



How visual experience shapes body representation

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ABSTRACT

We do not have a veridical representation of our body in our mind. For instance, tactile distances of equal measure along the medial-lateral axis of our limbs are generally perceived as larger than those running along the proximal-distal axis. This anisotropy in tactile distances reflects distortions in body-shape representation, such that the body parts are perceived as wider than they are. While the origin of such anisotropy remains unknown, it has been suggested that visual experience could partially play a role in its manifestation. To causally test the role of visual experience on body shape representation, we investigated tactile distance perception in sighted and early blind individuals comparing medial-lateral and proximal-distal tactile distances of stimuli presented on the ventral and dorsal part of the forearm, wrist, and hand. Overestimation of distances in the medial-lateral over proximal-distal body axes were found in both sighted and blind people, but the magnitude of the anisotropy was significantly reduced in the forearms of blind people. We conclude that vision does not drive the emergence of tactile distance anisotropies, but visual experience can however modulate its expression on some specific body parts.

1. Introduction

The representation of our body scaffolds our sense of self and therefore our identity (Longo, 2022). Intriguingly, we do not have a veridical body representation in our mind. For instance, the representation of body shape and size is distorted such that the width of the body parts is overestimated (Longo & Haggard, 2010, 2011). Distortions in body shape can produce anisotropy in perceived tactile distance between the medial-lateral (ML) and proximal-distal (PD) limb axes, where the ML distances are perceived as larger than the PD distances on various body parts (Longo & Haggard, 2011). Tactile distance anisotropies have been reported in many parts of the body including hands (Knight et al., 2014; Longo, 2020; Longo & Haggard, 2011), forearm (Green, 1982;

Knight et al., 2014), thigh (Green, 1982; Stone et al., 2018; Tosi & Romano, 2020), shin (Stone et al., 2018), feet (Manser-Smith et al., 2021), and face (Longo et al., 2020). Measuring tactile distance anisotropy, therefore, allows us to estimate the aspect ratio of a body part within the mental body model (Longo & Haggard, 2011).

What drives such body distortions is still unknown. Anisotropies in tactile body distance perception have been suggested to reflect the anisotropies in the geometry of tactile receptive fields. The receptive fields (RF) of neurons in somatosensory cortex representing the hairy skin of the limbs are generally oval-shaped, with the long axis running proximal-distally (Brooks et al., 1961; Longo & Haggard, 2011), and they are densely packed along the medial-lateral axis. This allows a greater count of “pixels” (pixel model proposed by Longo (Longo, 2022;

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Longo & Haggard, 2011)) in the medial-lateral axis, thereby increasing the perceived distance in this orientation. Moreover, tactile spatial acuity is higher for stimuli oriented medial-laterally compared to proximal-distally (Schlereth et al., 2001). Furthermore, tactile anisotropies are higher on less sensitive regions like arms, as compared to more sensitive areas like hands. Similarly, they are larger generally on the dorsal surface as compared to the ventral counterpart (Knight et al., 2014). However, if receptors indeed distort our perception of the physical world, it would be peculiar that during development and extended periods of interaction with objects, the mind and brain have not corrected such biases for skilled manual action (Bassolino & Becchio, 2023). Perceptual consistency, the idea that the mind generates a stable perception of the world despite what the receptors convey (e.g. across saccades) is a well described phenomenon in vision (Walsh & Kuliowski, 1998). In other words, our interaction with the world should have compensated for the sensory bias by imposing a perceptual bias on top of it for efficient interaction with objects. This suggests that the source of the anisotropy could also be found beyond the configuration of receptive fields (Bassolino & Becchio, 2023; Longo, 2022).

It is thought that the computation of tactile distances on different body parts are referenced against a mental representation of the body's shape and size (Longo, 2022). This mental representation draws from multiple sensory inputs (Azañón et al., 2016). Since vision is the dominant modality for spatial perception tasks (Alais & Burr, 2004; Charbonneau et al., 2013), it has been suggested that during tactile spatial processing, visual representations (e.g. visual imagery) are automatically activated to support tactile spatial discrimination (Sathian et al., 1997; Zangaladze et al., 1999). Likewise, the localization of touch in external space, i.e., taking postural information into account, is believed to take place in a visually-based representation, rather than purely tactual (Azañón & Soto-Faraco, 2008; Crollen et al., 2017; Röder et al., 2004).

