

**The neural basis of somatosensory remapping
develops in human infancy**

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Highlights

- Effects of limb position on somatosensory processing develop in human infancy.
- Young infants' spatial processing of touch does not incorporate limb position.
- Remapping touch across changes in posture at 10 months requires sight of the hands.
- By 10 months posture modulates early perceptual stages of processing.

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 changes in the way the brain processes somatosensory information in the first year of life which 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 whilst 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 onwards. 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

As adults when 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] this 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 across uncrossed- and crossed-hands postures. Because previous behavioural 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 enhancements 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 across both age groups (Figure 1), comprising several consecutive deflections within 500 ms following stimulus onset. Modulations of the SEPs by posture in the 10-month-olds were 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 (similarly to [14-17]).

--Insert Figure 1 about here--

We used a Monte Carlo simulation method (see Supplemental Information [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 following 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 an early effect of posture which was statistically reliable for 162 ms from 58 to 220 ms following 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 which 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 ($M = -.86$, $SD = 2.4$), $t(25) = 1.87$, $p = .037$, 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 to hand position in remapping tactile space [10, 21-25]. Multisensory neurons in primate premotor cortex have been identified which remap multisensory correspondences between touch and vision on

the basis of visual and proprioceptive cues to posture, both together and in isolation [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 Experiment 1 but this time we obscured their sight of their arms and hands with a black cloth (see Figure 2).

--Insert Figure 2 about here--

We again traced the emergence of statistically reliable effects of posture on a sample-point basis, but 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 (Experiment 1), and those who did not (Experiment 2), within the interval which was significant in the group who had sight of their arms (58-220 ms). A trend towards a greater posture effect in the infants with sight of their arms ($M = -2.63$, $SD = 2.45$) than those with no sight of their arms ($M = .49$, $SD = 5.33$), approached significance, $t(23) = 1.85$, two-tailed $p = .077$.

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, which modulates somatosensory processing. This contrasts with findings from adult humans and monkeys showing that 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. As 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 may be important in the development of external coding of touch [5, 7, 27, but see 28]. Here we investigate a different but overlapping hypothesis, namely, that it is sensorimotor experience of movements of the body, which 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 behaviours [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 behaviours in a reaching task. An attractive toy was presented on several trials 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 1 and a maximum of 7 midline-crossing reaches. We divided these infants into "Crossers" and "Non-crossers" groups on the basis of whether they had made a single reach which crossed the midline during the lateralised 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. Neither were there differences in the numbers of trials completed or reaches made (see Supplemental Information).

--Insert Figure 3 about here--

We ran separate Monte Carlo simulations examining the time course of reliable postural modulations of SEPs for the Crossers and Non-crossers groups, expecting greater posture effects in the Crossers group (see Figure 3). In the Crossers group, an effect of posture was observed for 94 ms from 298 to 392 ms (any sequence of consecutive significant t-tests which was longer than 86 ms was statistically reliable). No effect of posture was observed for the Non-crossers group. Comparing the “posture effect” (μV difference) for the Crossers and Non-crossers groups within the interval which was significant in the Crossers group (298-392 ms) failed to reveal the expected greater posture effect in the Crossers ($M = -4.35$, $SD = 4.42$) than the Non-crossers ($M = -2.68$, $SD = 7.02$), $t(24) = .75$, *n.s.* There was no significant correlation observed between the number of midline crosses and the posture effect in this SEP interval across all of the 8-month-olds, $r(26) = .19$, *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 following the stimulus) than 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 focussed 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 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 vs. Non-crossers) on somatosensory processing. Although we cannot rule out a role for midline crossing reaching, it seems

likely that sensorimotor experience may 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 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 which is supported by evidence of improvements in behaviour: 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 behavioural 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 may 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 vs. external) for encoding tactile stimuli and related

responses, prior to the emergence of changes to early perceptual tactile processes described above.

Changes in body posture represent a particular challenge when mapping 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 to 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] (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 which 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 4 discrete tactile stimuli presented to the hands one hand at a time in succession. Each stimulus lasted 200 ms, with interstimulus intervals varying randomly between 800 and 1400 ms. The order of hand stimulation was randomised with the constraint that each hand was stimulated twice on each trial. The experimenter changed the infants' hand posture between each trial (order 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.

--Insert Table 1 about here--

Brain electrical activity was recorded continuously via 128 electrode Hydrocel Geodesic Sensor Nets (Electrical Geodesic Inc.). Analyses of ERP data focussed 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 provided in the Supplemental Information).

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

Table 1: Participant characteristics in Experiments 1-3.

Figure legends

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, obtained in 6.5- and 10-month-old infants. A difference waveform was also obtained for each group by subtracting 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 taking part in Experiment 1 adopting the crossed-hands posture. (C) Topographical representations of the voltage distribution over the scalp in the 10-month-old infants from 150-200 ms following the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

Figure 2. Experiment 2: Somatosensory evoked potentials in crossed- and uncrossed-hands postures without sight of the hands in 10-month-old infants. (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 subtracting 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, analyses 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 towards the left.

Figure 3. Experiment 3: Somatosensory evoked potentials in crossed- and uncrossed-hands postures in 8-month-old infants who were either classified as “Crossers” or “Non-crossers”. (A) Grand averaged SEPs from central electrodes (C3, C4) contralateral to the stimulated hand depicted for both Crossers and Non-crossers groups of 8-month-old infants. A posture effect difference waveform was obtained in each group by subtracting the SEP waveform in crossed-hands posture from that in 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 Non-crossers, but the Crossers showed an effect between 298 and 392 ms. (B) A “Crosser” and a “Non-crosser” 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 following the tactile stimulus. Small black discs indicate the locations of the electrodes chosen for SEP analyses.

