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Correspondence and requests for materials should be addressed to E.N. (elena.nava@uni-hamburg.de)

Both developmental and adult vision shape body representations

Elena Nava[1], Tineke Steiger[2] & Brigitte Röder[1]

[1]Biopsychology and Neuropsychology, University of Hamburg, Von-Melle-Park 11, 20146 Hamburg, Germany, [2]Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Martinistr. 52, 20246 Hamburg, Germany.

Sense of body ownership and body representation are fundamental parts of human consciousness, but the contribution of the visual modality to their development remains unclear. We tested congenitally and late blind adults on a somatosensory version of the rubber hand illusion, and on the Aristotle illusion, in which sighted controls touching a single sphere with crossed fingers commonly report perceiving two. We found that congenitally and late blind individuals did not report subjectively experiencing the rubber hand illusion. However, in an objective measure, the congenitally blind did not show a recalibration of the position of their hand towards the rubber hand while late blind and sighted individuals did. By contrast, all groups experienced the Aristotle illusion. This pattern of results provides evidence for a dissociation of the concepts of body ownership and spatial recalibration and, furthermore, suggests different reference frames for hands (external space) and fingers (anatomical space).

Studies on congenitally amputated individuals have shown that the feeling of our own body might be partially innate[1,2]. Indeed, some congenitally amputated individuals report feeling the presence of their limbs even though they have never had any sensory experience of them (for a critical review, see[3]). For example[1], discuss the case of a woman with congenital aplasia of her four limbs, who nevertheless reported limb sensations. An extensive behavioural (i.e., mental rotation abilities for left/right position of visually presented hands and feet) and neuroimaging (i.e., mapping of sensorimotor cortex and cortical areas activated during voluntary movements) examination of the patient showed that she had an intact somatic representation of her missing body parts. In addition, transcranial magnetic stimulation (TMS) of the sensorimotor cortex elicited phantom sensations in her upper limbs, suggesting that the representation of the human body may have an innate basis. However, it still remains a matter of debate to which degree and what kind of experience defines body perception. For example, the role of multisensory input in shaping the development of body perception is still unexplored. Our brain constantly receives information from vision, audition, proprioception and touch and generates sensations on how we perceive the environment and ourselves. This multisensory characteristic of body perception allows us to perceive our body parts as our own and not someone else's (i.e., sense of body ownership). This multisensory perspective on development of body perception has been supported by several studies. Recently[4], has documented the existence of a multisensory organisation of peripersonal space for the whole body in the human posterior parietal cortex (PPC). The authors mapped human parietal areas that process visual and tactile stimuli when presented on or near the body. They showed, in accord with early results in nonhuman primates (for a review see[5]), that there is a direct overlap between tactile and visual maps for large parts of the body in the superior PPC. This 'multisensory homunculus' suggests that parietal areas representing the body integrate multisensory information in near space so that the individual's movements are constantly monitored. Moreover[6], have provided evidence for representations of perihand space not only in the human posterior parietal cortex but additionally in the premotor cortices, which activity appeared to be directly linked to changes in body perception.

Among the sensory modalities involved in shaping body perception, vision seems to play a crucial role, especially because of its influence on touch and proprioception. A series of experiments have documented that distorting or displacing vision often has dramatic influences on proprioception. These findings were attributed to vision being the most reliable sensory modality when acquiring information about the spatial position of body parts[7,8,27].

One of the most intriguing examples of visual capture on proprioception and touch comes from the classical experiment by[9], the so-called 'rubber hand illusion', in which participants experience the sensation of owning a hand that is not theirs. In this experiment, participants are seated with their left hand resting on a table while a screen hides their right hand. Next to their left hand, a visible rubber hand is placed. Two paintbrushes simultaneously stroke the rubber hand and the participant's hidden hand. After a short interval, participants have the distinct feeling that they are perceiving the stroking in the visible rubber hand and they feel as if the rubber hand was their own hand. Further experiments have shown that if participants are asked to point with the hidden (right) hand with eyes closed to the left hand, their pointing responses are displaced towards the rubber hand[9]. proposed that the rubber hand illusion is the result of the dominant role of vision when vision, touch and proprioception are integrated to update the body representation.

On a neural level[10], found that activity in the premotor cortex reflects the feeling of ownership of the hand during the elicitation of the rubber hand illusion, suggesting that the premotor cortex likely contributes to the self-attribution of body parts.

To further investigate the role of vision in triggering the illusion[11], blindfolded a group of participants in a paradigm that did not involve vision but was exclusively dependent on the integration of tactile and proprioceptive information from the two hands. The experimenter moved the participant's left index finger along the rubber hand while simultaneously stroking the right hand of the participant. The authors found that participants experienced a rubber hand illusion as well, which was accompanied by a similar activity in the ventral premotor cortex, as shown for the classical visual version. These results suggest that the integration of crossmodal signals from one's own body may underlie the feeling of body ownership.

Recently[12], employed the somatosensory version of the rubber hand illusion in a group of blind individuals. The authors hypothesised that if the perception of one's own body in space is essentially a multisensory experience involving visual, tactile and proprioceptive inputs, then the prolonged lack of one of these inputs could influence body representations.

Both qualitative and quantitative measures showed that blind individuals did not perceive the illusion, contrarily to the sighted controls who felt the touch at the location of the rubber hand and additionally showed a proprioceptive drift.

The authors proposed two different explanations to these findings: first, they suggested that blind individuals are not able to re-map the tactile input into an external reference frame as sighted individuals do. As a consequence, blind individuals are thought to be incapable of fusing the simultaneous stroking of the rubber hand and their own hand, which is the mechanism that likely allows sighted controls to experience the illusion.