The brain therefore uses visual information to create a mental representation of one's body shape (Longo, 2022). The way we visually experience our body, including the mental images we have of the location of body-parts such as knuckles and wrists, as well as the unique foreshortened perspectives of body parts such as the arms, could contribute to tactile anisotropy (Longo, 2022). When we stretch our arm out in front of us, our visual perspective of the arm will be foreshortened in the PD axis much more than the ML axis. A lifetime of experience seeing the arm in such foreshortened perspective may produce systematic distortions in how it is mentally represented.

Previous studies have assessed the role of vision in the distortion of hand shape using implicit methods, which require participants to localise landmarks such as knuckles or tips of the fingers. These studies have shown that the implicit perception of the hand shape is distorted in a similar fashion as the anisotropy observed in tactile distance: the hand width (i.e., the medial-lateral axis) is overestimated and the finger length (i.e., the proximal-distal axis) underestimated (Hidaka et al., 2020; Longo et al., 2015). Participants tested under both sighted and blindfolded conditions showed different magnitudes of distortions of the implicit hand maps (Longo, 2014). The representation of the hand was significantly more distorted in the sighted condition, which suggests that the distortion could be a result of multisensory interactions modulated by vision. In another study investigating how the different sensory modalities contribute to the perception of hand, it was seen that the distortion was higher in the case where the participants had access to both visual and haptic information or only the visual information, as opposed to the condition where they could access only haptic information (Coelho & Gonzalez, 2018).

Since vision has been seen to modulate tactile size perception (Taylor-Clarke et al., 2004) and implicit hand maps (Coelho & Gonzalez, 2018; Longo, 2014), it is suggested that vision could contribute towards tactile distance anisotropies (Longo, 2022). However, the causal impact of visual experience on tactile distance anisotropies remains untested. In this study, we assessed the role of visual experience on the anisotropies

of tactile distance perception underlying body shape representations by comparing tactile anisotropies in sighted controls (SC) and early blind (EB) individuals on different body parts and surfaces. We tested the participants with tactile distances oriented either medial-laterally or proximal-distally on their hand, wrist, and forearm in a two-alternative forced-choice paradigm. If the visual experience of the body contributes to anisotropies in tactile distance perception, we expect to observe differences in the magnitude of anisotropy between the two groups. On the other hand, an absence of group difference would suggest that intrinsic properties of the tactile receptive field may be the primary source for distorted body representation in touch.

2. Methods

2.1. Participants

We based our sample size on a previously published study (Knight et al., 2014) that measured tactile distance anisotropy on both – dorsal and ventral surfaces of the hand, wrist and forearm in the sighted population, using the same tactile stimuli. This study tested 15 sighted participants in a repeated measures design. We performed an a priori power analysis using the software G*Power (version 3.1) (Faul et al., 2007) with the reported effect sizes for the main effects and the interaction terms. Given the particular interest in the effect size of the interaction effect, which exhibited the smallest magnitude, we computed the sample size for the sighted group focussing on this term in a repeated-measures within-factors design. Using an effect size $f = 0.54$, $\alpha = 0.05$, and $power = 0.95$, the computed sample size for the sighted group was 11. This sample size was mirrored in the blind group. To ensure sufficient statistical power for detecting differences between the two groups and to accommodate exclusions resulting from poor curve fitting and variability in blindness duration, we recruited additional participants. Consequently, we tested 17 sighted individuals (SC) (11 females, mean age \pm SD: 33.47 ± 7.12 years old) and 19 early blind individuals (EB) (11 females, mean age \pm SD: 33.41 ± 7.33 years old).

Here, we attributed blindness to individuals with peripheral deficits and no additional neurologic problems (Table 1). The blind participants lost their sight or suffered from visual problems since birth that evolved towards complete blindness before 4 years of age. 11 blind participants reported residual vision with no pattern or color vision. Sighted participants had normal or corrected-to-normal vision. The details of the blind participants, obtained through extensive structured interviews, are summarised in Table 1.

The participants signed a written informed consent and were financially compensated for their participation. The experimental procedure was approved by the research ethics boards of the Center for Mind/Brain Sciences (CIMEC) and the University of Trento (Protocol 2016–012), and by The Code of Ethics of the World Medical Association, Declaration of Helsinki (Rickham, 1964).

2.2. Stimuli

The tactile stimuli (Fig. 1) consisted of three wooden blocks. Each wooden block was mounted with two metallic round-point pins. These pins were separated by fixed distances of either 2, 3, or 4 cm on each wooden block. These stimuli were very similar to those used in previous studies of tactile distance perception (Knight et al., 2014).

2.3. Procedure

The procedure was modelled on previous studies investigating tactile distance anisotropies (Chang & Longo, 2022; Knight et al., 2014). Participants sat blindfolded at a table. Stimuli were presented on both surfaces (dorsal and ventral) of the three body parts (forearm, wrist, and hand), resulting in six different locations. The midpoint between the two tactile-points for the wrist was taken as the narrowing between the ulna

Table 1
Clinical details of the blind participants.

