Congenital visual deprivation modulates the perception of own, but not others' body size

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Article

Keywords: body representation, blindness, early development, plasticity, body distortions, body metrics

Posted Date: February 15th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-215187/v1>

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Abstract

Neuropsychological reports of phantom sensations in congenital limb aplasia have often been taken as evidence of the existence of an innate, 'hard-wired', representation of the body in the brain that does not need to be constructed from, or updated by, online afferent sensory inputs, including vision. However, when asked to draw the contour of their own body and of an ideal body (i.e. body with perfect proportions), congenitally, but not late blind individuals, exhibited a magnified representation of their own body, specifically of their hands, in comparison to sighted controls. This over-representation did not extend to their ideal body model. These findings show that the representation of the own body metric is shaped by early visual experience, and that seeing one's own and other bodies early in development contributes to the construction of a unified internal model, in which 'own' and 'other' merge.

Introduction

Body representation is a heterogeneous concept which refers to perception, knowledge and evaluation of one's own body as well as of other bodies, including their metrics (body-parts size and shape). Almost two centuries ago, Weber (1834;1996) reported an illusion in which the perceived distance between two points on the skin increases or decreases depending on the skin region tested, so that the same physical distance is perceived as larger as the two stimuli are placed on high-receptor-density areas on the skin (e.g., fingertips), but is perceived as smaller on low-receptor-density areas (e.g., shoulders). Weber's illusion has often been proposed as evidence that there is a match between perceived size of body parts and their somatic representation in the primary somatosensory cortex (i.e., the cortical homunculus in S1; Penfield & Boldrey, 1937). However, as reported by Taylor-Clarke and colleagues (2004), this explanation fails to be fully satisfactory, as the illusion is much smaller in comparison to the cortical extent of body sizes (see also Longo & Haggard, 2011). That is, if our body proportions followed their cortical size representation in the homunculus, we would have disproportionate hands and lips, and probably impaired movements. Thus, Taylor-Clarke et al. (2004) proposed that there might be some compensatory mechanisms that rescale the distorted primary representations - based on receptor density - to an object-centred space. This process requires the brain to be informed about the actual metric properties of body parts, and since Weber's illusion clearly reveals that knowledge about own body metric is imprecise, there must be an experience-driven mechanism that accounts for such rescaling. Taylor-Clarke et al. (2004) suggested that visual feedback of own body parts is one of the factors that drives the rescaling of cortical representations to object-centred space (see also Longo & Sadibolova, 2013).

If vision plays a crucial role in compensating for the distortions in body size representations – i.e. keeping bodily size constant – one would expect that blind individuals, particularly congenitally blind who never experienced their bodies through vision, may have an overly distorted representation of their body size and shape, because loss of vision may reduce the effectiveness of the compensatory mechanisms adopted to rescale S1 representations (Giurgola, Pisoni, Maravita, Vallar & Bolognini 2019).

Furthermore, studies conducted in congenital limb aplasia (i.e., individuals born without one or more limbs) show that the lack of somatosensory and visual experience of the own limbs do not impair the emergence of phantom limb sensations (Flor, Nikolajsen & Jensen, 2006; Mezue & Makin, 2017). An innate, hard-wired, representation of the body and its parts has been proposed to account for such a mismatch between the absence of sensory inputs from the limbs and the feeling of having the missing limb (Berlucchi & Aglioti, 2010; Brugger, Kollias, Müri, Crelier, Hepp-Reymond & Regard, 2000). On the other hand, it is also possible that, although amputated patients cannot see their own limbs, they nevertheless see other people's body parts, and this visual feedback would be responsible of the maintenance of a representation of the own body size and shape. In other words, following sensorimotor deprivation, the representation of the own body might shift from a predominant somatosensory representation to a visually-based one.

Overall, evidence from studies conducted both in healthy and clinical populations suggests that the representation of body structure/form can develop without neither visual nor somatosensory feedback, and that the way we consciously perceive our body is aligned with organizing principles of the somatosensory system (Tamè, Azañón & Longo, 2019). However, to date the role of vision in the development and online update of body representation has been investigated in individuals whose vision was temporarily distorted or were directly lacking somatosensory information (as in the case of amputees), but who did not present a history of visual deprivation, either congenital or acquired in early development.

Thus, in this study, we aim at investigating the role of vision by assessing body metric representation in congenitally and late blind individuals who became totally blind after age 2. Congenitally and late blind individuals, as well as two groups of age-matched, blindfolded sighted controls, were asked to make a drawing of the contours of their own body (Gandevia & Phegan, 1999), as well as the contours of an ideal body (here defined as the prototype model of a human body; see Tamè et al., 2019). If vision does play an important role in shaping our perceived body representation, particularly its size and shape, blind individuals will draw their own body differently from sighted controls.