It has been argued that the default automatic remapping of sensory inputs into external coordinates is a result of visual experience during development. For example[13], tested congenitally and late blind individuals on a temporal order judgment task, in which participants were asked to indicate whether a tactile stimulus was presented first to their left or right index finger. The task was performed with the arms either crossed or uncrossed and at different SOAs (interval between the onset of the two stimuli). Crossing the hands typically results in a decline in TOJ performance, which has been attributed to a conflict of two references, a modality-specific, anatomical frame of reference and an external frame of reference[14,15]. Interestingly, late blind but not congenitally blind individuals experienced a crossing hand effect. These results suggest the existence of a sensitive phase for the default use of external reference frames for touch localization. Indeed, the reliable crossing effect of the late blind suggested that visual input during this phase irreversibly organises the brain in a way that touch is automatically recoded into external space.

As a second explanation of their data[12], suggested that blind individuals may have higher tactile discrimination abilities compared to sighted controls, so that touching an object that has a different texture (i.e., the rubber hand) from one owns hand could have made it more difficult to them to experience the sense of ownership for the rubber hand.

The study by[12] represents the first attempt to investigate sense of body ownership in blind individuals. However, a crucial issue was left unsolved. The authors tested ten blind individuals, five of which were congenitally blind, five of which were late blind (i.e., acquired blindness after birth) and did not analyse the data separately for these groups. Thus, the question of whether developmental vision – rather than visual status - shapes body representations as measured by the rubber hand illusion remains unanswered.

Therefore, in the first experiment of the present study we tested ten congenitally blind individuals, twelve late blind individuals and thirteen age-matched, temporarily blindfolded sighted controls on the somatosensory version of the rubber hand illusion. We hypothesised that if the rubber hand illusion can be explained as a conflict between external and anatomical centred coordinates, then congenitally blind individuals should not experience the illusion because the default use of an external frame of reference for touch localisation depends on early visual input[16]. By contrast, we expected late blind individuals, who automatically remap sensory stimuli into external coordinates, to be affected by the illusion.

To observe whether the rubber hand illusion influences other perceptual systems than touch, we tested our participants in an auditory localisation task as well, in which they had to report when they perceived a sound passing over their hand.

Finally, in a second experiment we tested five congenitally and three late blind individuals on the classical Aristotle illusion, first accounted by Aristotle (384–322 b.C.) in the essay "On dreams", in which the philosopher first reported that if one crosses two adjacent fingers (i.e., the middle finger over the index finger) and then touches with the crossed fingertips a small ball, he or she would commonly experience touching two balls. The current explanation is that when the two fingers are crossed and simultaneously touch the ball, only the outside part of the two fingers does so, which is an experience that fingers typically make when touching two separate objects. The brain does not seem to be able to take the crossed finger posture into account, when performing a single motor action, resulting in the typical illusion of perceiving two instead of one object. The Aristotle illusion has been interpreted as evidence for the assumption that fingers are coded by default in anatomical rather than external coordinates[26]. Since congenitally and late blind individuals as well as sighted controls do not differ in the use of anatomical frames of reference, we expected to observe the Aristotle illusion in all of these groups. Thus, this illusion served as control for the rubber hand illusion to show that congenitally blind individuals are in principle capable of perceiving and reporting illusions.

Results

Experiment 1: rubber hand illusion. *Qualitative reports of the illusion.* Figure 1 shows the mean responses to the 5 statements separately for the congenitally blind, the late blind and the sighted controls. Additionally, Table 1 reports the responses to the 5 statements provided by each participant. The responses were collected using a rating scale, with positive (+) responses ranging between +1 and +3 indicating agreement with the statement and negative (−) responses ranging between −1 and −3 indicating rejection of the statement.

Sighted controls rated the statement #1 ("I felt as if I was touching my left hand with my right index finger") on average 1.4 (SE = 0.5), with 11 out of 13 participants giving positive ratings (i.e., agreement to the statement). On the contrary, congenitally and late blind participants rated the statement negatively (−2.6 (SE = 0.4) and −2.0 (SE = 0.6), respectively). Only 1 congenitally blind and 2 late blind rated the statement positively (i.e., agreed with it). The difference in the number of positive vs. negative responses was significant when comparing sighted controls (positive: n = 11; negative: n = 2) with the congenitally (positive: n = 1; negative: n = 9; $p < 0.001$, two-tailed Fisher's exact test) and the late blind (positive: n = 2; negative: n = 10; $p = 0.001$, two-tailed Fisher's exact test) but not when comparing the two groups of blind participants.