Subject	Age	Sex	Residual vision	Onset	Total blindness	Cause of blindness
EB1	46	M	None	Birth	Birth	Optic nerve hypoplasia
EB2	31	M	None	Birth	Birth	Retinitis pigmentosa
EB3	39	M	Diffuse light	Birth	7 months	Retinal burn in incubator
EB4	28	F	Diffuse light	Birth	Birth	Microphthalmia
EB5	32	F	Diffuse light	Birth	Birth	Retinopathy
EB6	31	M	None	Birth	Birth	Retinal detachment
EB7	31	F	None	Birth	Birth	Premature retinopathy No congenital
EB8	37	F	None	Birth	Birth	Leber's congenital amaurosis
EB9	47	F	Diffuse light	Birth	Birth	Leber's congenital amaurosis
EB10	22	F	Diffuse light	Birth	Birth	Premature retinopathy
EB11	29	F	None	Birth	Birth	Retinopathy of prematurity
EB12	37	F	Diffuse light	Birth	Birth	Retinitis pigmentosa
EB13	30	F	Diffuse light	Birth	Birth	Retinopathy of prematurity
EB14	29	M	Diffuse light	Birth	3 year	Retinopathy of prematurity
EB15	30	F	Diffuse light	Birth	Birth	Toxoplasmosis during pregnancy
EB16	27	M	None	Birth	Birth	Retinitis pigmentosa
EB17	29	F	Diffuse light	Birth	8 months	Bilateral congenital glaucoma
EB18	48	M	None	Birth	Birth	Hypoglossal optic nerve impairment
EB19	33	M	Diffuse light	Birth	Birth	

bone and the hand. The midpoint for the hand was taken as approximately the center of the palm/dorsum. The midpoint for the forearm was the center point from wrist to the elbow or slightly shifted towards the wider part.

In each trial, participants were presented with two pairs of tactile

stimuli sequentially in each orientation, on the aforementioned locations. There were 5 types of stimulus pairs (ML/PD): 2/4, 2/3, 3/3, 3/2, 4/2 cm; with the first value denoting the distance in the medial-lateral axis and the second value denoting the distance in the proximal-distal axis. The order of the orientation within a stimulus pair was randomised. The experimenter presented the stimuli manually ensuring that the two points of each pair touched the skin simultaneously. Each presentation lasted approximately one second, with an inter-stimulus interval (ISI) of approximately one second. Participants indicated which of the pairs they perceived to be larger by verbally responding either “first” or “second”.

Each participant took part in 12 blocks of trials. These 12 blocks were made up of the six unique combinations of body part (forearm, wrist, hand) and surface (dorsal, ventral), each of which was presented twice. The 12 blocks were presented in a pseudorandomised order. The order of the blocks was also counterbalanced across participants. Each block included 20 trials, in which the 5 types of stimulus pairs were each presented 4 times in a pseudo-randomised order.

2.4. Statistical analyses

All analyses were performed using MATLAB 2020b (The MathWorks Inc., 2020) and R statistical software (R Core Team, 2023). The analyses were very similar to those used in previous studies (Chang & Longo, 2022; Knight et al., 2014). We measured the proportion of responses in which the medial-lateral (ML) distance was judged to be larger than the proximal-distal (PD) distance for each stimulus pair and plotted them as a function of the log-transformed ratio of stimulus pair (ML/PD). The log-transformation of the ratio (ML/PD) leads to a symmetric distribution around a ratio of 1 i.e. the ratio at which the distances in ML and PD axes were equal. Psychometric curves were fit to the data using the function *fitPsycheCurveLogit* available for MATLAB (<https://github.com/garethjns/PsychometricCurveFitting>). The goodness-of-fit was assessed using R-squared values. The Points-of-Subjective-Equality (PSEs) were calculated as the ratio of the stimulus pair (ML/PD) on the x-axis at which the psychometric function crossed 50 % on the y-axis, hence the point at which the participant was equally likely to say that each stimulus was larger. A PSE value lower than the ratio (stimulus pair ML/PD) of 1 imply a bias to perceive the ML distances to be larger than the PD distances (pair of tactile distances are perceived equal in size when the ML distance is smaller than PD). The PSE values obtained on log-transformed ratios of stimulus pair have thus been used for the