Figures

Figure 1

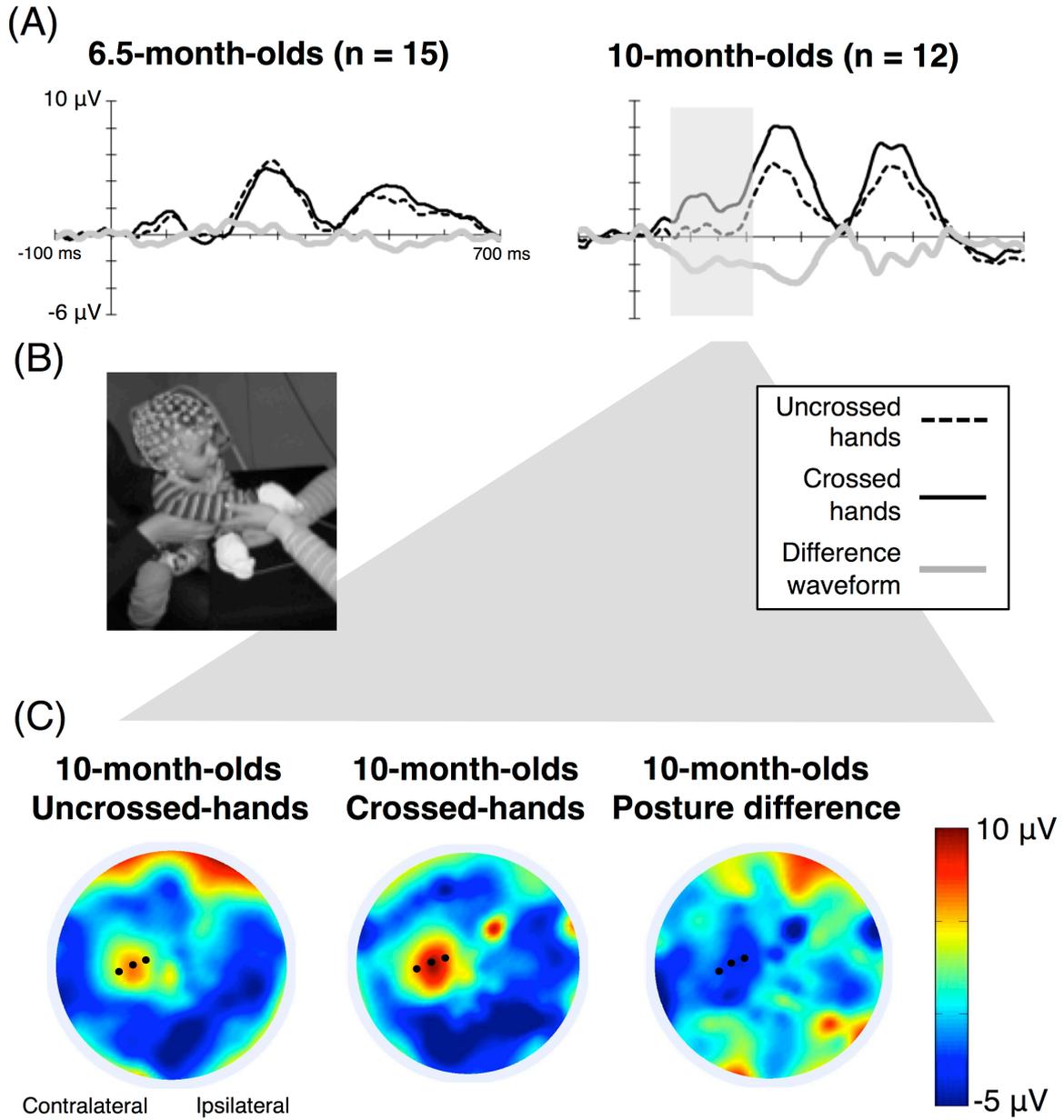
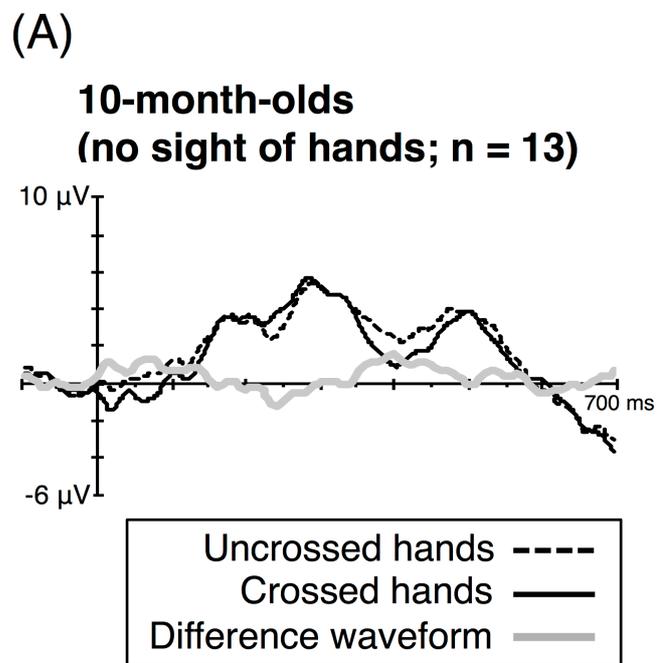


