Neural body maps in human infants: Somatotopic responses to tactile stimulation in 7-month-olds

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ABSTRACT

A large literature has examined somatotopic representations of the body in the adult brain, but little attention has been paid to the development of somatotopic neural organization in human infants. In the present study we examined whether the somatosensory evoked potential (SEP) elicited by brief tactile stimulation of infants' hands and feet shows a somatotopic response pattern at 7 months postnatal age. The tactile stimuli elicited a prominent positive component in the SEP at central sites that peaked around 175 ms after stimulus onset. Consistent with a somatotopic response pattern, the amplitude of the response to hand stimulation was greater at lateral central electrodes (C3 and C4) than at the midline central electrode (Cz). As expected, the opposite pattern was obtained to foot stimulation, with greater peak amplitude at Cz than at C3 and C4. These results provide evidence of somatotopy in human infants and suggest that the developing body map can be delineated using readily available methods such as EEG. These findings open up possibilities for further work investigating the organization and plasticity of infant body maps.

Introduction

A prominent feature of human somatosensory cortex is its somatotopic organization, such that the body surface is represented in a topographic fashion across the postcentral gyrus of the parietal lobe. This organization was first described by means of intracranial stimulation in adult patients undergoing epilepsy surgery (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950), leading to sustained interest in the properties of body maps in the human brain. More recent research has demonstrated that the somatotopic organization of the somatosensory cortex in adults can be mapped non-invasively using several neuroimaging techniques. A good deal of this work has involved functional magnetic resonance imaging (fMRI), but other methods have also proven useful for mapping the neural representation of the body surface. In particular, studies employing electroencephalography (EEG) and magnetoencephalography (MEG) have shown that evoked responses to stimulation of different body parts are somatotopically organized across the postcentral gyrus: The maximal amplitudes of responses to stimulation of the toes and feet occur most medially, the lips and tongue most laterally, and the hands and fingers in between (Dowman and Schell, 1999; Hari et al., 1984, 1993; Heed and Röder, 2010; Nakamura et al., 1998).

Although somatotopic responses to stimulation of different areas of the body surface have been documented in adults, much less is known about the ontogenesis of cortical body maps in the first months and years of life. To date, studies examining somatosensory evoked responses in human infants have mainly involved stimulation of a single body part. The most commonly studied body part has been the hand, with stimulation being delivered through electrical stimulation of the median nerve or tactile stimulation of the palm or fingertip. This work has shown that primitive somatosensory evoked responses can be detected in infants born as early as 25 weeks (Hrbek et al., 1973; Taylor et al., 1996), with the major components of these responses undergoing marked changes in latency and morphology until around two years of age, at which point the responses begin to more resemble those observed in adults (Pihko et al., 2009).

In infants, responses to hand stimulation are typically greatest over the central contralateral region (Hrbek et al., 1973; Nevalainen et al., 2008; Rigato et al., 2014), which is also the pattern observed in adults. This finding of a lateralized response to hand stimulation provides initial evidence for a somatotopic organization of somatosensory cortex in human infancy. However, a more comprehensive understanding of somatotopy in the infant brain can only be provided by studies examining neural responses to stimulation of multiple body parts. Delineating a body map ultimately relies on showing an orderly projection of neural responses to different areas of the body surface.

Some clinically-oriented EEG research with preterm infants (29 - 32 weeks postconceptional age) has employed tactile stimulation of hands and feet (Milh et al., 2007; Vanhatalo et al., 2009). In these studies, brushing of the hands was associated with increased activity at lateral central electrodes presumed to overly the hand areas, while

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brushing of the feet was associated with increased activity at the midline central electrode, which is presumed to overly the foot area. These results suggest an early-developing somatotopic organization of somatosensory cortex, although the unique nature of preterm EEG precludes direct comparisons with the brain responses of older infants and adults. Specifically, these studies were able to rely on responses that were visible in the raw EEG signal, and conventional somatosensory evoked responses were not computed.

