Current Biology 24, 1222–1226, June 2, 2014 http://dx.doi.org/10.1016/j.cub.2014.04.004

Report

The Neural Basis of Somatosensory Remapping Develops in Human Infancy

Silvia Rigato,[1,2] Jannath Begum Ali,[2] José van Velzen,[2] and Andrew J. Bremner[2,*]
[1]Department of Psychology, University of Essex, Colchester CO4 3SQ, UK
[2]Sensorimotor Development Research Unit, Department of Psychology, Goldsmiths, University of London, New Cross, London SE14 6NW, UK

Summary

When we sense a touch, our brains take account of our current limb position to determine the location of that touch in external space [1, 2]. Here we show that changes in the way the brain processes somatosensory information in the first year of life underlie the origins of this ability [3]. In three experiments we recorded somatosensory evoked potentials (SEPs) from 6.5-, 8-, and 10-month-old infants while presenting vibrotactile stimuli to their hands across uncrossed- and crossed-hands postures. At all ages we observed SEPs over central regions contralateral to the stimulated hand. Somatosensory processing was influenced by arm posture from 8 months onward. At 8 months, posture influenced mid-latency SEP components, but by 10 months effects were observed at early components associated with feed-forward stages of somatosensory processing. Furthermore, sight of the hands was a necessary pre-requisite for somatosensory remapping at 10 months. Thus, the cortical networks [4] underlying the ability to dynamically update the location of a perceived touch across limb movements become functional during the first year of life. Up until at least 6.5 months of age, it seems that human infants' perceptions of tactile stimuli in the external environment are heavily dependent upon limb position.

Results and Discussion

When, as adults, we feel a tactile sensation on one of our hands, we know where it comes from in external space irrespective of where our limbs rest; we are able to take account of limb position in mapping tactile space onto the external world. If human infants cannot do this, as some authors have proposed [3, 5–7], it would suggest that early perceptions of tactile space are heavily reliant on limb position [8, 9]. We investigated this possibility and the early development of tactile spatial representations by recording somatosensory evoked potentials (SEPs) from infants in age groups spanning 6.5 to 10 months of age. In adults, arm posture is known to modulate the early stages of somatosensory processing [1, 10–13]; we examined developmental changes in such effects of posture in infant SEPs.

In experiment 1, we presented 6.5- and 10-month-old infants with vibrotactile stimuli on the hands when their hands were both crossed and uncrossed. Because previous behavioral studies [3] have demonstrated the developmental improvements in orienting to tactile stimuli across changes in posture between 6.5 and 10 months of age, we expected to see parallel differences in postural modulations of somatosensory processing between these age groups. At scalp sites over the somatosensory cortex contralateral to the tactile stimuli, we observed similar SEPs in both age groups (Figure 1); these comprised several consecutive deflections within 500 ms after stimulus onset. Modulations of the SEPs by posture in the 10-month-olds manifested as increased positivity, in contrast to the increased negativity seen in adults [10, 11]. We observed no clearly defined SEPs at corresponding ipsilateral recording sites, and so we report only contralateral analyses across experiments 1–3 (similar to what is reported in [14–17]).

We used a Monte Carlo simulation method (see Supplemental Information available with this article online) [18] in which we were able to trace the time course of statistically reliable modulations of the SEPs by posture on a sample-point basis (intervals every 2 ms) across posture-difference waveforms (700 ms after stimulus onset) for each age group (see Figure 1). No effect of posture was observed in the 6.5-month-olds, but the 10-month-olds' SEPs demonstrated a statistically reliable early effect of posture for 162 ms, from 58 to 220 ms after stimulus onset (the simulation identified any sequence of consecutive significant t tests longer than 104 ms to be reliable).