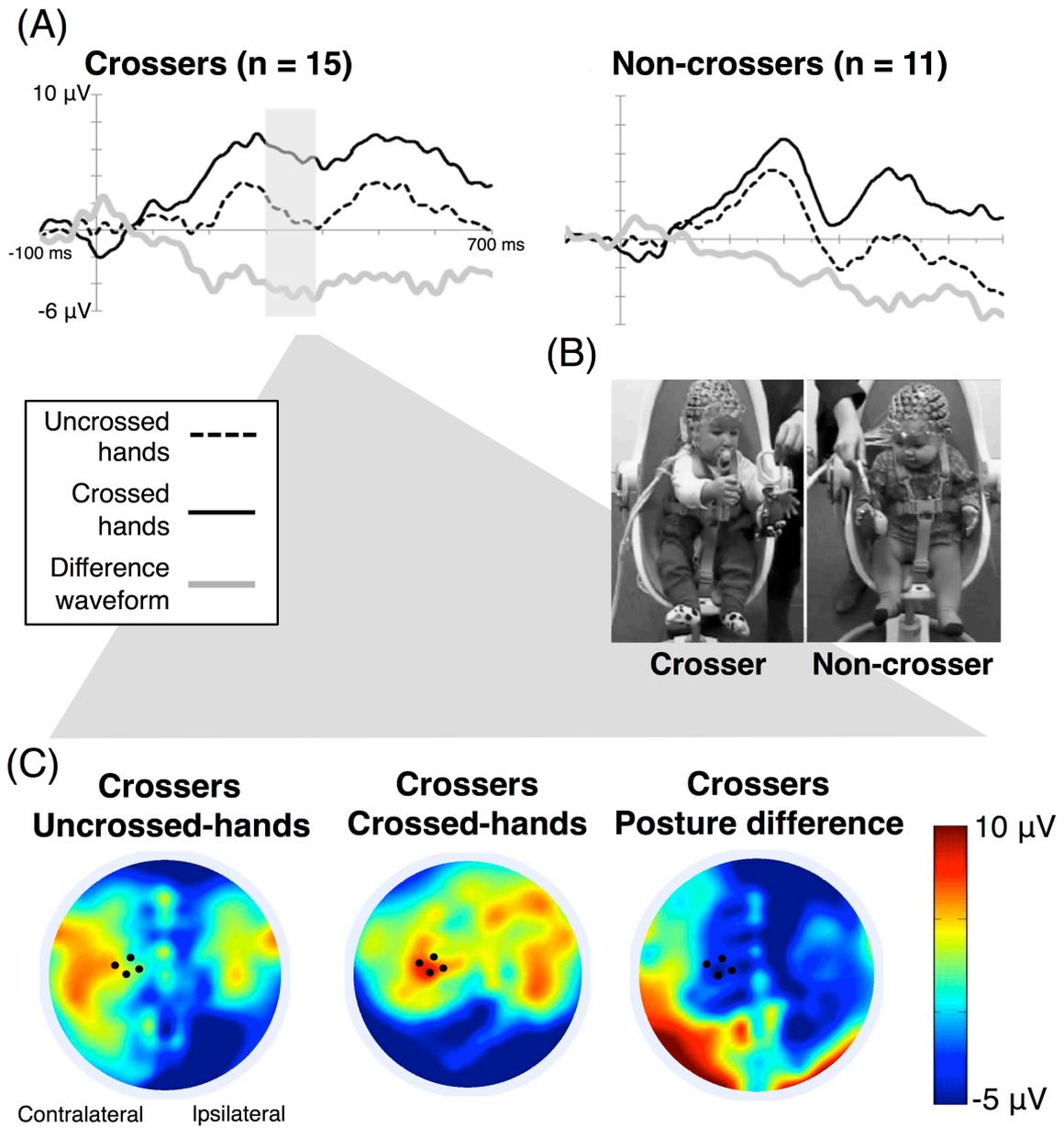
Figure 2



(B)