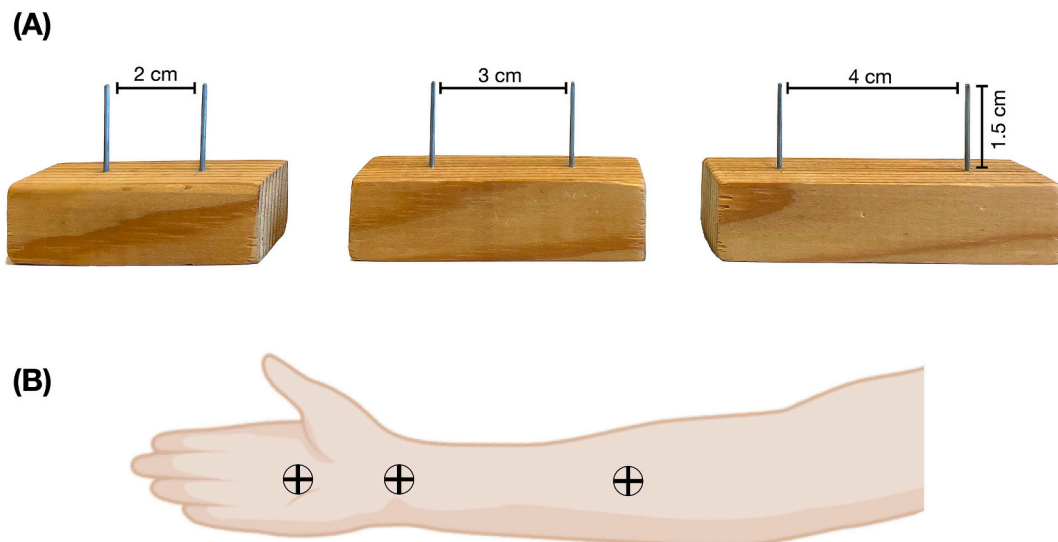


Fig. 1. (A) Tactile stimuli presented to the subjects on the dorsal and ventral surfaces of their hand, wrist and arm across two different orientations. (B) Locations on the ventral surface of the hand, wrist and arm where the stimuli were presented. Same locations were chosen on the dorsal surface of these body parts.

statistical analyses. We assessed differences between the PSEs across groups, body parts and surfaces using a Linear Mixed Model (LMM) implemented in R (R Core Team, 2023) using the *lmer* function. Group, body part, and surface predictors were entered as fixed effects, and the subject predictor was entered as a random effect.

3. Results

3.1. Curve fitting and goodness of fit

In accordance with previous studies (Chang & Longo, 2022; Knight et al., 2014), goodness-of-fit for the psychometric curve fitting was assessed using R-squared values. In our dataset, low R-squared values (R-squared value < 0.5) were obtained for three sighted participants on the dorsal forearm and one sighted participant on the ventral forearm. In contrast to the aforementioned studies, which involved the exclusion of entire subject's data based on this criterion, we excluded the PSE values corresponding to these locations in the sighted group. All the participants in the early blind group showed a good fit to the data.

3.2. Points of subjective equality (PSE)

Points of subjective equality (PSEs) obtained on log-transformed ratios (ML/PD stimulus pair) across all body parts and surfaces were compared against 0 (log-transformed ratio of 1) using one sample *t*-test and Holm's sequential Bonferroni correction to detect significant anisotropies. PSE values significantly below 0 indicate a reliable bias towards the distances in medial-lateral axis. In sighted controls, all PSEs were reliably less than 0 ($p < 0.05$) on all but ventral wrist and ventral hand locations. Interestingly, early blinds also showed significant anisotropies ($p < 0.05$) on all but ventral wrist location (Table 2). This shows that the bias to perceive tactile distances in the ML axis to be larger than the distances in the PD axis is present in blind individuals as well. The extent of the anisotropies was most pronounced on the forearms for both groups, with a noticeable decrease towards the hand and wrist areas. This is consistent with the pattern found by Knight and colleagues (Knight et al., 2014) (Fig. 2).

The PSE values were entered into an LMM, computed using the *lmer* function in R statistical software (R Core Team, 2023). The group (EB, SC), body part (forearm, wrist, and hand) and surface (dorsal, ventral) were entered as fixed effects and subject as a random effect.

Table 2
Statistical report of one-sample *t*-tests done on PSE values obtained on different locations in both sighted (SC) and early blind (EB) groups. Note that all statistical analyses were performed using the PSEs on logarithm scale, which were transformed back to ratios for reporting the mean. Asterisks denote the significant *p*-values after Holm's sequential Bonferroni correction.

