/little: $M = 41.75$, $SE = 6.4$; $t(70) = 4.01$, $p=.0004$, $dz = 2.88$] irrespectively of distal and proximal distance. We also found a main effect of Distances [$F(1,70) = 21.54$, $p<.0001$,

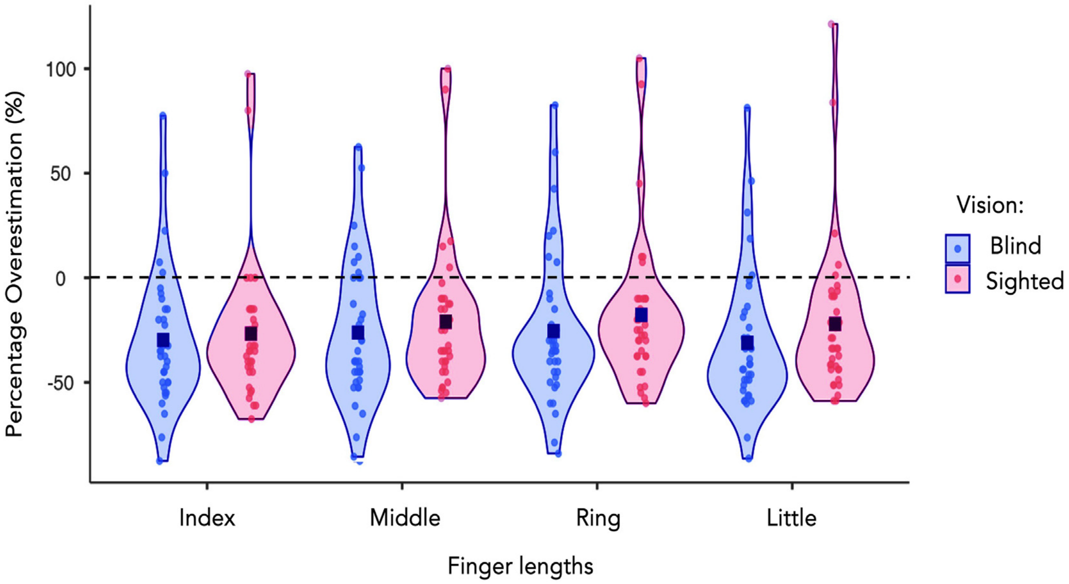

Fig. 3 – Percent overestimation [i.e., 100 x (judged length−actual length (2.5 cm))/actual length (2.5 cm)] of finger length. Clear underestimation was observed for both sighted and blind participants. No significant differences were found between subjective judged distances between blind and sighted participants. No differences were found between subjectively judged lengths between blind and sighted participants. Positive values indicate the degree of overestimation, negative values indicate the degree of underestimation, and zero indicates correct reports.