Figure 3



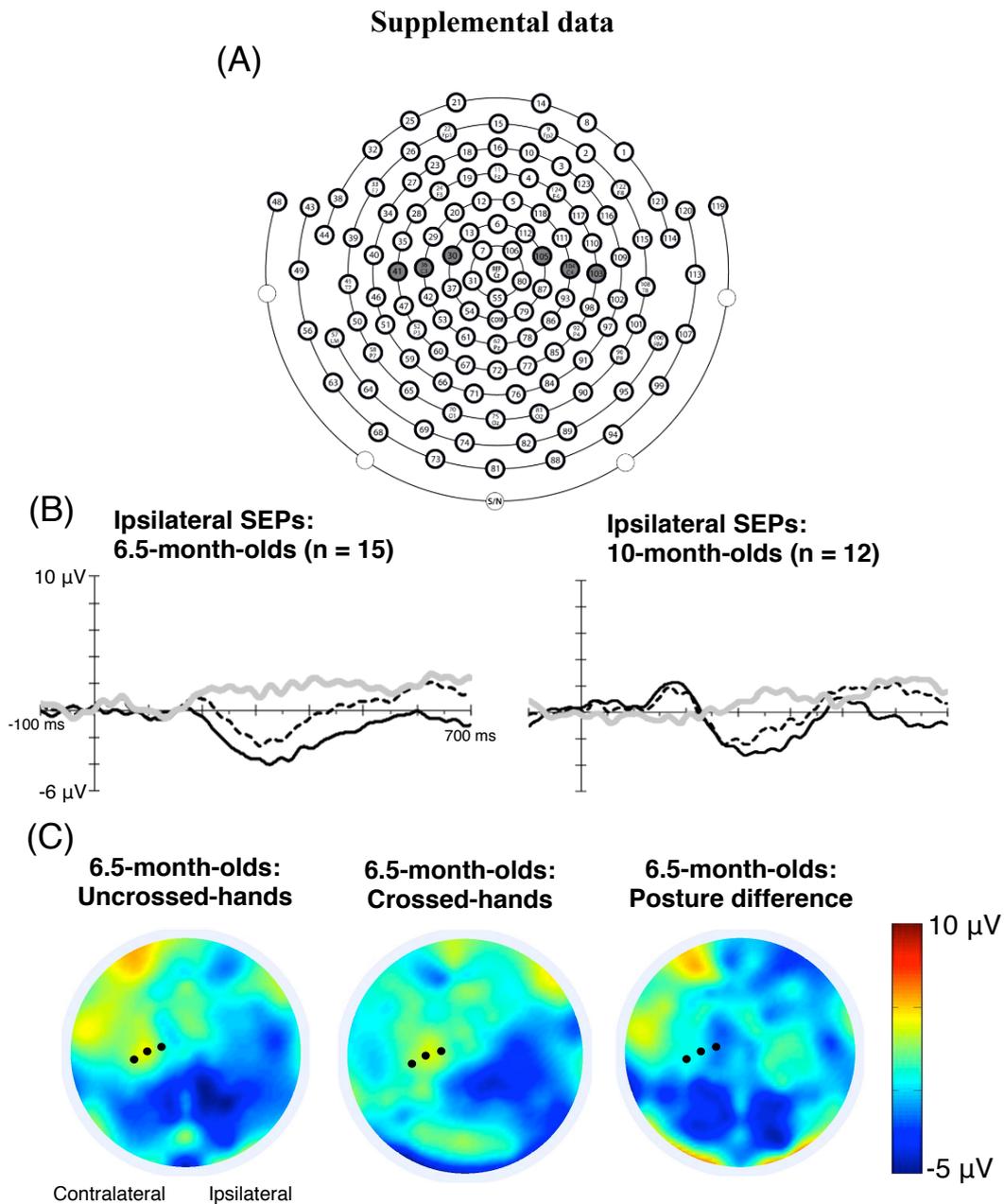


Figure S1 (related to Figure 1): Supplemental data from Experiment 1. (A) The layout of the Hydrocel Geodesic Sensor Net, and the electrodes which were selected for analysis in both Experiments 1 and 2 (C3: 30, 36, 41; C4: 103, 104, 105). (B) Grand averaged somatosensory evoked potentials in crossed- and uncrossed-hands postures from central electrodes (C3, C4) ipsilateral to the stimulated hand in 6.5-month-olds and 10-month-olds. As for the analyses of the contralateral SEPs reported in the manuscript, a sample-point analysis was carried out to determine at what point the posture conditions were reliably different. This analysis corrected for the autocorrelation of consecutive sample-points and multiple comparisons by using the Monte Carlo simulation method [S1] explained in the Supplemental Experimental Procedures. No effects of posture were found at sites ipsilateral to the stimulated hand in either age-group. The mean first order autocorrelation at lag 1 (estimated from our data, and used for our Monte Carlo simulations) was 0.99 for all of the datasets analysed. (C) Topographical representations of the voltage distribution over the scalp in the 6.5-month-olds. Both posture conditions and the posture difference maps are provided (from 150-200 ms following stimulus onset). Small black discs indicate the locations

of the electrodes chosen for SEP analyses. No effect of posture was observed in the SEPs gathered for this group.