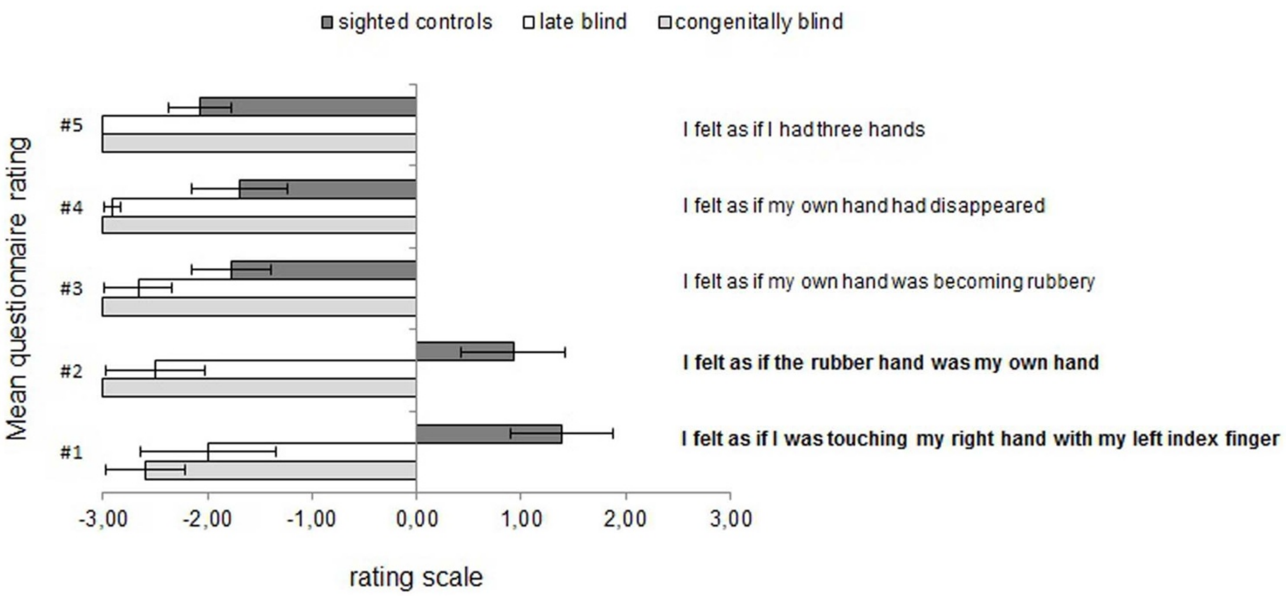

Figure 1 | **Qualitative measure of the illusion.** Rating from the questionnaire separately for congenitally blind (gray bars), late blind (white bars) and blindfolded controls (dark gray bars). Error bars indicate standard errors. Statements #1 and #2 indicate the illusion statements, while the other three statements were used as control statements for suggestibility. While blindfolded participants reported the illusion, congenitally and blind individuals strongly rejected the illusion statements.

Table 1 | Ratings of the questionnaire for the 5 statements for each participant

		illusion statements		control statements		
group	ID	#1	#2	#3	#4	#5
blindfolded controls	1	3	1	−3	−3	−1
	2	1	−1	0	−1	−3
	3	2	3	0	1	−3
	4	1	1	1	1	0
	5	2	1	−2	1	−1
	6	2	2	−3	−1	−1
	7	−3	−3	−1	−3	−3
	8	2	2	−1	−3	−1
	9	2	1	−3	−3	−3
	10	2	2	−2	−2	−2
	11	−2	−2	−3	−3	−3
	12	3	3	−3	−3	−3
	13	3	2	−3	−3	−3
congenitally blind	2	−3	−3	−3	−3	−3
	3	−3	−3	−3	−3	−3
	4	−3	−3	−3	−3	−3
	6	−3	−3	−3	−3	−3
	7	−3	−3	−3	−3	−3
	9	1	−3	−3	−3	−3
	10	−3	−3	−3	−3	−3
	11	−3	−3	−3	−3	−3
	15	−3	−3	−3	−3	−3
	16	−3	−3	−3	−3	−3
late blind	1	−3	−3	−3	−3	−3
	5	−3	−3	−3	−3	−3
	8	−3	−3	−3	−3	−3
	13	−3	−3	−3	−3	−3
	18	−3	−3	−3	−3	−3
	12	−3	−3	−3	−3	−3
	14	−3	−3	−3	−3	−3
	17	−3	−3	−3	−3	−3
	21	−3	−3	−3	−3	−3
	22	3	3	−3	−2	−3
	19	3	−3	1	−3	−3
	20	−3	−3	−3	−3	−3

On statement #2 ("I felt as if the rubber hand was my hand"), sighted controls rated the statement on average 0.9 (SE = 0.5), with 10 out of 13 participants giving positive ratings. Congenitally blind participants all gave negative ratings (mean = −3.0; positive: n = 0; negative: n = 10) and only 1 out of 12 late blind rated the statement as positive (mean = −2.5, SE = 0.5; positive: n = 1; negative: n = 11). The difference in the number of positive vs. negative responses was significant when comparing sighted controls with the congenitally blind ($p = 0.01$, two-tailed Fisher's exact test) and the late blind ($p = 0.02$, two-tailed Fisher's exact test) but not when comparing the two groups of blind participants.

The control statements were rated on average negatively by sighted (mean response for the three control questions was −1.9 (SE = 0.3), congenitally blind (mean response for the three control questions was −3) and late blind individuals (mean response for the three control questions was −2.9 (SE = 0.1)), suggesting that responses provided for statement #1 and #2 were not the result of suggestibility. Note that the average of the three control statements differed between congenitally blind participants and blindfolded controls ($p = 0.002$, two-tailed independent samples Mann-Whitney U test), and between late blind participants and blindfolded controls ($p = 0.007$, two-tailed independent samples Mann-Whitney U test), meaning that congenitally and late blind individuals rejected the control statements more than blindfolded controls did.

The strength of the experienced illusion (measured as the numerical average of each statement separately for each group) differed between sighted controls and congenitally blind participants ($p < 0.001$ for statement #1 and statement #2; two-tailed independent samples Mann-Whitney U test) and between sighted controls and late blind participants ($p = 0.01$ for statement #1, and $p = 0.01$ for statement #2; two-tailed independent samples Mann-Whitney U test) but did not differ between congenital and late blind participants ($p = 0.6$ for statement #1, and $p = 0.4$ for statement #2; two-tailed independent samples Mann-Whitney U test).