We next examined whether there was, as expected, a greater effect of posture in the 10-month-olds than the 6.5-month-olds. To do this, we calculated the "posture effect" (uncrossed-hands mean amplitude − crossed-hands mean amplitude; μV) for each participant within the interval that was significant in the 10-month-olds (58–220 ms). A one-tailed t test showed a greater posture effect in the 10-month-olds ($M = -2.63$, SD = 2.45) than the 6.5-month-olds ($M = -0.86$, SD = 2.4) ($t(25) = 1.87$, $p = 0.037$), confirming an increase in postural modulation of somatosensory processing between 6.5 and 10 months of age. Thus, whereas we find no evidence that arm posture influences processing of tactile stimuli at 6.5 months of age, by 10 months of age, as in adulthood [1, 10–13], posture modulated somatosensory processing. In the 10-month-olds, the distribution of this effect over central scalp sites and its early onset (also seen in adults [10, 11]) indicate that posture modulates the feed-forward stages of processing in somatosensory cortex [19, 20].

Adults use both visual and proprioceptive cues about hand position in remapping tactile space [10, 21–25]. Multisensory neurons that remap multisensory correspondence between touch and vision on the basis of visual and proprioceptive cues to posture, both together and in isolation, have been identified in primate premotor cortex [26]. To determine whether visual cues are necessary for postural modulation of touch at 10 months, in experiment 2 we presented an additional group of 10-month-olds with the same stimulus protocol as in experiment 1, but this time we used a black cloth to obscure their sight of their arms and hands (see Figure 2).

We again traced the emergence of statistically reliable effects of posture on a sample-point basis, but we found no effects across the recording epoch (Figure 2). We next looked for a significant difference in the posture effect (μV difference) between the 10-month-olds who had sight of their arms

*Correspondence: a.bremner@gold.ac.uk

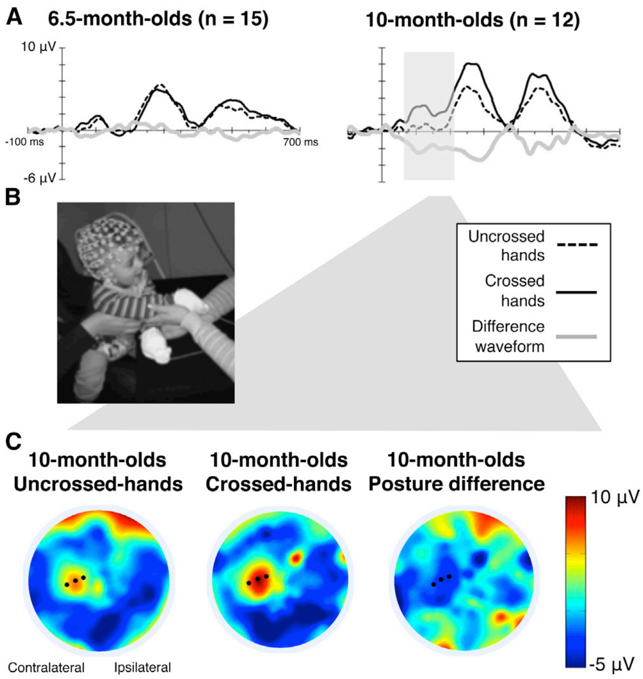

Figure 1. Experiment 1: Somatosensory Evoked Potentials in Crossed- and Uncrossed-Hands Postures, Compared between 6.5- and 10-Month-Old Infants

(A) Grand averaged SEPs in both posture conditions from central electrodes (C3, C4) contralateral to the stimulated hand are shown for 6.5- and 10-month-old infants. A difference waveform was also obtained for each group by subtraction of the SEP waveform in crossed-hands posture from that in uncrossed-hands posture. The shaded area indicates the time course of statistically reliable effects of posture on somatosensory processing. There was no effect of posture in the 6.5-month-olds, but a reliable effect was found between 58 and 220 ms in the 10-month-olds.

(B) A 6.5-month-old infant adopting the crossed-hands posture in experiment 1.

(C) Topographical representations of the voltage distribution over the scalp in the 10-month-old infants from 150–200 ms after the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

(experiment 1) and those who did not (experiment 2) within the interval (58–220 ms) that was significant in the group who had sight of their arms. A trend toward a greater posture effect in the infants with sight of their arms (M = −2.63, SD = 2.45) than in those with no sight of their arms (M = 0.49, SD = 5.33) approached significance, $t(23) = 1.85$, two-tailed p = 0.077.