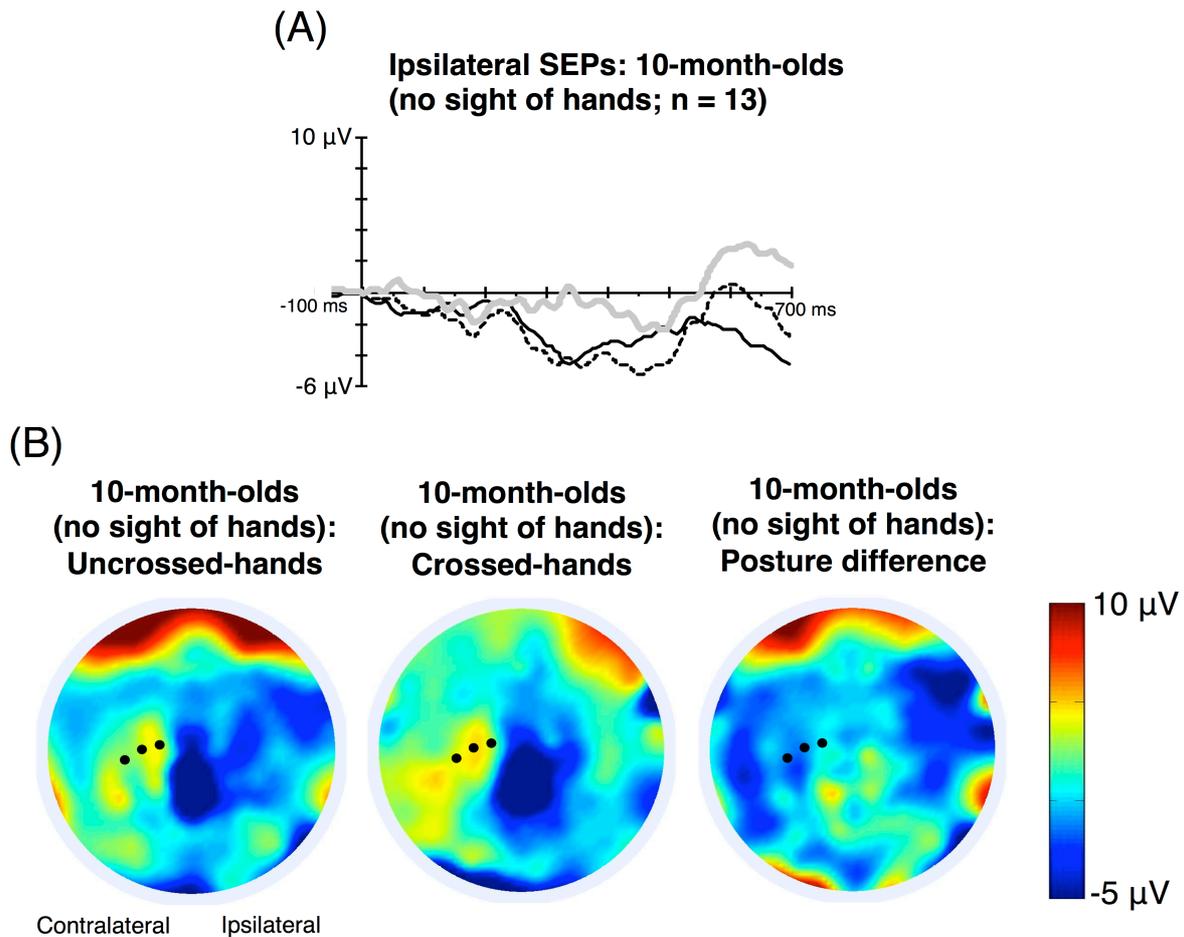


Figure S2 (related to Figure 2): Supplemental data from Experiment 2. The layout of the Hydrocel Geodesic Sensor Net, and the electrodes which were selected for analysis were the same in Experiment 2 as in Experiment 1 (see Figure S1). (A) Grand averaged somatosensory evoked potentials in crossed- and uncrossed-hands postures from central electrodes (C3, C4) ipsilateral to the stimulated hand in the 10-month-olds who did not have sight of their hands in Experiment 2. A sample-point analysis (see Figure S1) was carried out to determine at what point the posture conditions were reliably different. No effects of posture were found at sites ipsilateral to the stimulated hand. The mean first order autocorrelation at lag 1 (estimated from our data, and used for our Monte Carlo simulations) was 0.99 for all of the datasets analysed. (B) Topographical representations of the voltage distribution over the scalp in the 10-month-olds without sight of their hands. Both posture conditions and the posture difference maps are provided (from 150-200 ms following stimulus onset). Small black discs indicate the locations of the electrodes chosen for SEP analyses. No effect of posture was observed in the SEPs gathered for this group.