Furthermore, if the body model is innate (Longo, Long & Haggard, 2012; Melzack, 1990), and the visual exposure to the own body as well as to other people's body is uninfluential, the perception of one's own body should not differ from the perception of a prototypical, ideal, body.

Methods

Participants

Twenty-four participants took part in the study. Two groups of blind individuals (one congenitally blind and one late blind) and 2 groups of sighted adults took part in the experiment. The sample size was derived from previous studies that tested blind individuals (see e.g., Büchel, Price, Frackowiak & Friston, 1998; Guerreiro, Putzar & Röder, 2016), which had on average 5-6 blind individuals, as this population is not as large as the sighted one. Furthermore, we calculated a sensitivity power analysis based on

(minimum) required effect size, given the sample size, and obtained that for Mann-Whitney tests with 2 groups, $\alpha = 0.05$ and Power = 0.80, and 6 participants per group, an effect size of 2 is required. Note that all the significant comparisons between the blind and their respective controls exceeded this effect size.

The congenitally blind group consisted of 5 adults (3 females, mean age: 35.4, range: 26-40 years), and its sighted aged-matched control group comprised 5 adults (3 females, mean age: 36.4, range: 26-47). All congenitally blind participants were totally blind from both eyes since birth and had no pattern vision. Blindness was due to peripheral reasons in all participants: retinopathy of prematurity (N = 3), optic atrophy (N = 1) and unknown peripheral defect (N = 1).

The late blind group comprised 7 adults (2 females, mean age: 38.7, range: 19-60), and its sighted aged-matched control group comprised 7 adults (2 females, mean age: 38.8, range: 20-54). All late blind participants were totally blind from both eyes and had no pattern vision at the time of testing. Blindness was due to peripheral reasons in all participants, including retinitis pigmentosa (N = 3), macular degeneration (N = 2), glaucoma (N = 1), and unknown peripheral defect (N = 1). The blindness onset in the late blind group varied between 5 and 16 years of age, and the mean duration of blindness before taking part in the study varied between 14 and 50 years. All blind participants were Braille-readers at the time of testing, but they started at different stages in development depending on blindness onset. All participants were right-handed as assessed by self-report and with absence of tactile perception disorders. The study was approved by the Ethic Committee of the University of Milano-Bicocca, and all participants signed an informed consent before starting the experiment.

Stimuli and Procedure

The task consisted in drawing the outline of two bodies on tracing paper. Participants were told that one body had to be their own, as they imagine it to be; the other body had to be an ideal body, i.e., a body that participants imagined to have perfect proportions.

Before starting to draw, sighted participants were blindfolded, and all participants were allowed to explore the tracing paper to be able to fit the drawing within the paper's space. Furthermore, all participants performed two training-drawings before the target drawings, to familiarize with the procedure.

Participants were told that the bodies had to be a one-line drawing, i.e., to be performed without letting the marker detach from the paper, and that they had to draw only the external shape of the body, without details of inner parts of the body (e.g., mouth, eyes, hands, feet, etc). Participants were asked to start from the head and to keep the sheet right in front of them throughout the drawing. Half of the participants started by drawing their own body, while the other half started by drawing the ideal body. A representative picture of the original draw for each group is depicted in Figure 1.

Data analysis

Each body draw was sampled using 62 landmarks representative of the different body parts as shown in Figure 1 (last panel). A picture of each draw was taken keeping the camera flattened aligned on the top of