Finally, we explored the strength of the illusion within each group by comparing the mean response of statement #1 and statement #2 with the mean response of all three control statements, as recently performed in studies investigating the rubber hand illusion[17–19]. For sighted controls, statement #1 ($p = 0.002$, one-tailed Wilcoxon signed ranks test) and statement #2 ($p = 0.003$, one-tailed Wilcoxon signed ranks test) differed from the control statements, providing evidence that blindfolded controls experienced the illusion. On the contrary, and as expected, because both congenitally and late blind individuals rejected the illusion statements, we found no difference between the illusion and the control statements (see Table 1).

Proprioceptive and auditory drifts. For both pointing and auditory tasks, the average drift of each participant was entered separately for each group into a Shapiro-Wilk test for normality distribution. Because all groups showed normally distributed means (all $p > 0.06$), we analysed the pointing and auditory tasks with t-tests.

One sighted control participant was excluded from the analysis because he reported not hearing the sound of the auditory stimulus.

Figure 2 shows the drift (calculated as the difference between the average responses before and after stimulation with the rubber hand) towards the rubber hand in the pointing and auditory localisation tasks for each group.

We compared the proprioceptive and auditory drifts towards the rubber hand between groups by means of independent-samples t-tests. Results showed that congenitally blind individuals differed from the blindfolded controls on the proprioceptive ($t(21) = 3.8$, $p = 0.001$) and auditory drifts ($t(21) = 3.1$, $p = 0.005$), while late blind individuals did not differ from blindfolded controls on neither the proprioceptive ($t(23) = 1.3$, $p = 0.2$) nor the auditory ($t(23) = 0.6$, $p = 0.6$) drift. Moreover, the congenitally blind differed from the late blind in the proprioceptive ($t(20) = 4.2$, $p = 0.001$) and the auditory drift ($t(20) = 2.8$, $p = 0.01$).

In order to observe whether participants of each group experienced or did not experience a drift as a consequence of the illusion induction phase, we compared the performance on the pointing and the auditory localisation task for each group before and after the induction of the rubber hand illusion using paired t-tests.

Sighted controls showed a strong perceptual drift in the proprioceptive ($t(12) = 5.1$, $p < 0.001$) and in the auditory task ($t(11) = 3.4$, $p = 0.006$), while congenitally blind participants did not show any drift in neither the proprioceptive ($p = 0.1$) nor the auditory task ($p = 0.2$). By contrast, late blind participants showed a drift in both the proprioceptive ($t(11) = 5.6$, $p < 0.001$) and the auditory task ($t(11) = 2.7$, $p = 0.02$).

Because late blind participants differed in their complete blindness onset and in the level of vision prior to their total loss of sight (i.e., visual impairment vs. normal sight), we analysed the proprioceptive and auditory drifts for the late blind group separately for the participants who were born with full vision and lost it at different times in life ($n = 4$) and the participants who were born with severe visual impairments and completely lost vision in childhood or adulthood ($n = 8$). We did not find any difference between these sub-groups ($p > 0.3$, Mann Whitney U test, for both auditory and proprioceptive drifts).

Furthermore, to observe whether the illusion increased in the late blind as a function of blindness onset and/or years of blindness, we correlated these factors separately with the two drift score. For both factors we did not find any significant correlation (all $p > 0.1$).

To document whether subjective reports of the illusion and the drift are linked, we correlated the average rating of the illusion questions (question 1 and 2) separately with the proprioceptive and auditory drifts and separately for congenitally blind, late blind and controls (Spearman correlations). We did not find a significant correlation between sense of ownership and drift for neither group (all $p > 0.1$).

To assess whether the differences between congenitally blind individuals on the one side, and late blind participants and sighted controls on the other side, can be explained by different tactile or auditory discrimination abilities (e.g., congenitally blind individuals possessing enhanced tactile and/or auditory abilities), we compared the average response of each group in the baseline condition (i.e., proprioceptive and auditory performance before the illusion was induced, see Fig. 3), separately for the proprioceptive and auditory localisation task. No difference between groups was obtained in neither the proprioceptive (congenitally vs. late blind: $t(20) = 1.0$, $p = 0.3$; congenitally blind vs. sighted controls: $t(21) = 0.7$, $p = 0.5$; late blind vs. sighted controls: $t(23) = 1.9$, $p = 0.07$) nor the auditory baseline scores (congenitally vs. late blind: $t(20) = 1.7$, $p = 0.2$;