Group: Sighted Controls (SC)						
Body Part	Surface	Mean	t-statistic	df	p-value	Cohen's d
Arm	Dorsal	0.5476	-14.4274	13	0*	-3.86
Arm	Ventral	0.6605	-7.4647	15	0*	-1.87
Wrist	Dorsal	0.8795	-4.0747	16	0.009*	-1.51
Wrist	Ventral	0.9735	-0.9924	16	0.3358	-0.56
Hand	Dorsal	0.7929	-6.2094	16	0*	-0.99
Hand	Ventral	0.9509	-2.2917	16	0.0358	-0.24

Group: Early Blinds (EB)						
Body Part	Surface	Mean	t-statistic	df	p-value	Cohen's d
Arm	Dorsal	0.7125	-8.4691	18	0*	-1.94
Arm	Ventral	0.8022	-5.5593	18	0*	-1.28
Wrist	Dorsal	0.8737	-3.6317	18	0.0019*	-0.83
Wrist	Ventral	0.9569	-1.4188	18	0.173	-0.33
Hand	Dorsal	0.8366	-6.116	18	0*	-1.4
Hand	Ventral	0.8956	-3.9758	18	0.0009*	-0.91

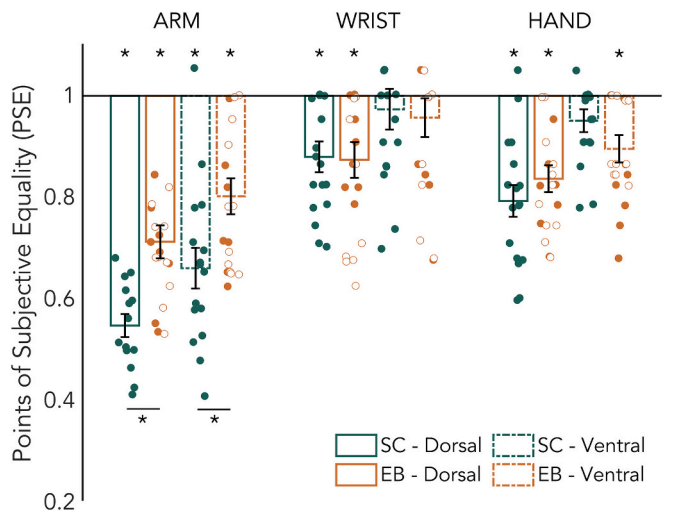


Fig. 2. Points of subjective equality (PSEs) for Arm, Wrist, and Hand, split between Ventral (dashed lines) and Dorsal (plain lines) Surfaces in sighted controls (SC; Green) and early blind (EB; Orange) individuals. Each dot represents an individual subject's data point. In the EB group, filled dots indicate the blind individuals without residual vision, while the unfilled circles indicate the blind individuals with faint light perception (see Section 2.1). All the statistical analyses (in-text) on PSEs have been performed on the log-transformed values. Here, in this figure, the PSE values are back-transformed for reporting the mean so that the PSEs below 1 represent the tactile distance anisotropy (bias towards ML distance being perceived to be larger than PD distance). Asterisks denote significant differences between the anisotropies on the arm of the SC and the EB groups at $p < 0.05(*)$ level. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We observed a significant main effect of group ($F(1,34) = 6.08, p = 0.018, \omega^2 = 0.125$) suggesting that the sighted individuals generally showed higher anisotropy than the blind individuals. There was a significant main effect of body part ($F(2,167) = 79.83, p < 0.001, \omega^2 = 0.482$) due to the heightened anisotropy on the arms, and a main effect of surface ($F(1,167) = 33.29, p < 0.001, \omega^2 = 0.160$) which revealed larger anisotropies present on the dorsal surface in comparison to the ventral surface in both the sighted and the blind groups. This difference between the surfaces is consistent with the previous results obtained in (Knight et al., 2014; Longo & Haggard, 2011).

We also observed a significant interaction of group X body part ($F(2,167) = 13.63, p < 0.001, \omega^2 = 0.130$). To explore the interaction, post-hoc two-sample *t*-tests were performed (*p*-values were subjected to the Holm-Bonferroni correction). Anisotropies were significantly higher for the sighted than the blinds on the forearm (two-sample *t*-test, $t(66) = -4.52, p = 0.0000, d = 0.998$). There were no significant differences between the two groups on the wrist (two-sample *t*-test, $t(70) = 0.39, p = 0.6984, d = 0.070$) and hand (two-sample *t*-test, $t(70) = 0.08, p = 0.9330, d = 0.013$).