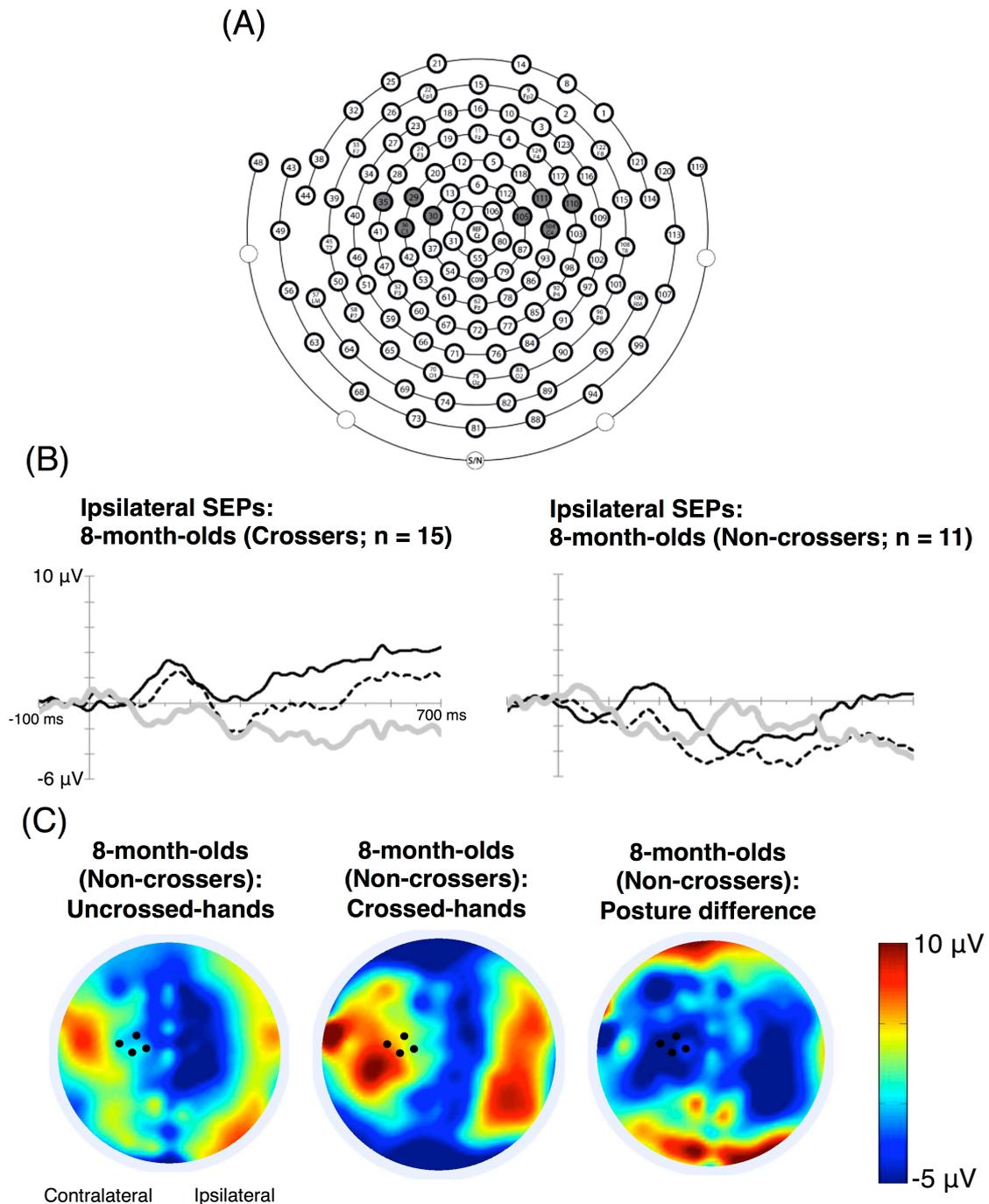


Figure S3 (related to Figure 3): Supplemental data from Experiment 3. (A) The layout of the Hydrocel Geodesic Sensor Net, and the electrodes which were selected for analysis in Experiment 3 (C3: 29, 30, 35, 36; C4: 104, 105, 110, 111). (B) Grand averaged somatosensory evoked potentials in crossed- and uncrossed-hands postures from central electrodes (C3, C4) ipsilateral to the stimulated hand in the 8-month-old Crossers and Non-crossers. A sample-point analysis (see Figure S1) was carried out to determine at what point the posture conditions were reliably different in these groups. No effects of posture were found at sites ipsilateral to the stimulated hand in either group. The mean first order autocorrelation at lag 1 (estimated from our data, and used for our Monte Carlo simulations) was 0.99 for all of the datasets analysed. (C) Topographical representations of the voltage distribution over the scalp in the 8-month-old Non-crossers. Both posture conditions and the posture difference maps are provided (from 340-390 ms following stimulus onset). Small black discs indicate the locations of the electrodes chosen for SEP analyses. No effect of posture was observed in the SEPs gathered for this group.

Group	Reaching task				Mullen motor scores			VABS motor scores		
	Trials completed	Reaches	Midline crosses	% midline crosses	Gross	Fine	Gross	Fine	Gross	Fine
Crossers n = 15 (8m, 7f)	M = 10.6 SD = 2.2 Range = 6-12	M = 10.5 SD = 2.4 Range = 5-12	M = 2.2 SD = 1.7 Range = 1-7	M = 20 SD = 14 Range = 8-58	M = 12.5 SD = 1.2 Range = 7-15	M = 13.0 SD = 2.5 Range = 10-18	M = 15.6 SD = 3.7 Range = 7-24	M = 12.1 SD = 2.0 Range = 9-16		
Non-crossers n = 11 (3m, 8f)	M = 11.4 SD = 1.8 Range = 6-12	M = 11.2 SD = 2.4 Range = 4-13	M = 0 SD = 0 Range = 0	M = 0 SD = 0 Range = 0	M = 13.1 SD = 1.9 Range = 11-15	M = 14.6 SD = 2.8 Range = 11-18	M = 15.6 SD = 4.5 Range = 12-24	M = 12.9 SD = 2.5 Range = 10-16		

Table S1 (related to Figure 3): 8-month-olds' performance in the reaching task and motor scales administered in Experiment 3. Infants in the two 8-month-old reaching groups (Crossers and Non-crossers) were compared on age, the number of reaching trials presented, number of reaches made and gross and fine motor abilities using the Mullen Scales of Early Learning and the Vineland Adaptive Behaviour Scale (VABS) (further details provided below). Independent samples t-tests showed that the two groups did not differ on any of these measures ($t < 1$, n.s., see Table S2).

Variable	Means (SD)		t-test statistics			
	<i>Crossers</i>	<i>Non-crossers</i>	<i>t</i>	<i>df</i>	<i>p</i>	<i>d</i>
No. of midline crosses	2.2 (1.7)	.0 (.0)				
% of midline crosses	20.0 (13.8)	.0 (.0)				
Age (days)	257.9 (13.4)	255.7 (13.3)	.4	24	.4	.2
Trials presented	10.6 (2.2)	11.4 (1.8)	.93	24	.36	.4
Reaches made	10.5 (2.4)	11.2 (2.4)	.68	24	.50	.3
Mullen gross motor score	12.5 (1.2)	13.1 (1.9)	.47	24	.36	.5
Mullen fine motor score	13.0 (2.5)	14.6 (2.8)	.94	24	.16	.6
VABS gross motor score	15.6 (3.7)	15.6 (4.5)	0.0	24	1.0	0
VABS fine motor score	12.1 (2.0)	12.9 (2.5)	.79	24	.44	.4

Table S2 (related to Figure 3): Independent samples t-tests of age, reaching performance and motor ability scores comparing the Crossers and Non-crossers groups of 8-month-olds in Experiment 3.