Another set of findings relevant to investigating neural body maps in infancy comes from EEG studies examining the scalp topography of mu rhythm (6-9 Hz) responses during production of hand and foot actions (Marshall et al., 2013). When 14-month-old infants carried out an action with their hand, mu rhythm desynchronization was greater at the lateral central electrodes (C3 and C4) than over the midline central electrode (Cz). Conversely, when infants carried out an action with their foot, mu rhythm desynchronization was greater over the midline electrode than over the more lateral central sites. This pattern of findings echoes results in adults showing a somatotopic response of the mu rhythm during action execution (Pfurtscheller et al., 1997).

In the present study, we examined whether somatotopic representations of the body can be studied using EEG and well-controlled, brief tactile stimuli delivered to the hands and feet of 7-month-old infants. To our knowledge, this is the first developmental study in which the evoked responses to stimulation of multiple body parts have been quantitatively compared. Based on the existing studies with preterm newborns (Milh et al., 2007; Vanhatalo et al., 2009), we predicted that the amplitude of the somatosensory evoked potential (SEP) to tactile stimulation of infants' feet would be greater at the midline central electrode (Cz) than at the more lateral electrodes (C3 and C4). For stimulation of infants' hands, we predicted that the amplitude of the SEP would be greater at C3 and C4 than at Cz. We also expected the amplitude of the response to hand stimulation to be maximal in the hemisphere contralateral to the tactile stimulation (Rigato et al., 2014).

Materials and Method

Participants

The analyses were based on data from 17 infants (mean age = 29 weeks; range = 25 to 34 weeks, 8 male). An additional 16 infants participated in the study, but were excluded from analyses because of hardware problems ($n = 3$), or an insufficient number of artifact-free trials (less than 8) in one or more of the four conditions due to fussiness ($n = 4$), or excessive movement ($n = 9$). All participating infants were born within three weeks of their due date and had not experienced chronic health issues or developmental problems. The study procedures were approved by the Institutional Review Board at Temple University. Written informed consent was provided by the infant's parent or guardian prior to the start of the experiment.

Tactile stimulation

Tactile stimuli were delivered to infants' hands and feet using an inflatable membrane mounted in a plastic casing (10 mm diameter; MEG International Services; see Fig. 1). A similar device for producing tactile stimulation has been used in prior EEG and MEG studies (Pihko and Lauronen, 2004; Pihko et al., 2009). Each membrane was inflated by a short burst of compressed air delivered via flexible polyurethane tubing (3 m length, 3.2 mm outer diameter). The compressed air delivery was controlled by STIM stimulus presentation software in combination with a pneumatic stimulator unit (both from James Long Company) and an adjustable regulator that restricted airflow to 100 psi.

For each tactile stimulus, a trigger generated by the stimulus presentation software caused a solenoid in the pneumatic stimulator to open for 10 ms. Expansion of the membrane began 20 ms after trigger onset and peaked 20 ms later. The expansion and subsequent contraction of

Fig. 1. Photo of the plastic membrane (10 mm diameter) used to deliver tactile stimulation to infants' hands and feet.

the membrane lasted around 60 ms in total. In order to ensure that the solenoid operation was not audible to the infant, the pneumatic stimulator unit and the regulator were located in an adjacent room, behind a closed door. The tubing carrying the compressed air entered the testing room through a small hole in the wall that was filled with soundproofing material.

Procedure

Infants were fitted with an EEG cap (see Section 2.4) while seated on their caregiver's lap. Four tactile stimulators were then attached to the infant, one at the midpoint of the dorsal surface of each hand and foot (see Fig. 1). The stimulators were attached using double-sided adhesive electrode collars in combination with medical tape, and were then covered with a tubular bandage to hold them firmly in place.