the sheet at a constant distance of 25 centimetres (cm). Subsequently, the experimenter, by using an image modification software (i.e., Microsoft Paint) extracted the values of each point in pixel coordinates. Pixel coordinates of landmarks were coded and averaged, thus resulting in a map for each draw. Then, for visualization purposes, we used Generalized Procrustes Analysis (GPA) to average the different configurations for each group across participants. This procedure aligns sets of homologous landmarks, removing differences in location and rotation thus highlighting differences in shape (Bookstein, 1997). Note that we kept the information about scale. To perform the GPA we used *Shape*, a MATLAB toolbox from Dr. Preston (<https://www.maths.nottingham.ac.uk/personal/spp/shape.php>), based on an algorithm derived from Gower (1975) and Ten Berge (1977). Based on the approach adopted in previous studies (Medina, Tamè & Longo, 2018; Tamè, Bumpus, Linkenauger & Longo, 2017), using a similar logic we focused our analyses on the size of the body comparing it between the different groups. First, we investigated whether the overall configuration of the 62 landmarks representing the whole body was changing in size as a function of the different group tested (i.e., congenitally blind vs control and late blind versus control) for the two type of requested drawings. Similarly to Medina et al. (2018), we quantified the size of each configuration by calculating the centroid size, as well as the root mean square of the distance from each of the 62 points from their centre of mass (or centroid, see Bookstein 1997; Zelditch, Swiderski & Sheets, 2012). For each participant, we calculated the centroid size (in pixel units) for the different configurations of points for the whole body as well as for three set of body parts, namely hands, feet and head. We focused on these body parts, because we hypothesised that hands, selectively, and not other body parts, would be distorted in blind individuals. Thus, feet and head were taken as control body parts to observe whether the hypothesised change in hand representation is highly specific or generalises to other body parts. The rationale of this comparison was dictated by the fact that human hands and feet are serially homologous structures that have co-evolved (Rolian, Lieberman & Hallgrímsson, 2010), showing several similarities (Manser-Smith, Tamè, Longo, 2018; Manser-Smith, Tamè, Longo, 2019) and some differences (Manser-Smith, Romano, Tamè, Longo, 2021) in their representations.

To further explore the hypothesis that hands, but not other body parts, could be differently represented in blind individuals, we conducted a second analysis to calculate the estimated size of the fingers of the hands. On such configurations, we calculated the differences in the estimation of the fingers' length between groups (i.e., congenitally and late blind individuals vs sighted controls) and drawing conditions (i.e., own vs ideal body). As shown in the graphical depiction of Figure 2, for each finger, we calculated the middle points (B) between the base of the most proximal phalange of each finger (distance between A and C). Then, to estimate the finger's length, we calculated the Euclidean distance between this middle point (B) and the tip of the finger (D) using the *pdist* Matlab function (MathWorks, Natick, MA). The raw data have been made publicly available via the Open Science Framework and can be accessed at <https://osf.io/ahuyyp/>.

Body sizes were then compared between groups by means of Mann–Whitney U test, considering the size of the drawn whole bodies and the single body parts (hands, feet and head); single body part sizes were

computed as the proportion between single body part and whole body (i.e., % single body part = single body part/whole body*100).

Results

Whole body. Congenitally blind individuals drew their own body larger than that of the control group ($U = 1.00$, $p = 0.02$, Cohen's $d = 2.54$, Fig. 3, left panel); however, no difference emerged between the two groups for the ideal body ($U = 6.00$, $p = 0.22$, Fig. 3, right panel).

No difference emerged between the size of the whole body drawn by late blind and their controls, both for own body ($U = 18.00$, $p = 0.41$, Fig. 4, left panel) and ideal body ($U = 21.00$, $p = 0.66$, Fig. 4, right panel).

Hand. The congenitally blind drew the right and left hand as larger in comparison to controls, but this was only true for their own right ($U = 2.50$, $p = 0.04$, Cohen's $d = 2.05$, Fig. 5, upper panel) and left hand ($U = 1.00$, $p = 0.02$, Cohen's $d = 2.34$, Fig. 5, upper panel) but not for the ideal right ($U = 0.00$, $p = 0.24$, Fig. 5, lower panel) and left hand ($U = 12.50$, $p = 0.99$, Fig. 5, lower panel). On the contrary, right and left hand representation was similar between late blind and their controls (own right hand: $U = 24.00$, $p = 0.95$; ideal right hand: $U = 28.50$, $p = 0.60$, own left hand: $U = 25.00$, $p = 0.95$; ideal left hand: $U = 29.00$, $p = 0.56$, Fig. 6).

Head. No difference emerged between the congenitally blind and their controls for both own head ($U = 7.00$, $p = 0.25$) and ideal head ($U = 6.00$, $p = 0.17$), as well as between the late blind and their controls for both own head ($U = 34.00$, $p = 0.21$) and ideal head ($U = 18.50$, $p = 0.44$).

Foot. No difference emerged between the congenitally blind and controls for both own right foot ($U = 15.00$, $p = 0.60$) and ideal right foot ($U = 17.00$, $p = 0.34$), as well as between the late blind and controls (own right foot: $U = 26.50$, $p = 0.80$; ideal right foot: $U = 38.50$, $p = 0.07$). The same results emerged for the left foot: congenitally blind vs. controls, own left foot ($U = 13.50$, $p = 0.83$) and ideal left foot ($U = 17.00$, $p = 0.33$); late blind vs. controls, own left foot ($U = 22.50$, $p = 0.79$) and ideal left foot ($U = 33.00$, $p = 0.26$).