The lack of posture effect in the 10-month-olds who could not see their hands indicates that it is primarily visual limb posture, at this age, that modulates somatosensory processing. This contrasts with findings from adult humans and monkeys, for whom both proprioceptive and visual signals concerning the limbs, alone or combined, play roles in somatosensory remapping [10, 21–26]. The current findings suggest that infants are immature in their use of static proprioceptive cues to hand position and that somatosensory modulation by visual hand position drives remapping at 10 months.

In experiment 3, we examined the emergence of somatosensory remapping in 8-month-olds. Because 10-month-old infants show influences of posture on the early perceptual stages of somatosensory processing, we asked whether, at an earlier point in the emergence of somatosensory remapping, posture also influences early stages of processing. Experiment 3 also investigated experiential factors driving the emergence of somatosensory remapping in infancy. Research with blind individuals indicates that visual perceptual experience might be important in the development of external coding of touch ([5, 7, 27], but see [28]). Here we investigated a different but overlapping hypothesis, namely, that sensorimotor experience of movements of the body is what drives the development of somatosensory remapping.

The emergence of somatosensory remapping in the crossed-hands posture between 6.5 and 10 months of age (observed in experiment 1 and in [3]) is developmentally contiguous with the first reaches that infants make across the body midline [29–31]. Given some individual differences in midline crossing behaviors [31], we reasoned that we might observe associations in the acquisition of midline crossing and somatosensory remapping across infants.

We first examined 8-month-olds' spontaneous midline-crossing behaviors in a reaching task. During several trials, an attractive toy was presented within reach across three locations: at the midline or over the infant's left or right shoulders. Eleven of the infants tested made no midline-crossing reaches at all. The other 15 infants made at least one and a maximum of seven midline-crossing reaches. We divided these infants into "crossers" and "noncrossers" on the basis of whether they had made a single reach which crossed the midline during the lateralized trials of the reaching task (see Figure 3). There were no significant differences in the age of the groups or in their performance on standardized tests of motor ability.

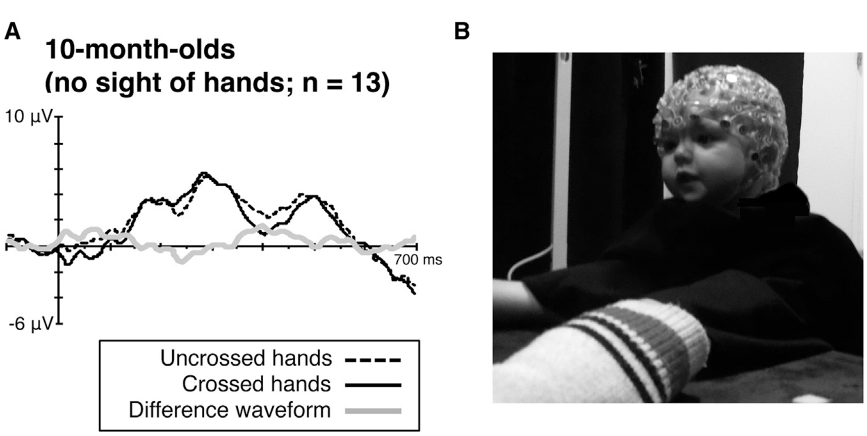

Figure 2. Experiment 2: Somatosensory Evoked Potentials in Crossed- and Uncrossed-Hands Postures in 10-Month-Old Infants Who Could Not See Their Hands

(A) Grand averaged SEPs in both posture conditions from central electrodes (C3, C4) contralateral to the stimulated hand. A posture difference waveform was obtained by subtraction of the SEP waveform in crossed-hands posture from that in the uncrossed-hands posture. No effects of posture were observed at any time point. Collapsing across posture conditions revealed no differences between the SEPs in experiment 2 and those from the 10-month-olds in experiment 1.

(B) A 10-month-old taking part in experiment 2. The experimenter's arms holding the infant's hands under the gown are visible extending toward the left.