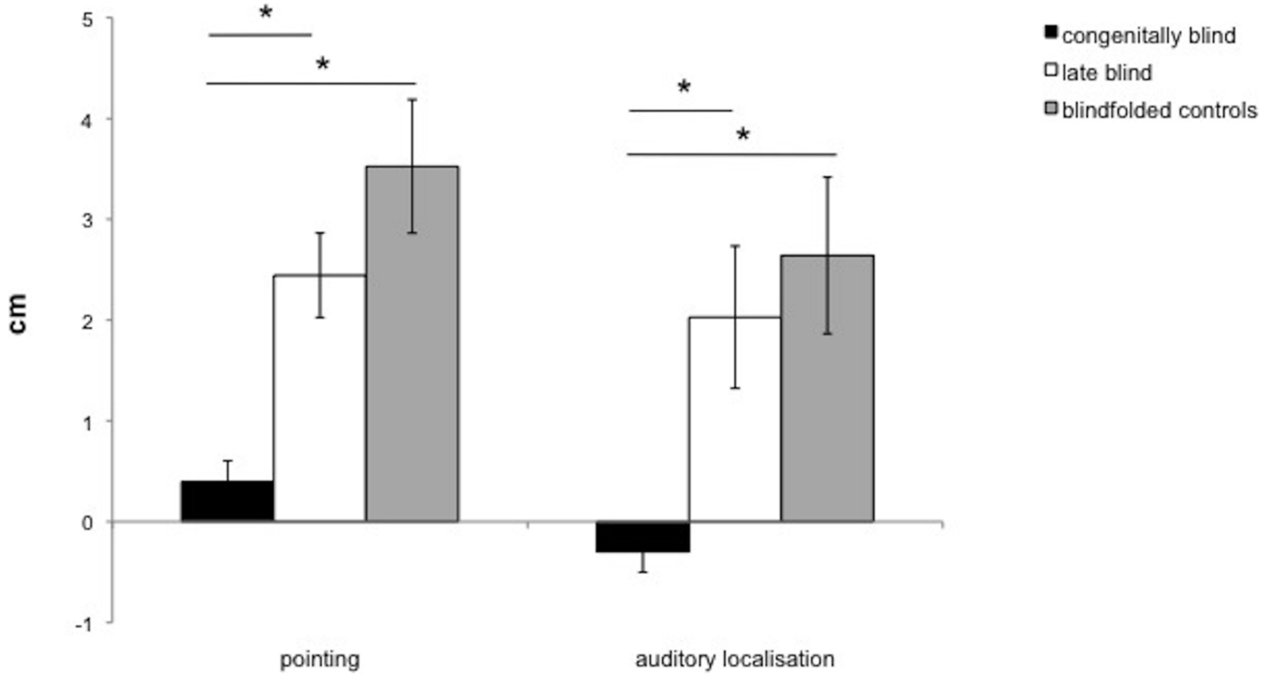

Figure 2 | **Quantitative measure of the illusion.** Proprioceptive and auditory drift (calculated as the difference between the average responses before and after stimulation with the rubber hand) for congenitally blind, late blind and blindfolded controls. Error bars indicate standard errors. Blindfolded controls and late blind individuals showed a proprioceptive and auditory drift, while congenitally blind individuals remained unaffected.

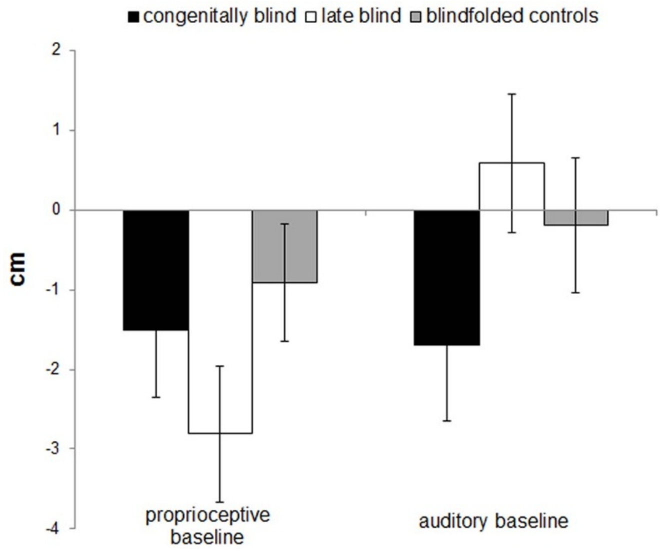

Figure 3 | **Proprioceptive and auditory baseline.** Proprioceptive and auditory baseline (calculated as the average response before stimulation with the rubber hand) for congenitally blind, late blind and blindfolded controls. Error bars indicate standard errors. No difference emerged between groups.

congenitally blind and sighted controls (t(20) = 1.3, p = 0.2; late blind vs. sighted controls: t(22) = 0.7, p = 0.5).

Finally, to exclude that any difference between blind individuals and blindfolded controls could be attributed to the administration of the test by a different experimenter, we compared the proprioceptive and auditory drifts of blind and controls as a function of which experimenter tested. More precisely, we split the data for the proprioceptive and auditory drifts of all participants in two (according to which experimenter tested them) and compared the data on independent samples t-test. For both blind participants (proprioceptive drift: t(20) = 0.4, p = 0.7; auditory drift: t(20) = 0.3, p = 0.8) and blindfolded controls participants (proprioceptive drift: t(11) = 1.7, p = 0.1; auditory drift: t(11) = 0.3, p = 0.7), we found no difference that could be attributed to the two different experimenters.

Aristotle illusion. The five congenitally blind, the three late blind and the six blindfolded controls reported perceiving one sphere when touching it with uncrossed fingers, but all reported perceiving two spheres when the fingers were crossed. On average, participants reported perceiving the illusion immediately after touching the sphere with crossed fingers.

Discussion

In the present study we investigated the role of early vision for the development of the body representation by testing a group of blind individuals with different ages at blindness onset (i.e., congenitally vs. late) on a somatosensory version of the classic rubber hand illusion.

We found that congenitally and late blind participants did not report perceiving the rubber hand illusion. In contrast, sighted controls subjectively perceived the strokes at the location of the rubber hands and reported the feeling of the rubber hand being part of their body. Thus, we were able to replicate the somatosensory rubber hand illusion shown in earlier studies[11,12].

Furthermore, when tested on proprioceptive and auditory drifts towards the rubber hand, blindfolded controls showed a drift on both measures, thus indicating that the stroking had spatially recalibrated the location of their other hand.

On the contrary, and in accord with their subjective percept, congenitally blind individuals did not display any drift in neither the proprioceptive nor the auditory task. Interestingly, and in contrast to their subjective report late blind individuals showed proprioceptive and auditory drifts that were indistinguishable from those of the blindfolded controls.

Because we found different results for congenitally and late blind participants in relation to sense of body ownership (as assessed by the questionnaire) and remapping of touch (as assessed by the proprioceptive and auditory drifts), we will discuss these findings separately and at the end we will try to reconcile both data sets into a broader framework for body representation.