Supplemental experimental procedures

Participant characteristics, details of participant exclusion, ethical scrutiny and consent arrangements

Infants who appeared to be upset, or who moved excessively were classified as being fussy. If fussiness was identified at any point during the experiment then testing was terminated. For all of the experiments reported in this manuscript, participants were required to complete a minimum of 20 artefact free trials across both posture conditions to be included in analyses (additionally, for Experiment 3, participants needed to complete a minimum of 9 reaching trials). If testing was stopped before these criteria were reached then the infant was excluded from analysis on the basis of fussy behaviour. In Experiment 1 an additional nine 6.5-month-olds were excluded from the analyses (7 because of fussy behaviour, 2 because of equipment failure), and an additional four 10-month-olds were excluded from the analyses because of fussy behaviour. In Experiment 2 an additional 8 infants were excluded from the analyses because of fussy behaviour. In Experiment 3 an additional five 8-month-olds were excluded from the analyses because of fussy behaviour (4 participants) and equipment failure (1 participant).

Informed consent was obtained from the parents. The testing took place only if the infant was awake and in an alert state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London, and the Research Ethics Committee of the Department of Psychological Sciences, Birkbeck, University of London.

Design considerations

The design of the experiments reported in this paper take into account a number of factors which bear mentioning as they are specific to infant participants. Firstly, whereas it is considered valuable to gather behavioural and physiological data simultaneously in adult ERP investigations, this is typically not possible with infant participants as it is not possible to give infants instructions as to how or when to respond behaviourally. Behavioural data are often gathered separately (indeed this is recommended by [S2]) using experimental paradigms specifically designed to elicit observable behavioural responses (e.g. preferential looking). In order to limit the influence of movement-related artefacts, infant ERP studies tend to be designed in such a way as to discourage behavioural responses.

As described in the Experimental Procedures, vibrotactile stimuli were presented to infants' palms, one palm at a time in quite rapid succession; each stimulus was delivered to the palm for 200 ms, with interstimulus intervals varying randomly between 800 and 1400 ms. We used this rapid presentation method in order to maximise the number of tactile trials which we could present to each infant thereby improving the resilience of the gathered ERPs to noise and other artefacts. In order to prevent shifts in overt attention towards the tactile stimuli, we also put in place procedures to minimize such orienting responses. In order to do this, an experimenter, during presentation of the tactile stimuli, attracted the infant's visual attention centrally with an engaging facial expression and direct eye-contact (see below). We

were able to rule out a role of any residual orienting responses in the observed posture effects, as all of the significant postural modulations of SEPs occurred well in advance of the time at which infants of these ages will typically orient towards a touch. We observed posture effects in the SEPs between 58-220 ms (10-month-olds), and 298-392 ms (8-month-olds) following stimulus onset, whereas behavioural studies [S3] have demonstrated that infants make visual orienting responses to tactile stimuli much later, at average latencies of ~2 seconds in 10-month-olds, and ~3.5 seconds in 6.5-month-olds.

Additional information concerning experimental stimuli and procedures

In Experiment 1, the vibrotactile stimuli were presented via tactors comprising bone-conducting hearing aids (Audiological Engineering, Somerville, MA, US) driven at 220 Hz by a pure tone generator and amplifier and controlled by an EPRIME script. The tactors used in Experiments 2 and 3 were in house custom-built voice coils which were again driven with a 220 Hz sine wave, and very similar in their vibrotactile properties to those used in Experiment 1.

All infants were tested in a dimly lit room, seated on their parent's or a caregiver's lap with their forearms resting on a small table. Experimenter A faced the infant across the table, while Experimenter B was seated outside the room observing the infant's behaviour on a video monitor and triggering the presentation of the tactile stimuli. The testing session was recorded for data coding purposes. The tactors were fixed to the infant's palms with elastic straps, one in each hand. The infant's hands and the tactors were then covered by small cotton mittens (see Figure 1). Experimenter A, who was blind to the side of stimulus presentation, held the infant by each wrist and bounced his or her hands three times while saying "One, two, three, woo!". On reaching "woo!", Experimenter A held the infant's attention with an engaging facial expression and direct gaze, and at the same time placed and held the infant's hands into the appropriate posture (crossed-hands or uncrossed-hands), approximately 10 cm apart, one on either side of the midline. At this point, Experimenter B triggered the presentation of a trial (a sequence of four tactile stimuli). Between every trial the posture of the baby's arms was changed (order was counterbalanced between participants). This procedure was the same across all three experiments. In Experiment 2 visual information about the hands, the arms, and their postures was eliminated by covering the arms of the infant with a black cloth after fixing the tactors to the palms (Figure 2).

The 6.5- and 10-month-old infants in Experiment 1 were presented with an average of 96 and 101 vibrotactile stimulations, respectively. In Experiment 2, the 10-month-old infants were presented with an average of 117 vibrotactile stimulations. In Experiment 3 the Crossers group of 8-month-olds were presented with an average of 82 vibrotactile stimulations, and the Non-crossers group of 8-month-olds were presented with an average of 80 vibrotactile stimulations.