Infants received a total of 240 tactile stimuli, 60 to each hand and foot. The protocol consisted of 8 blocks, with 2 blocks of stimuli being delivered to each effector. During each block the infant received 30 stimuli to one of the effectors with an interstimulus interval that varied randomly between 3 and 4 seconds (in 200 ms increments). The order of the blocks was randomized between participants, and the full protocol lasted approximately 16 minutes. Throughout the presentation of the tactile stimuli, an experimenter sat facing the infant (60 cm away) and displayed a spinning toy resembling a windmill. The spinning feature was activated using a button located on the toy's handle. To prevent the observation of the button-press action from potentially influencing sensorimotor activation (Saby et al., 2013), the handle of the toy was hidden behind a black screen during presentation of the spinning action.

The experimental session was recorded on video for the purpose of coding any infant movement. During recording, a vertical interval time code (VITC) was placed on the video signal that was aligned with EEG collection at the level of one video frame. For each of the 240 tactile stimuli, the epoch from 1000 ms before to 1000 ms after the onset of the stimulus was coded offline as containing: (i) no movement, (ii) small movements, or (iii) large/repetitive movements. Epochs were coded as containing no movement if all parts of the infant's upper and lower limbs remained still for the entire 2000 ms coding period. Epochs were coded as containing small movements if the infant made small, isolated movements with one or several limbs, such as bending a finger or flexing an ankle. Epochs were coded as containing large movements if they included gross body movements or large, repetitive movement of a limb (e.g., kicking a leg or batting a hand). For the primary analyses, trials containing large (but not small) movements were excluded in order to maximize the numbers of trials in the evoked potential averages. However, supplementary analyses were also carried

out in which trials were excluded if any movement (large or small) occurred (see Supplementary Material).

EEG apparatus and methods

The EEG signal was recorded using a lycra stretch cap (Electro-Cap International) with 21 electrodes (Fp1, Fp2, F3, F4, Fz, F7, F8, C3, C4, Cz, T7, T8, P3, P4, Pz, P7, P8, O1, O2, M1, M2) placed according to the 10-20 system. Scalp electrode impedances were accepted if they were at or below 30 kilohms. The signal from each electrode was amplified using optically isolated, custom bioamplifiers with high input impedance (>1 GΩ; SA Instrumentation) and was digitized using a 16-bit A/D converter (+/- 5 V input range). Bioamplifier gain was 4000 and the hardware filter (12 dB/octave rolloff) settings were .1 Hz (high-pass) and 100 Hz (low-pass). The signals were collected referenced to the vertex (Cz) with an AFz ground.

Data processing and analysis were carried out using a combination of the EEG Analysis System from James Long Company and the EEGLAB toolbox for MATLAB (Delorme and Makeig, 2004). The EEG signals were re-referenced to an average of the left and right mastoids before being low-pass filtered at 30 Hz and segmented into 800 ms epochs. Epochs were excluded if they contained ocular or muscle artifact or if the amplitude of the EEG at central sites (C3, Cz, C4) exceeded ± 250 μV.

SEPs were computed for each participant relative to a prestimulus baseline of -100 ms to 0 ms, with time zero corresponding to the onset of membrane expansion at the skin surface. The mean numbers of trials included in the averages were 31 for stimulation of the left foot (range 16-54), 35 for the right foot (range 21-53), 27 for the left hand (range 8-51), and 34 for the right hand (range 16-57). Given that the purpose of the test was to assess infant neural somatotopic organization, the analysis focused on the amplitude of responses at central electrode sites (C3, Cz, C4) overlying sensorimotor cortex.

Results

Analyses of the SEPs focused on the most prominent feature of the grand-averaged waveforms, which was a positive component peaking around 175 ms after onset of the tactile stimulus (Fig. 2). In order to quantify this component, mean amplitude at the three electrode sites of interest were computed for each participant across the 100 to 250 ms time period. Mean amplitude was then compared across sites and stimulus conditions using a repeated-measures analysis of variance (ANOVA) with two factors—electrode (C3, Cz, C4) and body part stimulated (left hand, left foot, right hand, right foot). In the results below, Greenhouse-Geisser corrected values are reported when the sphericity assumption was not met.