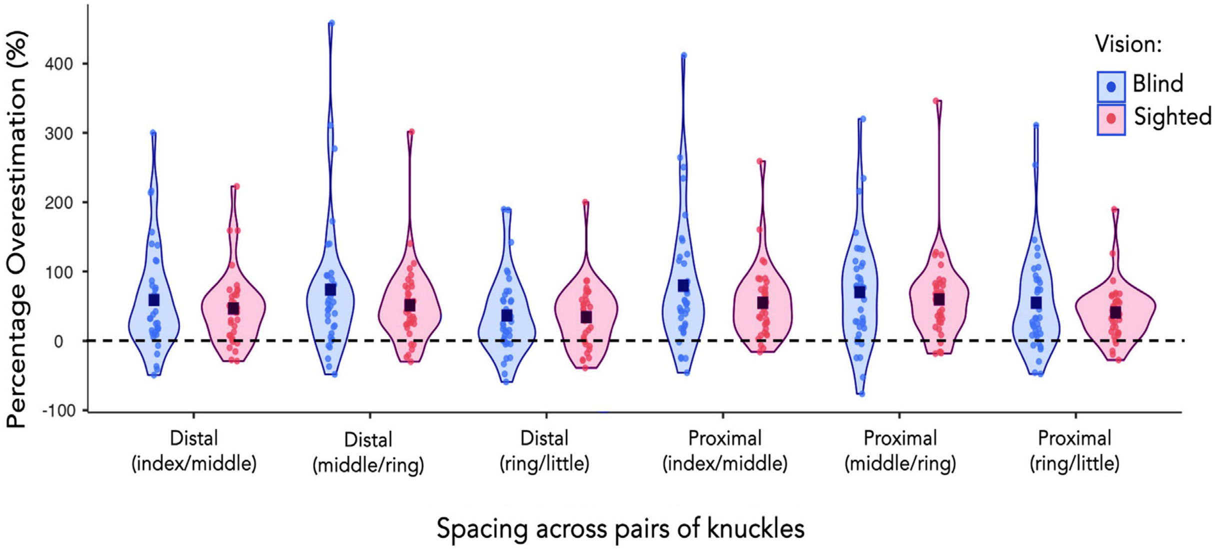

Fig. 4 – Percent overestimation [i.e., 100 x (apparent distance–objective distance)/objective distance] of spacing across pairs of knuckles. Clear overestimation was observed for both sighted and blind participants, but no differences were found between these two groups. Positive values indicate the degree of overestimation, negative values indicate the degree of underestimation, and zero indicates correct reports.

$\eta^2 = .005$] due to higher overestimation when participants had to estimate proximal distances than distal distances [Distal: M = 50.4, SE = 7.02; Proximal: M = 60.2, SE = 7.6; t(70) = - 4.64, *p*<.0001, *dz* = 1.34]. No interaction effects were found at all, and no differences between groups were found [F(1,70) = 1, *p*=.32, $\eta^2 = .01$].

5. Discussion

In the present study, we investigated the role of vision in body representation by testing blind and sighted individuals with different degrees of visual experiences and blindness onset (i.e., congenitally vs. late) on a tactile distance estimation task on the hand and fingers dorsum. We found the typical distortions observed in previous studies (Longo et al., 2015; Longo & Golubova, 2017; Longo & Haggard, 2010, 2011; Tamè, Bumpus, et al., 2017; Tamè et al., 2022) across all participants, irrespective of their visual experiences (note that no differences were also found between late and congenital participants). Blind and sighted participants showed an overestimation of the distances between touches orientated with the mediolateral hand and finger axis, but no significant differences in this bias (both in overestimation and underestimation direction) were found between the groups.

According to previous literature, vision appears to play a crucial role in the formation of body perception and seems to be the most reliable sensory modality when it comes to acquiring information on the spatial position of body parts (de Vignemont, Ehrsson, & Haggard, 2005; Marino, Stucchi, Nava, Haggard, & Maravita, 2010; Pavani, Spence, & Driver, 2000). Nevertheless, in our study, it seems that vision does not strongly influence the represented spatial configuration of the skin surface of the hand and fingers. This might suggest that hand distortions, and by extension, body representation, might be a structural feature unaffected by changes due to visual deprivation. For example, studies on congenitally amputated individuals (e.g., congenital limb aplasia) have revealed that the feeling of the own body (i.e., body representation) might be partially innate (Brugger et al., 2000; Melzack, 1997). Indeed, some congenital amputees report experiencing the presence of their limbs while having no sensory experience with them (Price, 2006). These examples are in line with a general idea of a body model, by which the internal representation of our body and its parts are hardwired.