The first finding (i.e., that blind individuals were unaffected by the subjective feeling of owning the rubber hand) is in line with the results of[12], who recently tested ten blind individuals on the somatosensory version of the rubber hand illusion and did not find a subjective illusion in their blind sample either. Since these authors did not distinguish between congenitally and late blind individuals within their sample, they were not able to distinguish the role of early vision and current visual status for the emergence of a subjectively perceived rubber hand illusion. By contrast, we found differences between these groups in the objective measures (drift) but not in the subjective measures (questionnaire).

The main finding of the present study is that while congenitally blind did not show any drift towards the rubber hand in neither the pointing nor auditory task, the late blind had drifts that were indistinguishable to those of sighted controls in both the pointing and auditory task.

The different results for congenitally and late blind can find an answer in the role of early vision in the development of the automatic encoding of touch into external coordinates. More precisely, studies have shown that the location of tactile stimuli is automatically transformed from anatomical, skin-based coordinates to external spatial coordinates[29]. Such a remapping of touch is necessary in order to relate tactile input to inputs of other sensory modalities in particular vision. Indeed, vision has been suggested to dominate the other sensory modalities in spatial processing[28], so that all sensory inputs are likely remapped into visual-external coordinates. This hypothesis was supported by cumulating evidence that congenitally blind adults did not seem to automatically recode touch into external coordinates[20]. In general, in contrast to sighted and late blind individuals, congenitally blind adults do not seem to derive external coordinates if the task does not require doing so. In the present study, there was no need to externally remap the strokes at the hidden hand. While sighted and late blind participants recalibrated the external location of their hand based on the proprioceptive feedback of the hand being moved to stroke the rubber hand, congenitally blind participants did not. Because the earliest blindness onset of one of our late blind participants was 3 years of age, we can speculate that experiencing vision prior to this age is crucial in order to develop the mechanisms that allow for an automatic encoding of touch in external coordinates.

It could be claimed that the absence of drift in the congenitally blind may be the result of enhanced tactile, auditory and/or proprioceptive skills that these participants may have developed as a consequence of sensory loss[25]. The lack of any group differences in the proprioceptive and auditory baselines renders this alternative explanation, however, rather unlikely.

It remains to be discussed why late blind individuals showed a dissociation between their subjective report of the illusion and the perceptual drift measures. First, it is important to note that the correlations ran between the subjective ratings and the drifts did not yield any significant result for none of the groups, suggesting that these two measures indicate different aspects of the rubber hand illusion and more generally of the sense of body ownership. Indeed[21], reported that external remapping of touch and the subjective feeling of body ownership are dissociated under different experimental conditions. More precisely[21], measured the proprioceptive drift repeatedly after 10, 40 or 120 seconds in the classical visuo-tactile version of the rubber hand illusion. At the end of each trial the subjective feeling of body ownership was assessed with a questionnaire. Interestingly, not only in the synchronous, but also in the asynchronous condition the proprioceptive drift increased as a function of the number of measurements taken (i.e., the authors observed that the drift was the larger the more often the stroking was interrupted to measure the proprioceptive drift). However, this change in proprioceptive drift did not correspond to changes in the subjective feeling of body ownership, as measured with questionnaires. The authors concluded that the processes underlying the proprioceptive drift are independent from the processes (including visuo-tactile integration) that caused the feeling of body ownership as assessed with questionnaires. Thus, the feeling of ownership and the spatial updating of the perceptual world with respect to the body seem to be independent at least in some situations. Our results confirm and extend these proposals to the somatosensory rubber hand illusion by demonstrating a full dissociation between both processes in the late blind group.

While subjectively reporting to feel to be touching one owns hand while actually touching the rubber hand may involve the so-called "body image", mislocating the position of one owns hand may involve the so-called "body schema". The notions of body image and body schema[22,23], are still a topic of vivid debate (see[24]), and may be defined as follows: while body image refers to a conscious visual representation of the body as can be observed from the outside, the body schema is an unconscious postural model of the body that constantly tracks and updates the position of the body parts in space.

Therefore, it could be speculated that late blind individuals adapt their body image to their current visual status. By contrast, they still automatically remap sensory input in external space due to the fact that they had acquired the mechanisms that cause an automatic recoding of touch into external space. It has been shown that the spatial remapping process remains unchangeable after development[16]. As a consequence of the latter, the late blind recalibrate their body schema as sighted individuals do.

Finally, we have shown that all blind individuals, irrespective of blindness onset, experienced the Aristotle illusion, a tactile illusion that arises when the brain fails to integrate the atypical crossed finger posture with the perceived tactile information. Because we did not find any difference between blind and sighted controls on this illusion, we interpret this result as evidence for the proposal that in contrast to the hands, the fingers are represented predominantly in anatomical coordinates, which are used independent of visual experience[26].

In conclusion, our study has demonstrated that the rubber hand illusion failed to show up in congenital blind adults and is not subjectively reported by late blind individuals. We have additionally demonstrated that the illusion in late blind individuals dissociates, in that these participants did not report the qualitative experience but showed proprioceptive and auditory drifts towards the rubber hand. Finally, we have demonstrated that congenitally and late blind individuals, did experience an Aristotle illusion, which was indistinguishable from the illusion reported by sighted individuals. Thus, the rubber hand illusion and the Aristotle illusion seem to arise from different spatial representations.

Methods

Participants. Ten congenital (two females, mean age = 36 years of age, range: 26–49 years of age), twelve late blind (six females, mean age = 48 years of age, range: 27–67 years of age) and thirteen sighted participants (seven females, mean age = 42 years of age, range: 27–64) took part in the rubber hand illusion experiment. All sighted controls reported to be right-handed, while one congenital and two late blind reported to be left-handed. Moreover, one congenital and one late blind were ambidextrous.