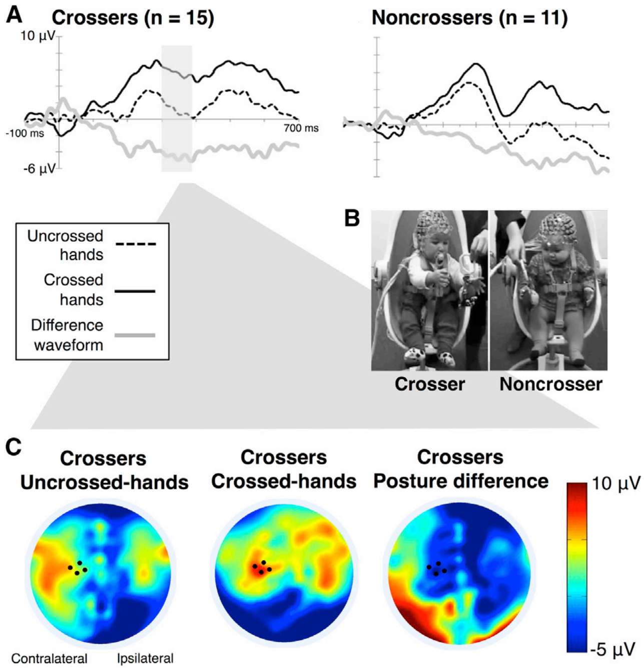

Figure 3. Experiment 3: Somatosensory Evoked Potentials in Crossed- and Uncrossed-Hands Postures in 8-Month-Old Infants Who Were Classified as Either “Crossers” or “Noncrossers”

(A) Grand averaged SEPs from central electrodes (C3, C4) contralateral to the stimulated hand are depicted for both crosser and noncrosser groups of 8-month-old infants. A posture effect difference waveform was obtained in each group by subtraction of the SEP waveform in the crossed-hands posture from that in the uncrossed-hands posture. The shaded area indicates the time course of reliable effects of posture on somatosensory processing. There was no effect of posture in the noncrossers, but the crossers showed an effect between 298 and 392 ms.

(B) A “crosser” and a “noncrosser” 8-month-old showing distinctive reaches in the reaching task of experiment 3.

(C) Topographical representations of the voltage distribution over the scalp in the crossers from 340–390 ms after the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

Neither were there differences in the numbers of trials completed or reaches made (see Supplemental Information).

We ran separate Monte Carlo simulations to examine the time course of reliable postural modulations of SEPs for the crossers and noncrossers; we expected greater posture effects in the crossers (see Figure 3). In the crossers, an effect of posture was observed for 94 ms, from 298 to 392 ms (any sequence of consecutive significant t tests longer than 86 ms was considered statistically reliable). No effect of posture was observed for the noncrossers. Comparing the “posture effect” (µV difference) for the crossers and noncrossers within the interval (298–392 ms) that was significant in the crossers group failed to reveal the expected greater posture effect in the crossers ($M = -4.35$, SD = 4.42) than in the noncrossers ($M = -2.68$, SD = 7.02), ($t(24) = 0.75$, not significant [n.s.]). There was no significant correlation observed between the number of midline crosses and the posture effect in this SEP interval across the 8-month-olds, $r(26) = 0.19$, n.s.

Thus, posture modulates somatosensory processing in 8-month-old infants, although only in a group of infants who had a tendency to cross their hands over the midline in a prior reaching task. The effect of posture in this group began at a later phase of the SEPs (298 ms after the stimulus) than it did for the 10-month-olds in experiment 1, indicating that, at this earlier stage of development, posture modulates touch beyond the initial feed-forward phase of somatosensory processing. The less focused distribution of the posture effect (see in Figure 3) also suggests that a wider range of brain areas (perhaps beyond SI and SII) are recruited in 8-month-olds.

No influence of posture on somatosensory processing was seen in a group of 8-month-olds who were virtually identical in age and motor ability but who demonstrated no tendency to place their hands across the midline. Nonetheless, there was no statistically reliable influence of group (crossers versus noncrossers) on somatosensory processing. Although we cannot rule out a role for cross-midline reaching, it seems likely that sensorimotor experience might not be the only factor in the emergence of somatosensory remapping. As mentioned, visual experience in early life has been implicated in the external coding of touch [5, 7]. It is also possible that maturational brain changes [20] (e.g., in the corpus callosum [32–34]) occurring between 6 and 10 months influence both somatosensory remapping and the ability to adopt a wider range of body and limb postures.