In Experiment 3, prior to EEG recording, infants were tested on: i) the Mullen Scales of Early Learning (current edition [S4]), ii) the Vineland Adaptive Behaviour Scale (VABS, current

edition [S5]), and iii) a reaching task designed to measure any tendency to cross the midline and based on [S6]. The Mullen and VABS are assessment scales for infants and toddlers measuring overall cognitive development using domains including language, visual reception and motor abilities. For this study, we used only the gross and fine motor scales from these batteries.

In the reaching task, infants were seated in a specialist baby chair (Bloom Loft high chair) placed upright at a 90° angle from the cradle (horizontal) position, and secured with adjustable straps. Two cameras were used to record reaching behaviours, one placed at the midline, and the other at a 30° angle from the midline. Video data were coded off-line. The object which the infants were presented with was a stuffed tiger face toy (7 cm in diameter) which made a tinkling sound when shaken. On each trial the researcher, standing behind the baby chair, presented the toy at arm length in front of: i) the infant's left shoulder, ii) right shoulder, or iii) midline, until the infant touched the toy or 30 seconds had elapsed. Testing continued until a minimum of 9 and a maximum of 18 trials had been completed (and thus a minimum of 3 and a maximum of 6 trials at each presentation position). Infants were presented with a minimum of 9 reaching trials (3 trials in each of the reach locations) and a maximum of 18, and all made a reach response on virtually all of those trials. The order of presentation positions was counterbalanced across participants. Only lateral trials (left and right shoulder) were analysed. In order for a reach to be counted, infants had to either grasp the toy (with one or both hands) or to have brought one or both of their hands within a fist sized distance of the toy (the same criteria were used by [S6]). Unimanual reaches across the midline and reaches across the midline which formed part of a bimanual reach were both counted as midline crossing. Those participants who crossed their midline at least once were allocated to the "Crossers" group. The remaining participants who did not cross the midline once were allocated to the "Non-crossers" group.

EEG acquisition methods

Brain electrical activity was recorded continuously via a Hydrocel Geodesic Sensor Net (Electrical Geodesic Inc.), consisting of 128 silver-silver chloride electrodes evenly distributed across the scalp. The vertex served as the reference. The electrical potential was amplified with 0.1 to 100 Hz band-pass, digitized at a 500 Hz sampling rate, and stored on a computer hard disk for off-line analysis. The data were analysed off-line using NetStation 4.5.1 analysis software (Electrical Geodesic Inc.). Continuous EEG data were low-pass filtered at 30 Hz using digital elliptical filtering, and segmented in epochs from 100 ms before until 700 ms after stimulus onset. Segments with eye movements and blinks were detected visually and rejected from further analysis. Artefact-free data were then baseline-corrected to the average amplitude of the 100 ms interval preceding stimulus onset, and re-referenced to the average potential over the scalp. Finally, individual and grand averages were calculated.

On average, the number of trials considered for the analyses in Experiment 1 was 38 for uncrossed-hands posture and 35 for crossed-hands posture for the 6.5-month-old infants, and

37 for uncrossed-hands posture and 35 for crossed-hands posture for the 10-month-olds. In Experiment 2, the number of trials considered for the analyses was 32 for uncrossed-hands posture and 33 for crossed-hands posture. In Experiment 3, the average number of trials considered for analysis was 24 in the uncrossed-hands posture and 26 trials for the crossed-posture. In the Non-crossers group, the average number of trials used in the analyses were 26 in the uncrossed-hands posture and 27 in the crossed-hands posture. In the Crossers group, trial numbers were 22 and 25 respectively.

In order to select electrodes for ERP analysis we first identified scalp regions based on a continuous series of topographic maps across the recording epoch. These indicated stimulus-related hotspots, as expected, in areas surrounding C3 and C4 of the 10-20 system. Next, electrodes within these C3 and C4 areas were visually inspected in order to identify a representative sample of electrodes, symmetrical across the hemispheres, that showed the most pronounced SEP components as well as low levels of inter-participant variability. This resulted in slightly different but overlapping clusters of electrodes between the individual experiments. The electrodes considered were: 30, 36, 41, 103, 104, 105 in Experiments 1 and 2, and 29, 30, 35, 36, 104, 105, 110, 111 in Experiment 3 (see Figure S3).

ERP analyses

We compared posture conditions for the contralateral ERPs using paired t-tests at each sample point (2 ms intervals). In order to establish the precise onset of the effects of remapping on somatosensory processing, a sample-point analysis across 700 ms following stimulus onset was carried out to determine the time course over which the ERPs elicited in the posture conditions differed. We corrected for the autocorrelation of consecutive sample-points by using a Monte Carlo simulation method [S1]. This method began by estimating the average first order autocorrelation present in the real difference waveforms across the temporal window noted above (the mean first order autocorrelation at lag 1 was .99 for all datasets analysed). Next, 1000 datasets of randomly generated waveforms were simulated, each waveform having zero mean and unit variance at each time point, but having the same level of autocorrelation as seen on average in the observed data. Each simulated dataset also had the same number of participants and time-samples as in the real data. Two-tailed one-sample t-tests (vs. zero; $\alpha = .05$, uncorrected) were applied to the simulated data at each time point, recording significant vs. non-significant outcomes. In each of the 1000 simulations the longest sequence of consecutive significant t-test outcomes was computed. The 95th percentile of that simulated distribution of “longest sequence lengths” was then used to determine a significant difference waveform in the real data; specifically, we noted any sequences of significant t-tests in our real data which exceeded this 95th percentile value. This method thus avoids the difficulties associated with multiple comparisons and preserves the type 1 error rate at .05 for each difference waveform analysed.

Supplemental references

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