There were no significant main effects of electrode, $F_{(2, 32)} = .721$, $p = .494$, or body part stimulated, $F_{(3, 48)} = .314$, $p = .815$. As predicted from the hypothesis of neural somatotopy, there was a significant interaction between these factors, $F_{(3.67, 58.63)} = 6.37$, $p < .001$. The results of post-hoc tests were consistent with a somatotopic patterning
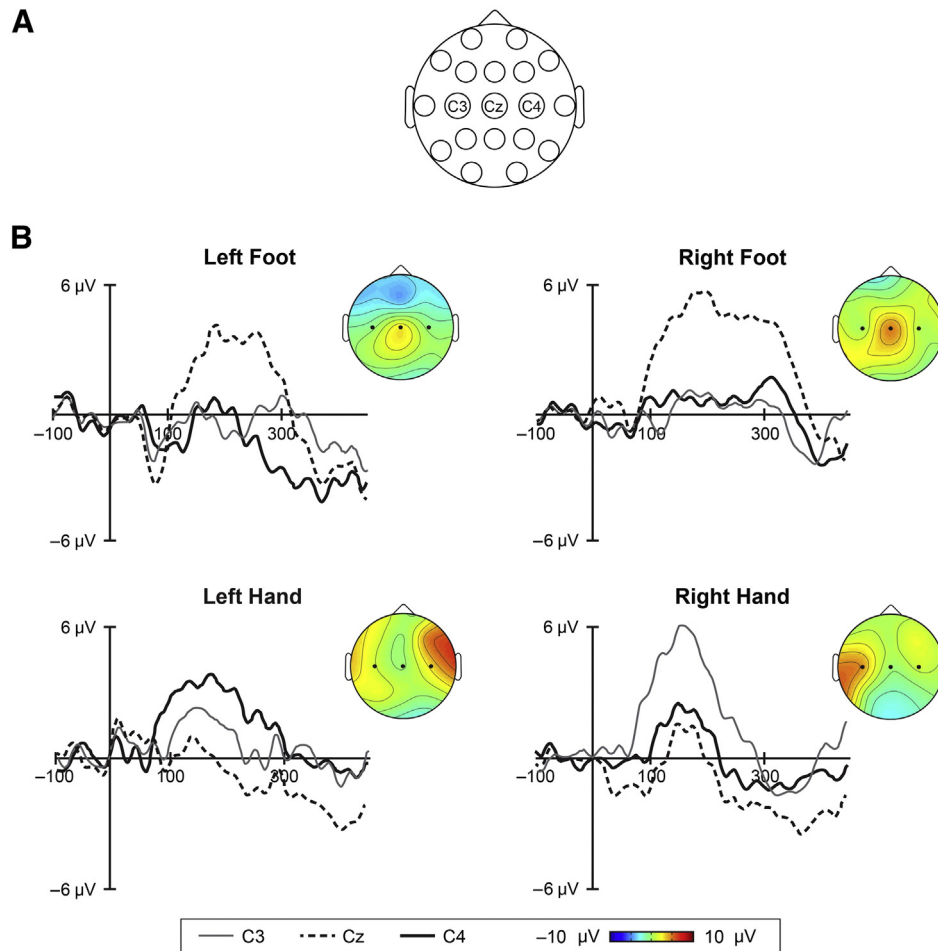
Fig. 2. Infant Somatosensory Evoked Potentials. (A) The location of the central electrodes included in the analysis. (B) Grand averaged responses at C3, Cz, and C4 in response to stimulation of each hand or foot. The tactile stimulus elicited a large positive component peaking around 175 ms that was organized somatotopically. For the left and right foot stimulation, the amplitude of this peak was greatest at the midline central electrode (Cz). For left and right hand stimulation, the amplitude of this peak was greatest at lateral central electrodes (C3 and C4). Scalp maps of mean amplitude between 100 to 250 ms are shown to the right. The central electrodes are indicated by black dots.

of the evoked response at central sites. For stimulation of the left foot, mean amplitude was significantly greater at Cz compared to C3 and C4, $t(16) = 3.48$, $p = .003$ and $t(16) = 2.84$, $p = .012$, respectively. Stimulation of the right foot was also associated with significantly greater mean amplitude at Cz compared to C3 and C4, $t(16) = 3.41$, $p = .004$, $t(16) = 3.28$, $p = .005$. For stimulation of the left hand, mean amplitude was significantly greater at C4 compared to Cz, $t(16) = 2.17$, $p = .046$, but mean amplitude at C4 was not significantly different from mean amplitude at C3, $t(16) = 1.23$, $p = .238$. For right hand stimulation, mean amplitude was significantly greater at C3 compared to both Cz, $t(16) = 3.38$, $p = .004$, and C4, $t(16) = 2.15$, $p = .048$.