Irrespective of the developmental processes involved, we have demonstrated dramatic changes in infants’ processing of tactile information across the first year of life. At 6.5 months of age, posture plays no role in SEPs, yet by 10 months arm position influences the early feed-forward stages of somatosensory processing. This represents strong evidence that somatosensory remapping across changes in limb position emerges in the first year, a conclusion that is supported by evidence of improvements in behavior: orienting responses to tactile stimuli on the hands across changes in arm posture also improve between 6.5 and 10 months [3]. An important contribution of the current study is to demonstrate, using electrophysiological recordings, the stages of processing at which posture plays a role across these ages. Whereas improvements in behavioral orienting responses to tactile stimuli could be driven by changes in perceptual and post-perceptual processes alike, emerging effects of posture on the early stages of somatosensory processing (experiment 1) unambiguously point to the emergence of a new mode of tactile spatial perception. Interestingly, early in the emergence of these processes, postural remapping of touch appears to occur later in processing. It could be that at 8 months infants are at an initial developmental stage in which they are required to resolve conflict between different frames of reference (anatomical versus external) for encoding tactile stimuli and related responses, prior to the emergence of changes to the early perceptual tactile processes described above.

Changes in body posture represent a particular challenge when individuals must map touches in external space (see [35]). Although 6.5-month-old infants are able to locate and orient to tactile stimuli when their hands are in typical positions [3], we have shown striking changes subsequently in the way the infant brain processes touch. Infants come to learn to use cues about limb position (initially visual cues only) to remap where touches are in the external world. The first evidence of this is in 8-month-olds and appears to occur at somatosensory processing stages associated with stimulus evaluation and responding. In 10-month-olds, remapping becomes perceptual, a function of the early feed-forward stages of processing in somatosensory cortex.

That there are developmental changes in how touch is mapped onto external space shows that, in agreement with arguments made by Molyneux and Locke over 300 years ago [36]

Table 1. Participant Characteristics in Experiments 1–3

	Group	n	Sex	Mean Age (Days)	Age Range (Days)
Experiment 1	6.5-month-olds	15	7 f, 8 m	198 (SD = 8.3)	185–214
	10-month-olds	12	7 f, 5 m	304 (SD = 12.3)	288–322
Experiment 2	10-month-olds	13	9 f, 4 m	302 (SD = 10.7)	279–315
Experiment 3	8-month-old crossers	15	7 f, 8 m	258 (SD = 13.4)	243–279
	8-month-old noncrossers	11	8 f, 3 m	256 (SD = 13.3)	241–283

(and also with the recent work of Held and colleagues [37]), humans are not provided a priori with an ability to represent space across sensory modalities. This conclusion places strong qualifications on accounts of multisensory development that argue that certain "amodal" aspects of sensory stimulation, such as spatial location, are readily available to perception in early life [38–40]. Early perceptions of tactile space are solipsistic in that they are strongly anchored to the usual position of the limbs. Infants have to learn how touch maps onto the external world across changes in limb position.

Experimental Procedures

Table 1 provides the characteristics of all participant groups (experiments 1–3). Across experiments 1–3, ERPs were recorded while infants were presented with vibrotactile stimuli to their palms. A single tactor was attached to each of the infants' hands. Each trial comprised four discrete tactile stimuli presented to the hands, one hand at a time in succession. Each stimulus lasted 200 ms, and interstimulus intervals varied randomly between 800 and 1,400 ms. The order of hand stimulation was randomized under the constraint that each hand was stimulated twice on each trial. The experimenter changed the infants' hand posture between each trial (order was counterbalanced). The stimulus presentation protocol was designed in such a way as to discourage overt orienting responses to the tactile stimuli (see Supplemental Information). Testing took place until the infant became fussy and inattentive.

Brain electrical activity was recorded continuously via 128 electrode Hydrocel Geodesic Sensor Nets (Electrical Geodesic, Inc.). Analyses of ERP data focused on central sites (C3 and C4) contralateral to the stimulated hand (see Supplemental Information). In experiment 3, prior to EEG recording, the infants were tested on a battery of motor scales and a reaching task designed to measure any tendency to cross the midline (full details are provided in the Supplemental Information).