For all blind individuals, blindness was due to peripheral deficits and was not associated to other impairments (see Table 2 for details about the blind participants).

Table 2 | Characteristics of participants and experiment(s) they took part to

ID	Gender	Age	Etiology of blindness	Age at blindness onset	Handedness	Rubber hand illusion	Aristotle illusion
2	m	40	Retinopathy	congenital	right	x[x]	
3	m	26	Retinopathy	congenital	right	x	
4	m	34	Retinitis pigmentosa	congenital	both	x	
6	m	47	Retinal degeneration	congenital	right	x	
7	m	33	Eye cancer	congenital	right	x	
9	m	29	Retinoblastoma	congenital	right	x	
10	m	49	Retinoblastoma	congenital	right	x	
11	f	29	Detached retina	congenital	right	x	
15	m	39	Lack of oxygen during birth	congenital	right	x	
16	f	30	Retinitis pigmentosa	congenital	left	x	
23	m	35	Retinoblastoma	congenital	right		x
24	m	46	Retinal degeneration	congenital	right		x
25	m	49	Retinopathy of prematurity	congenital	right		x
26	f	48	Retinopathy of prematurity	congenital	right		x
27	f	48	Glaucoma	congenital	right		x
1	f	27	Retinitis pigmentosa	14 years, before visually impaired *	left	x	
5	f	42	Glaucoma	6 years, before visually impaired *	right	x	
8	m	36	Retinitis pigmentosa	8 years, born myopic **	right	x	
12	m	41	Retinitis pigmentosa	3 years	both	x	
13	f	42	Retinopathy	20 years, visually impaired since age 5 years **	left	x	
14	m	46	Optic nerve atrophy	22 years	right	x	
17	m	49	Retinitis pigmentosa	22 years	right	x	
18	f	67	Glaucoma	unspecific, progressive, late blindness	right	x	
21	f	44	Eye infection	18 years, before visually impaired *	right	x	
19	m	54	Retinitis pigmentosa	18 years, before visually impaired *	right	x	x
20	m	67	Diabetes mellitus	23 years	right	x	x
22	f	63	Glaucoma	30 years, visually impaired since birth **	right	x	x

[x] indicates the experiment to which the single participant took part.
*the time point in which visual impairment started and the degree of it were not specified.
**the degree of visual impairment was not specified.

For all blind participants, inclusion criterion was complete blindness or minimal light sensitivity with no ability to functionally use this sensation, nor did they have pattern vision.

The same inclusion criterion was used for testing the Aristotle illusion, for which five congenital (two females, mean age = 45 years of age, range: 35–49 years of age) and three late blind individuals (one female, mean age = 61 years of age, single age: 54, 63, 67 years of age) took part in the study (see Table 2 for details about these groups of participants), age-matched with six sighted controls (three females, mean age = 55 years of age, range: 31–64 years of age). While the three late blind took part in the rubber hand illusion as well, the five congenitally blind participants were recruited to take part in the Aristotle illusion only.

All blind participants did not use sensory substitution devices and all of them were proficient Braille readers.

For both experiments, all participants were healthy, sighted controls had normal or corrected-to-normal vision and all had no prior experience with the two illusions.

Sighted controls were blindfolded during the whole duration of the experiment.

Informed consent was obtained from all participants before the beginning of the experiment.

The experiment was performed in accordance with the guidelines and regulations of the Helsinki Declaration. The protocol was approved by the ethical committee of the German Society for Psychology on human research.

Experimental design. *Rubber hand illusion.* Before starting the experiment, all participants were informed about the experimental set-up, about the experimental tool (i.e., the rubber hand), and received a short description of the tasks (i.e., tactile and auditory tasks) they were supposed to perform (see section below). Note that the instructions were also repeated during the experiment.

Blind individuals were allowed to manually explore the rubber hand before the experiment commenced. Sighted controls were blindfolded before entering the experimental room and remained blindfolded throughout the whole experiment, and were also allowed to manually explore the rubber hand. We did not allow the control group to see the experimental set-up to provide blind and blindfolded controls a largely similar experience.

Participants were asked at the beginning of the experiment to sit on a chair, and the experimenter then placed the participant's arms, with the palms facing downwards, to rest on a table. Participants were allowed to re-adjust the position of their arms so that they could feel as comfortable as possible.

A life-sized plastic hand was then placed between the participant's hands, at a distance of 15 cm between the participant's left index finger and the rubber hand's index finger.

The rubber hand could be a right or left hand according to the participant's non-dominant hand, which had to be held still throughout the experiment.

The participant, the rubber hand and the experimenter wore identical surgical gloves to avoid differences in tactile perception of the hand surface.

The stimulation consisted in having the experimenter moving the index finger of the participant's dominant hand on the rubber hand mostly between the knuckles of the index and the middle finger. At the same time, the experimenter stroked the same part of the non-dominant hand of the participant, synchronizing the stroking of both hands as closely as possible. Each stroke was maximum 5 cm long, lasting approximately 1 second each and applied in a proximal-to-distal direction.

For all the participants, this type of stimulation was performed 3 times, each one lasting approximately 90 seconds.

Proprioceptive and auditory drifts towards the rubber hand. Before and after exposure to the rubber hand, participants performed two tasks: pointing and auditory localisation. The tasks were used to measure whether the felt position of the participant's non-dominant hand would change (i.e., the drift) after the stroking session.