However, there was no significant interaction of group X surface ($F(1,167) = 2.16, p = 0.1438, \omega^2 = 0.006$) and body part X surface ($F(2,167) = 0.56, p = 0.5731, \omega^2 = 0.00$). There was also no significant interaction for group X body part X surface ($F(2,167) = 0.60, p = 0.5498, \omega^2 = 0.00$).

4. Discussion

In this study, we compared the anisotropy in tactile distance perception on the ventral and dorsal surfaces of the arm, wrist, and hand between the sighted and the blind individuals as a means to infer the role of visual experience in the development of the representation of body shape.

We found significant tactile anisotropies in both sighted and blind,

suggesting significant distortion of shape such that the width is perceived wider irrespective of visual experience. The anisotropies are strongest on the arm and decrease in magnitude towards the wrist and hand. The observation that the anisotropy decreases with the known increase in tactile acuity across body parts corroborates previous findings in the sighted individuals (Knight et al., 2014). Interestingly, the blind individuals showed a similar bias for overestimating tactile distances in the medial-lateral axis suggesting that visual experience is not necessary to produce body-shape distortions. These results suggest that the anisotropies in tactile distance perception occur primarily because of the low-level properties of the tactile receptive fields and somatosensory processing, in accordance with the “pixel model” proposed by Longo (Longo & Haggard, 2011).

Interestingly however, we found that the magnitude of the anisotropy was significantly higher on the arm of the sighted than the blind participants; with no between-group differences on the wrist and hand. Why do the differences in the magnitude of anisotropy between groups occur specifically on the arm? The arm, with its intrinsic lower tactile acuity compared to the hand and wrist, would be more susceptible to a “practice effect” (Goldreich & Kanics, 2003; Sathian, 2000), as the blinds (when compared to the sighted) could use this body part more in their daily life, for instance, to judge the distance between an object on a table and their body. The forearm often comes in contact with other objects, like a desk, and can be used for exploration by the blind population. Future experiments could test the differences between sighted and the blind individuals on body parts that have a similar organization of tactile receptive fields and lower acuity but with no expected differences in use (e.g., the upper arm or the calf). Secondly, the mental representation of the arm, crafted through visual experience, could be susceptible to alterations stemming from changes in its foreshortened perspective or the visual biases associated with its elongated and slender shape. Arms are typically long and slender, which may introduce certain visual biases or predispositions in how we perceive their shape.

Consistent with prior research (Knight et al., 2014; Longo, 2020; Longo & Haggard, 2011), we also observed a higher level of anisotropy on the dorsal surface compared to the ventral surface of the body parts, independently of visual experience. This difference can again be attributed to the basic properties of tactile receptive fields distinctive of the two surfaces (Longo, 2022; Longo & Haggard, 2011) in both groups. The receptive fields on the hairy dorsal surface are generally oval shaped and less dense. On the contrary, the receptive fields on the ventral surface are more circular, smaller, and denser (Powell & Mountcastle, 1959). In line with this observation, previous studies have consistently reported smaller or absent anisotropies on the palm of the hand compared to the dorsum (Longo, 2020).

It is important to note that our study focuses on body shape, a specific aspect of the more general topic of body representation, which also include body schema and body image (Berlucchi & Aglioti, 2010). In line with the present study, it is worth noting that visual degradation affects the relative weight of body schema (sensorimotor) and body image (visual) in the mental representation and spatial transformation of the body (Giovaola et al., 2022). In addition, previous studies suggest that congenitally blind individuals are “immune” to the nonvisual version of the rubber hand illusion (Nava et al., 2014; Petkova et al., 2012) potentially due to changes in multisensory integration of tactile and proprioceptive signals (Radziun et al., 2024) which links to recent models of the interaction between body representation and different types of vision (Coelho & Gonzalez, 2024).

In summary, our study explored the impact of visual experience on tactile distance anisotropies by comparing sighted and blind people. Our findings indicate that the absence of visual experience does not lead to variations in anisotropies on the hand and wrist. However, there is a significant reduction in tactile anisotropy on the arms of blind individuals, suggesting that visual experience plays a considerable role in shaping tactile perception, at least in specific body areas. Whether the alteration of tactile anisotropy is due to a change in use of this body part

in blind people or an alteration in the visual grounding of touch (e.g. through change in foreshortened perspective) remains to be elucidated. We conclude that intrinsic tactile mechanisms like the shape of tactile receptive fields (Longo, 2022; Longo & Haggard, 2011) are likely the main driver behind the expression of tactile anisotropies; but that vision also plays a role either through an influence on mental body representation in the sighted and/or differences in tactile experience in the blind. We conclude that vision does not drive the emergence of tactile distance anisotropies, but visual experience can however modulate its expression on some specific body parts.