A variation in sensory input, e.g. the presence or absence of access to the visual channel, would therefore appear to have no decisive influence on the spatial representation of the body to the extent that variations can be detected (Coelho et al., 2017; Longo, 2014; Shahzad et al., 2025). The persistence of similar distortions of body representation (e.g., of the hand) in blind and sighted individuals may indicate that the fundamental architecture of body ownership may be hardwired and linked to multisensory integration, where different cross-modal signals from one's body contribute to this sensation. Indeed, somatosensory and proprioceptive systems provide continuous feedback about the body's position and movement. These inputs might be sufficient to maintain an accurate body representation even without visual information. For example, haptic feedback and proprioception can compensate for the lack of visual input, ensuring that the body schema remains intact, suggesting the use of an anatomically rather than externally anchored reference system for tactile localization (Rincon-Gonzalez, Naufel, Santos, & Helms Tillery, 2012). Furthermore, the existence of similar finger distortions for blind and sighted individuals reinforces the proposal that fingers are predominantly represented in anatomical coordinates through a somatotopic representation or finger schema, which is used independently of visual experience

(Haggard, Kitadono, Press, & Taylor-Clarke, 2006; Röder, Föcker, Hötting, & Spence, 2008). This also aligns with previous studies showing an identical perception of Aristotle's Illusion between blind and sighted individuals (Benedetti, 1985; Nava, Steiger, & Röder, 2014).

Our results appear in contrast with studies suggesting that vision distorts tactile size constancy, a mechanism that could account for body distortions. Indeed, as shown by Longo and Sadibolova (2013), when participants were induced to believe (through the mirror box illusion) that they were seeing their stimulated left while, although they see a reflection of their right hand, their estimates of the perceived size of touch were reduced when they were allowed to see. On the contrary, the estimates were more accurate when participants looked at an object or the contralateral hand.

While this study seems to strongly suggest that vision plays a crucial role in modulating tactile size constancy, it could be claimed that the method cannot be fully comparable to the visual deprivation approach. In other words, in the study by Longo and Sadibolova (2013), participants were not deprived of vision; rather, their vision was temporarily altered. This might suggest that temporary alterations of vision can distort the tactile percept; however, long-term visual deprivation might stabilise tactile size constancy mechanisms.

In a recent intriguing report, Shahzad et al. (2024) investigated how visual experience can shape body representation by testing tactile distance perception on the ventral and dorsal part of the forearm, wrist and hand in blind and sighted participants. Although they found a reduced magnitude on the forearm tactile distance estimation for the blind participants, no difference was found between the groups for the other body parts tested, namely wrist and hand. Their findings are compatible with our results, suggesting that although visual experiences may contribute in some way to body representation (e.g., forearm), they are not in themselves a key element influencing whole-body tactile representation. Notably, the blind individuals showed a bias similar to that observed in the sighted participants for overestimating tactile distances on the limbs medial–lateral axis, suggesting that visual experience does not critically contribute to the tactile body shape distortions. In line with their results, we also found that visual deprivation does not appear to lead to changes in hand and fingers anisotropy, although visual experience could play an important role in shaping other specific body areas (e.g. forearm in the study by Shahzad et al., 2024).

In general, the stability of body representation despite visual deprivation has significant implications for our understanding of sensory processing and neural plasticity. It suggests that the brain's representation of the body is a robust feature maintained through multisensory integration and neural plasticity. Future studies investigating the specific neural mechanisms underlying this stability could provide deeper insights into how the brain integrates sensory information to maintain a coherent body schema.

CRediT authorship contribution statement

Michelle Giraud: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Luigi Tamè:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Elena Nava:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Scientific transparency statement

DATA: All raw and processed data supporting this research are publicly available: https://osf.io/7fp5c/?view_only=752ec52043f749e9a9b4f2326a63dce0.
CODE: All analysis code supporting this research is publicly available: https://osf.io/7fp5c/?view_only=752ec52043f749e9a9b4f2326a63dce0.
MATERIALS: This research did not make use of any materials to generate or acquire data.
DESIGN: This article reports, for all studies, how the author(s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.
PRE-REGISTRATION: No part of the study procedures was preregistered in a time-stamped, institutional registry prior to the research being conducted. No part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted.
For full details, see the Scientific Transparency Report in the supplementary data to the online version of this article.

Declaration of competing interest

The authors declare no conflict of interest.

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Supplementary data

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