We further explored the differences in hand size that emerged between the congenitally blind and their controls, by analysing the finger length of both own and ideal hands of all participants.

Congenitally blind individuals represented the thumb ($U = 0.00$, $p = 0.009$, Cohen's $d = 3.00$), index finger ($U = 2.00$, $p = 0.03$, Cohen's $d = 2.20$), middle finger ($U = 3.00$, $p = 0.04$, Cohen's $d = 1.93$), and ring finger ($U = 2.00$, $p = 0.03$, Cohen's $d = 2.20$) of the own right hand as longer compared to their sighted controls. There was no difference in the length representation of the right little finger ($p = 0.12$, Fig. 5, upper right panel).

The congenitally blind also represented the thumb ($U = 0.00$, $p = 0.009$, Cohen's $d = 3.00$), index finger ($U = 0.00$, $p = 0.009$, Cohen's $d = 3.00$), middle finger ($U = 0.00$, $p = 0.009$, Cohen's $d = 3.00$), and little finger ($U = 2.00$, $p = 0.003$, Cohen's $d = 2.20$) of their left hand as longer than the respective fingers of their sighted controls. No difference emerged for the ring finger of the left hand ($p = 0.12$, Fig. 5, upper left panel).

Importantly, these differences only applied to their own fingers, but not to the ideal hand (all fingers of the right hand $p > 0.11$; all fingers of the left hands $p > 0.11$).

Furthermore, no difference emerged between the finger's length of the late blind and their controls, both for their own left (all fingers $p > 0.08$, except for a difference in the thumb, $p = 0.03$) and right hand (all fingers $p > 0.17$) and ideal left (all fingers $p > 0.22$) and right hand (all fingers $p > 0.27$, see Fig. 6).

Discussion

Our study yielded two main findings: first, vision influences the internal representation of the body metrics, that is, the mental image that we have of our own body size and shape. Indeed, with respect to sighted controls, congenitally, but not late blind individuals, exhibited an enlarged representation of their body, particularly of the fingers of their hands. The specificity of this over-representation could be due to two interrelated mechanisms.

The over-representation of the hands in congenitally blind individuals could be accounted by mechanisms of experience-dependent plasticity associated to the extensive use of the hands. Indeed, most blind individuals are Braille readers, and this has shown to induce both functional and cortical changes in the somatosensory cortex (Sterr, Müller, Elbert, Rockstroh, Pantev & Taub, 1998; Pascual-Leone & Torres, 1993). However, if it were only a matter of experience-dependent plasticity induced by Braille reading, we would have seen hand representational changes in late blind individuals too, since all our participants, irrespective of blindness onset, had experience with Braille reading, and all started learning it in the schoolyears.

The difference in tactile experience between the congenitally and late blind should be sought in the very first years of life: touch is the very first sense to develop and provides infants the access to explore their surrounding environment as well as their bodies (for a review see, Bremner & Spence, 2017). However, starting by age 6 months, infants massively integrate vision in their motor activities (i.e., grasping, reaching), and these strong sensori-motor interactions appear to be promoted by crossmodal transfers of object's features that are already present at birth (Sann & Streri, 2007). In comparison to sighted infants, congenitally blind infants can only rely on their hands to explore the world, and this may trigger compensatory, experience-dependent plastic changes associated to hand use. This is in line with studies showing that only congenital, but not late blind, exhibit a series of use-dependent functional and structural brain changes, which are associated with enhanced functions on different tactile and auditory tasks (Goldreich & Kanics, 2003; Müller, Niso, Samiee, Ptito, Baillet & Kupers, 2019; Wong, Gnanakumaran & Goldreich, 2011; Wan, Wood, Reutens & Wilson, 2010; Ricciardi, Handjaras, & Pietrini, 2014).

A second mechanism that may have contributed to the development of the hand over-representation could be the reduction of rescaling of neural signals, from a distorted representation based solely on receptor density, to an object-centred spatial coding likely driven by visual experience. As shown by the study of Taylor-Clarke et al. (2004), manipulations of visual feedback of own body size modulates the

perceived tactile distance across body parts (i.e., finger and forearm); this clearly shows that primary somatosensory representations can be altered by visual experience.