The first task consisted in pointing the index finger of the dominant hand towards the middle finger of the non-dominant hand, which was placed under a small glass table (60 cm length × 30 cm width × 40 cm height). Participants had to make the pointing movement over the table, on which a measuring tape was placed. After each pointing, the experimenter manually took the response by typing the number of cm in the computer. Plus (+) and minus (−) signs were used to identify the direction of the pointing, with '+' indicating the pointing in the direction of the rubber hand and '−' indicating the pointing beyond the participant's own middle finger.

The auditory localisation consisted in detecting when a continuous tone (600 Hz, 40 dB) presented over the participant's non-dominant hand was perceived to be passing over the middle finger. The stimulus was produced by a tactile stimulator wrapped into cellular material and was slowly moved over the participant's hand. We used the small glass table for the pointing task as reference to move the auditory stimulus. In other words, the auditory stimulus moved along the horizontal axis of the small glass table from its extreme left side to its extreme right side (and back). The auditory stimulus was kept approximately at the level of the participant's ears and was moved manually by the experimenter at a constant velocity (approximately 3 cm a second). The participant had to say "stop" when she perceived that the sound was exactly over the middle finger of her non-dominant hand. The experimenter took then the response exactly as described for the tactile task and typed it into the computer.

Both tasks were performed three times before and after the stroking session.

The drifts from both tasks were calculated as the difference of error before and after the rubber hand induction session.

Questionnaire (qualitative experience of the illusion). At the end of the experiment participants were asked to complete a questionnaire consisting of 5 statements adapted from[9] and[11]. A seven-item rating scale was used, with responses ranging between ± 3. Plus 3 would indicate a strong agreement with the statement, whereas −3 would indicate a strong disagreement and 0 a neutral response (i.e., neither agree nor disagree). All participants responded orally to the questions posed by the experimenter.

The first two statements were designed to correspond to the illusion (1. "I felt as if I was touching my left hand with my right index finger"; 2. "I felt as if the rubber hand was my hand"; note that statement #1 was rephrased for left handers). The other three statements were unrelated to the illusion and, accordingly to previous studies[9,11], served as control statements for suggestibility (3. "I felt as if my hand was becoming rubberish"; 4. "I felt as if my hand had disappeared"; 5. "I felt as if I had three hands").

Procedure. All participants were informed about the experiment before it started and particularly that the experimenter would use the participant's hand to stroke a rubber hand.

All sighted participants were blindfolded prior to entering the experimental room to avoid seeing the experimental set-up and remained blindfolded throughout the experiment.

All participants were asked to comfortably sit on a chair and place the non-dominant hand on the table with the palm facing downwards. Once a comfortable position was found, the participant was asked to keep her non-dominant hand still throughout the experimental session.

The experiment would start by measuring pointing and auditory localisation. The order of the two tasks was randomised between participants.

Then, participants were exposed to the rubber hand illusion, followed by the pointing and auditory tasks, again randomised in their order between participants. The stroking of the rubber hand and the participant's hand was repeated 3 times (sessions) in a row. At first, the experimenter asked the participant to simply say "stop" when she perceived that something had changed in her body perception. In case of immediate sensation of anything changing in their body perception, the experimenter would ask the participant to provide more details about the type of experience felt (note that none of our participants experienced any change in body perception after the first stroking session). If participants did not say anything, stroking would last up to a maximum of 90 seconds. We used this condition to see whether the illusion itself or any other bodily experience could be elicited by the stroking without providing any specific instruction about the feeling that should be perceived. On the second stroking session, participants were explicitly asked to say "stop" as soon as they felt that they were stroking their own hand and not the rubber hand. The stimulation would stop when response was provided or after a maximum of 90 seconds.

The last stroking session consisted of 90 seconds stroking without asking the participant to report any feeling.

Participants would then undergo the testing of the pointing and auditory localisation tasks. Finally, they would be asked to answer a questionnaire.

The experiment took overall 20 minutes to complete.

One sighted control did not take part in the auditory task because he reported being slightly hearing impaired.

Note that in this study we only measured the effects of synchronous stroking on the reported feeling and the perceptual drifts. This choice was driven by two main reasons. First, the literature about the rubber hand illusion clearly reports that only synchronous stroking leads to an experience of the illusion (as reported subjectively, see[27]) and to its correspondent perceptual drift (as measured with pointing, see[9,11]). Second, a recent study by[21] found that repeating asynchronous stroking leads to perceptual drift too, which suggests that a comparison between synchronous and asynchronous stroking should be taken with caution. Moreover, because we were interested in group comparisons (i.e., congenital and late blind vs. blindfolded controls), we wanted to focus on the condition that triggers the illusion the most.

It should also be noted that only two experimenters were allowed to perform this experiment to avoid different tactile pressures, duration of the stimulation, and synchronicity of the stimulation of the rubber hand and the participant's hand. The two experimenters tested an equal number of congenitally blind, late blind and blindfolded controls. Note that no difference emerged as a consequence of having two instead of one experimenter (see p. 11 for further details).

Aristotle illusion. A small sphere was placed on the palm of the non-dominant hand of the participant. Both blind participants and blindfolded controls were asked to touch the sphere with the index and middle finger and to tell how many spheres they perceived to be touching. Participants were then asked to cross the middle finger over the index finger of their dominant hand and to keep this position while moving the tips of the crossed fingers over the small sphere. Participants were then asked to report again the number of spheres they perceived to be touching as soon as they felt them. The response was taken manually by the experimenter, who typed it into the computer.

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Author contributions

E.N. and B.R. designed the experiments; E.N. and T.S. performed the experiments; E.N. analysed data; E.N. and B.R. wrote the manuscript.

Additional information

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