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CRediT authorship contribution statement

Iqra Shahzad: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Valeria Occelli:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Eléonore Giraudet:** Resources. **Elena Azañón:** Writing – review & editing, Methodology, Conceptualization. **Matthew R. Longo:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **André Mouraux:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Olivier Collignon:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

I have shared the link to my data/code at the attach file step in the manuscript anonymously.

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Appendix A. Supplementary data

The data and code are available at the following link: https://osf.io/2j7fn/?view_only=91c1689303ac49f2b40bca061fd1bc74. Supplementary data to this article can also be found online at [<https://doi.org/10.1016/j.cognition.2024.105980>].

References

- Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, 14(3), 257–262. <https://doi.org/10.1016/j.cub.2004.01.029>
- Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. *Current Biology*, 18(14), 1044–1049. <https://doi.org/10.1016/j.cub.2008.06.045>

- Azañón, E., Tamè, L., Maravita, A., Linkenauger, S. A., Ferrè, E. R., Tajadura-Jiménez, A., & Longo, M. R. (2016). Multimodal contributions to body representation. *Multisensory Research*, 29(6–7), 635–661. <https://doi.org/10.1163/22134808-00002531>
- Bassolino, M., & Becchio, C. (2023). The ‘hand paradox’: Distorted representations guide optimal actions. *Trends in Cognitive Sciences*, 27(1), 7–8. <https://doi.org/10.1016/j.tics.2022.09.010>
- Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research*, 200(1), 25–35. <https://doi.org/10.1007/s00221-009-1970-7>
- Brooks, V. B., Rudomin, P., & Slayman, C. L. (1961). Peripheral receptive fields of neurons in the CAT’S cerebral cortex. *Journal of Neurophysiology*, 24(3), 302–325. <https://doi.org/10.1152/jn.1961.24.3.302>
- Chang, K.-C., & Longo, M. R. (2022). Similar tactile distance anisotropy across segments of the arm. *Perception*, 51(5), 300–312. <https://doi.org/10.1177/03010066221088164>
- Charbonneau, G., Véronneau, M., Boudrias-Fournier, C., Lepore, F., & Collignon, O. (2013). The ventriloquist in periphery: Impact of eccentricity-related reliability on audio-visual localization. *Journal of Vision*, 13*(12), 20. <https://doi.org/10.1167/13.12.20>
- Coelho, L. A., & Gonzalez, C. L. (2018). The visual and haptic contributions to hand perception. *Psychological Research*, 82(5), 866–875. <https://doi.org/10.1007/s00426-017-0870-x>
- Coelho, L. A., & Gonzalez, C. L. R. (2024). Perception, action, and the body model. *Neuropsychologia*, 196, Article 108853. <https://doi.org/10.1016/j.neuropsychologia.2024.108853>
- Crollen, V., Lazzouni, L., Rezk, M., Bellemare, A., Lepore, F., & Collignon, O. (2017). Visual experience shapes the neural networks remapping touch into external space. *The Journal of Neuroscience*, 37(42), 10097–10103. <https://doi.org/10.1523/JNEUROSCI.1213-17.2017>
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191. <https://doi.org/10.3758/BF03193146>
- Giovaola, Y., Rojo Martinez, V., & Ionta, S. (2022). Degraded vision affects mental representations of the body. *Visual Cognition*, 30(10), 686–695. <https://doi.org/10.1080/13506285.2023.2186997>
- Goldreich, D., & Kanics, I. M. (2003). Tactile acuity is enhanced in blindness. *The Journal of Neuroscience*, 23(8), 3439–3445. <https://doi.org/10.1523/JNEUROSCI.23-08-03439.2003>
- Green, B. G. (1982). The perception of distance and location for dual tactile pressures. *Perception & Psychophysics*, 31(4), 315–323. <https://doi.org/10.3758/BF03202654>
- Hidaka, S., Tucciarelli, R., Azañón, E., & Longo, M. R. (2020). Tactile distance adaptation aftereffects do not transfer to perceptual hand maps. *Acta Psychologica*, 208*, Article 103090. <https://doi.org/10.1016/j.actpsy.2020.103090>
- Knight, F. L. C., Longo, M. R., & Bremner, A. J. (2014). Categorical perception of tactile distance. *Cognition*, 131(2), 254–262. <https://doi.org/10.1016/j.cognition.2014.01.005>