Our results suggest that this rescaling may be reduced in congenitally blind individuals, and this may keep their hand representation more distorted with respect to the sighted. Furthermore, because late blind did not present any difference in body representation compared to their sighted controls, we suggest that the rescaling from a cortical representation to an object-centred space develops and stabilizes permanently through visual experience in the first years of life. Thus, it appears to be a plastic function in case of visual adjustment (as in Taylor-Clarke et al., 2004), but not in case of complete visual loss.

An intriguing finding about the blind individual's hand representation is that it was not only the absolute size of the hand to be perceived as larger in comparison to sighted controls, but rather the length of the fingers that drove this difference; indeed, only congenitally – but not late blind - individuals drew their fingers longer in comparison to their sighted controls. In this regard, it is worth mentioning a series of studies by Longo and colleagues (2010; 2014), showing that the implicit hand representation of own hand structure in sighted individuals is remarkably distorted: sighted individuals underestimate the length of their own fingers while overestimating their own hands in width. This appears to be the opposite direction of what exhibited by congenitally blind individuals. Thus, it could be that vision reduces the perceived finger length, which would be in line with the rescaling hypothesis, by which the brain, in the attempt to compensate for a bias at the primary somatosensory level (i.e., S1; Giurgola et al., 2019), exceeds in the opposite direction, resulting in an underestimation of finger length at a perceptual level. A recent study has shown that some compensatory mechanisms are already taking place at an early stage of the tactile processing in the sensorimotor cortices. Indeed, the reconstructions of the shape of skin space in S1 and primary motor cortices reveal that it is distorted in a way that matches the perceptual shape of skin space (Tamè, Tucciarelli, Sadibolova, Sereno & Longo, 2021).

Our second main finding suggests that this alteration only applies to the representation of own body, but not to the concept of body itself (i.e., ideal body). Congenitally blind individuals over-represented their own hand size and length, but not the size and shape of an ideal body. This result is particularly relevant since it suggests that there could be an innate body representation that goes beyond both somatosensory (as in the case of amputees) and visual feedback (Longo et al., 2012). The fact that congenitally and blind individuals represented the ideal body similarly to sighted controls reveals that vision does not guide the internal knowledge of the body parts and their proportions; hence, a likely innate representation of a standard body model may be in place despite any sensory experience. However, the dissociation in own and ideal body representation in the congenitally blind reveals that vision may contribute to the development of an internal representation of one's own body. Following congenital vision loss, the perception of 'my body' vs. 'other bodies' may remain separated, but merged in typical development.

In conclusion, our study shows that vision contributes to the development and consolidation of an internal representation of one's own body, while it does not contribute to a more general, semantic representation of the body.

Declarations

Authors' contribution:

N.B., E.N. and S.G. developed the study concept and study design. Testing and data collection were performed by E.N. and S.G. L.T. performed the data analysis. E.N. drafted the manuscript, and N.B., L.T. and S.G. provided critical revisions. All authors approved the final version of the manuscript for submission.

Acknowledgements

We are very grateful to all blind participants for taking part in this study, and in particular to Cristian Bernareggi, for helping with the recruitment and data collection.

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Figures

Figure 1

Examples of drawings made by a representative congenitally blind, late blind and sighted control participant. The panel on the right displays an example of drawing, onto which the 62 landmarks were applied.

Figure 2

Graphical depiction of the distances between landmarks used to estimate the finger's length (Euclidean distance between points B and D) where A and C represent the conjunction points of the most proximal phalange of the finger. B (intersection of the dashed lines) represents the middle point between A and C. D represents the tip of the finger. These landmarks refer to the middle finger as an example, but the same procedure was applied to all the fingers.

Figure 3

Whole body and single body parts sizes between the congenitally blind and their age-matched sighted controls for own body (left panel) and ideal body (right panel). Schematic drawings in red lines denote the congenitally blind, while the black lines denote the sighted controls.

Figure 4

Whole body and single body parts sizes between the late blind and their age-matched sighted controls for own body (left panel) and ideal body (right panel). Schematic drawings in blue lines denote the late blind, while the black lines denote the sighted controls.

CONGENITALLY BLIND VS CONTROLS

Figure 5

Left- and right-hand length comparison between the congenitally blind and their age-matched sighted controls for own body (upper panel) and ideal body (lower panel). Schematic drawings in red lines denote the congenitally blind, while the black lines denote the sighted control.

LATE BLIND VS CONTROLS

Figure 6

Left- and right-hand length comparison between the late blind and their age-matched sighted controls for own body (upper panel) and ideal body (lower panel). Schematic drawings in blue lines denote the late blind, while the red lines denote the sighted controls.