Supplemental Information

Supplemental Information includes three figures, two tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.04.004.

Acknowledgments

This research was supported by European Research Council grant 241242 (European Commission Framework Programme 7), awarded to A.J.B.. We thank the infants who took part and their parents, and also Elisa Carrus, Rob Davis, Maurice Douglas, Alan Pickering, and researchers at the Goldsmiths Infant Lab and the Centre for Brain and Cognitive Development at Birkbeck University of London.

Received: January 11, 2014
Revised: March 11, 2014
Accepted: April 1, 2014
Published: May 22, 2014

References

1. Azañón, E., and Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. Curr. Biol. *18*, 1044–1049.
2. Azañón, E., Longo, M.R., Soto-Faraco, S., and Haggard, P. (2010). The posterior parietal cortex remaps touch into external space. Curr. Biol. *20*, 1304–1309.
3. Bremner, A.J., Mareschal, D., Lloyd-Fox, S., and Spence, C. (2008). Spatial localization of touch in the first year of life: Early influence of a visual spatial code and the development of remapping across changes in limb position. J. Exp. Psychol. Gen. *137*, 149–162.
4. Graziano, M.S.A. (2006). Progress in understanding spatial coordinate systems in the primate brain. Neuron *51*, 7–9.
5. Röder, B., Rösler, F., and Spence, C. (2004). Early vision impairs tactile perception in the blind. Curr. Biol. *14*, 121–124.
6. Pagel, B., Heed, T., and Röder, B. (2009). Change of reference frame for tactile localization during child development. Dev. Sci. *12*, 929–937.
7. Ley, P., Bottari, D., Shenoy, B.H., Kekunnaya, R., and Röder, B. (2013). Partial recovery of visual-spatial remapping of touch after restoring vision in a congenitally blind man. Neuropsychologia *51*, 1119–1123.
8. Hall, G.S. (1898). Some aspects of the early sense of self. Am. J. Psychol. *9*, 351–395.
9. Piaget, J. (1952). The Origins of Intelligence in Children, Cook, M. (trans.) (New York: International Universities Press Inc.).
10. Rigato, S., Bremner, A.J., Mason, L., Pickering, A., Davis, R., and Van Velzen, J. (2013). The electrophysiological time course of somatosensory spatial remapping: Vision of the hands modulates effects of posture on somatosensory evoked potentials. Eur. J. Neurosci. *38*, 2884–2892.
11. Soto-Faraco, S., and Azañón, E. (2013). Electrophysiological correlates of tactile remapping. Neuropsychologia *51*, 1584–1594.
12. Overvliet, K.E., Azañón, E., and Soto-Faraco, S. (2011). Somatosensory saccades reveal the timing of tactile spatial remapping. Neuropsychologia *49*, 3046–3052.
13. Groh, J.M., and Sparks, D.L. (1996). Saccades to somatosensory targets. I. behavioral characteristics. J. Neurophysiol. *75*, 412–427.
14. Desmedt, J.E., Brunko, E., and Debecker, J. (1976). Maturation of the somatosensory evoked potentials in normal infants and children, with special reference to the early N1 component. Electroencephalogr. Clin. Neurophysiol. *40*, 43–58.
15. Pihko, E., and Lauronen, L. (2004). Somatosensory processing in healthy newborns. Exp. Neurol. *190* (*Suppl 1*), S2–S7.
16. Pihko, E., Nevalainen, P., Stephen, J., Okada, Y., and Lauronen, L. (2009). Maturation of somatosensory cortical processing from birth to adulthood revealed by magnetoencephalography. Clin. Neurophysiol. *120*, 1552–1561.
17. Wolff, P.H., Matsumiya, Y., Abroms, I.F., van Velzer, C., and Lombroso, C.T. (1974). The effect of white noise on the somatosensory evoked response in sleeping newborn infants. Electroencephalogr. Clin. Neurophysiol. *37*, 269–274.
18. Guthrie, D., and Buchwald, J.S. (1991). Significance testing of difference potentials. Psychophysiology *28*, 240–244.
19. Hari, R., and Forss, N. (1999). Magnetoencephalography in the study of human somatosensory cortical processing. Philos. Trans. R. Soc. Lond. B Biol. Sci. *354*, 1145–1154.
20. Nevalainen, P., Lauronen, L., and Pihko, E. (2014). Development of human somatosensory cortical functions – what have we learned from magnetoencephalography: A review. Front Hum Neurosci *8*, 158. http://dx.doi.org/10.3389/fnhum.2014.00158.
21. Kennett, S., Spence, C., and Driver, J. (2002). Visuo-tactile links in covert exogenous spatial attention remap across changes in unseen hand posture. Percept. Psychophys. *64*, 1083–1094.
22. Azañón, E., and Soto-Faraco, S. (2007). Alleviating the 'crossed-hands' deficit by seeing uncrossed rubber hands. Exp. Brain Res. *182*, 537–548.
23. Làdavas, E. (2002). Functional and dynamic properties of visual peripersonal space. Trends Cogn. Sci. *6*, 17–22.
24. Lloyd, D.M., Shore, D.I., Spence, C., and Calvert, G.A. (2003). Multisensory representation of limb position in human premotor cortex. Nat. Neurosci. *6*, 17–18.
25. Medina, J., and Coslett, H.B. (2010). From maps to form to space: Touch and the body schema. Neuropsychologia *48*, 645–654.