- Longo, M. R. (2014). The effects of immediate vision on implicit hand maps. *Experimental Brain Research*, 232(4), 1241–1247. <https://doi.org/10.1007/s00221-014-3840-1>
- Longo, M. R. (2020). Tactile distance anisotropy on the palm: A meta-analysis. *Attention, Perception, & Psychophysics*, 82(4), 2137–2146. <https://doi.org/10.3758/s13414-019-01951-w>
- Longo, M. R. (2022). Distortion of mental body representations. *Trends in Cognitive Sciences*, 26(3), 241–254. <https://doi.org/10.1016/j.tics.2021.11.005>
- Longo, M. R., Amoruso, E., Calzolari, E., Ben Yehuda, M., Haggard, P., & Azañón, E. (2020). Anisotropies of tactile distance perception on the face. *Attention, Perception, & Psychophysics*, 82(7), 3636–3647. <https://doi.org/10.3758/s13414-020-02079-y>
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences*, 107(26), 11727–11732. <https://doi.org/10.1073/pnas.1003483107>
- Longo, M. R., & Haggard, P. (2011). Weber’s illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance*, 37(3), 720–726. <https://doi.org/10.1037/a0021921>
- Longo, M. R., Mancini, F., & Haggard, P. (2015). Implicit body representations and tactile spatial remapping. *Acta Psychologica*, 160*, 77–87. <https://doi.org/10.1016/j.actpsy.2015.07.002>
- Manser-Smith, K., Tamè, L., & Longo, M. R. (2021). Tactile distance anisotropy on the feet. *Attention, Perception, & Psychophysics*, 83(8), 3227–3239. <https://doi.org/10.3758/s13414-021-02339-5>
- Nava, E., Steiger, T., & Röder, B. (2014). Both developmental and adult vision shape body representations. *Scientific Reports*, 4(1), 6622. <https://doi.org/10.1038/srep06622>
- Petkova, V. I., Zetterberg, H., & Ehrsson, H. H. (2012). Rubber hands feel touch, but not in blind individuals. *PLoS One*, 7(4), Article e35912. <https://doi.org/10.1371/journal.pone.0035912>
- Powell, T. P. S., & Mountcastle, V. B. (1959). Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey: A correlation of findings obtained in a single unit analysis with cytoarchitecture. *Bulletin of the Johns Hopkins Hospital*, 105, 133–162.
- R Core Team. (2023). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Radziun, D., Korczyk, M., Szwed, M., & Ehrsson, H. H. (2024). Are blind individuals immune to bodily illusions? Somatic rubber hand illusion in the blind revisited. *Behavioural Brain Research*, 460, Article 114818. <https://doi.org/10.1016/j.bbr.2023.114818>
- Rickham, P. P. (1964). Human experimentation. Code of ethics of the world medical association. Declaration of Helsinki. *British Medical Journal*, 2(5402), 177. <https://doi.org/10.1136/bmj.2.5402.177>
- Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Current Biology*, 14(2), 121–124. <https://doi.org/10.1016/j.cub.2003.12.054>
- Sathian, K. (2000). Practice makes perfect: Sharper tactile perception in the blind. *Neurology*, 54(12), 2203–2204. <https://doi.org/10.1212/WNL.54.12.2203>
- Sathian, K., Zangaladze, A., Hoffman, J. M., & Grafton, S. T. (1997). Feeling with the mind’s eye. *Neuroreport*, 8(18), 3877–3881. <https://doi.org/10.1097/00001756-199712220-00008>
- Schlereth, T., Magerl, W., & Treede, R.-D. (2001). Spatial discrimination thresholds for pain and touch in human hairy skin. *Pain*, 92(1), 187–194. [https://doi.org/10.1016/S0304-3959\(00\)00484-X](https://doi.org/10.1016/S0304-3959(00)00484-X)
- Stone, K. D., Keizer, A., & Dijkerman, H. C. (2018). The influence of vision, touch, and proprioception on body representation of the lower limbs. *Acta Psychologica*, 185, 22–32. <https://doi.org/10.1016/j.actpsy.2018.01.007>
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, 7(3), 219–220. <https://doi.org/10.1038/nn1199>
- The MathWorks Inc. (2020). *MATLAB version: 9.9.0.1570001 (R2020b)*. Natick, Massachusetts: The MathWorks Inc.. <https://www.mathworks.com>
- Tosi, G., & Romano, D. (2020). The longer the reference, the shorter the legs: How response modality affects body perception. *Attention, Perception, & Psychophysics*, 82(7), 3737–3749. <https://doi.org/10.3758/s13414-020-02074-3>
- Walsh, V., & Kulikowski, J. (Eds.). (1998). *Perceptual constancy: Why things look as they do*. Cambridge University Press.
- Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, 401(6753), 587–590. <https://doi.org/10.1038/44139>