26. Graziano, M.S.A. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. Proc. Natl. Acad. Sci. USA *96*, 10418–10421.
27. Röder, B. (2012). Sensory deprivation and the development of multisensory integration. In Multisensory Development, A.J. Bremner, D.J. Lewkowicz, and C. Spence, eds. (Oxford: Oxford University Press), pp. 301–322.
28. Eardley, A.F., and van Velzen, J. (2011). Event-related potential evidence for the use of external coordinates in the preparation of tactile attention by the early blind. Eur. J. Neurosci. *33*, 1897–1907.
29. Morange, F., and Bloch, H. (1996). Lateralisation of the approach movement and the prehensile movement in infants from 4 to 7 months. Early Dev. Parent. *5*, 81–92.
30. Provine, R.R., and Westerman, J.A. (1979). Crossing the midline: Limits of early eye-hand behavior. Child Dev. *50*, 437–441.
31. van Hof, R., van der Kamp, J., and Savelsbergh, G.J.P. (2002). The relation of unimanual and bimanual reaching to crossing the midline. Child Dev. *73*, 1353–1362.
32. Teicher, M.H., Dumont, N.L., Ito, Y., Vaituzis, C., Giedd, J.N., and Andersen, S.L. (2004). Childhood neglect is associated with reduced corpus callosum area. Biol. Psychiatry *56*, 80–85.
33. Barkovich, A.J., and Kjos, B.O. (1992). Gray matter heterotopias: MR characteristics and correlation with developmental and neurologic manifestations. Radiology *182*, 493–499.
34. Ballesteros, M.C., Hansen, P.E., and Soila, K. (1993). MR imaging of the developing human brain. Part 2. Postnatal development. Radiographics *13*, 611–622.
35. Bremner, A.J., Holmes, N.P., and Spence, C. (2008). Infants lost in (peripersonal) space? Trends Cogn. Sci. *12*, 298–305.
36. Locke, J. (1694/1979). An Essay Concerning Human Understanding, Peter H. Nidditch, ed. (Oxford: Clarendon Press).
37. Held, R., Ostrovsky, Y., de Gelder, B., Gandhi, T., Ganesh, S., Mathur, U., and Sinha, P. (2011). The newly sighted fail to match seen with felt. Nat. Neurosci. *14*, 551–553.
38. Bahrick, L., and Lickliter, R. (2012). The role of intersensory redundancy in early perceptual, cognitive and social development. In Multisensory Development, A.J. Bremner, D.J. Lewkowicz, and C. Spence, eds. (Oxford: Oxford University Press), pp. 183–206.
39. Filippetti, M.L., Johnson, M.H., Lloyd-Fox, S., Dragovic, D., and Farroni, T. (2013). Body perception in newborns. Curr. Biol. *23*, 2413–2416.
40. Bahrick, L.E. (2013). Body perception: Intersensory origins of self and other perception in newborns. Curr. Biol. *23*, R1039–R1041.