Although our analyses focused on central sites, inspection of the scalp maps suggested that stimulation of each hand was also associated with a positive response in the evoked potential over the contralateral temporal region (Fig. 2). For stimulation of the right hand, mean amplitude from 100 to 250 ms post stimulus was significantly greater at the contralateral temporal electrode (T7) compared to the ipsilateral temporal electrode (T8), $t(16) = 3.18$, $p = .006$. For stimulation of the left hand, the difference between the mean amplitudes at T7 and T8 was not statistically significant, $t(16) = 1.61$, $p = .128$.

As noted in Section 2.3, the comparisons presented above involved trials in which the infants were either completely still or showed only small movements. Supplementary analyses examined the pattern of findings when only trials in which the infants were completely still were included. Although the numbers of trials in the averages were lower, the pattern of responses in these analyses remained very similar to the main results presented above (see Supplementary Material).

Discussion

Research using EEG and MEG methods with adults has demonstrated that somatotopic representations of the body in the human cortex can be mapped by examining the spatial patterning of evoked responses to somatosensory stimulation of different body parts (Baumgartner et al., 1993; Hari et al., 1993; Nakamura et al., 1998). However, relatively little is known about the electrophysiological signature of the body map in infancy, when evoked responses to somatosensory stimulation have a considerably different morphology than those in adults (Lauronen et al., 2006; Pihko et al., 2009).

In the present study we quantified the SEP at central electrode sites to brief tactile stimuli delivered to the left and right hands and the left and right feet of 7-month-old infants. We employed a within-subjects design in which each individual infant received stimulation to all four body parts. Hypothesizing that the topography of the SEP response would reflect a somatotopic pattern, we expected that the stimulation of infants' feet would be associated with a prominent response at the midline central electrode (Cz), which is assumed to overly the foot area of sensorimotor cortex. We also expected tactile stimulation of the hands to elicit a large evoked response at more lateral central electrodes (C3 and C4), which is assumed to overly the hand areas. While prior infant EEG work suggests a somatotopic pattern (Milh et al., 2007; Vanhatalo et al., 2009), previous studies have not directly compared the amplitude of SEPs across central electrode sites as a function of the stimulation of multiple body parts.

The SEP response to the tactile stimuli was primarily characterized by a large positive component peaking at around 175 ms. In line with our hypothesis, this component showed evidence of a somatotopic organization. Specifically, for stimulation of the left and right feet the mean amplitude of the positive component was significantly greater at the midline central electrode (Cz) than at the left and right central electrodes (C3 and C4). For stimulation of the left and right hands, mean amplitude was significantly greater at the contralateral central electrode compared to the midline electrode. For the right hand condition, mean amplitude at the contralateral site (C3) was also greater than mean amplitude at the ipsilateral electrode (C4). For left hand

stimulation, the difference in amplitude between the two lateral central electrodes was not statistically significant.

One possible explanation for the lack of a difference between C3 and C4 for left hand stimulation is that the number of trials that were free of large movements and artifacts was lowest for this condition, which may have resulted in a less than optimal signal to noise ratio for these comparisons. It is also possible that the brief tactile stimuli employed here may be less effective in eliciting a clearly lateralized response compared to more intense forms of stimulation. For instance, differences in the method and duration of the stimulation may be one reason that the waveforms in Rigato et al. (2014), which were elicited by a prolonged vibrotactile stimulus, have a somewhat different shape then those reported here.

As a starting point for clarifying the somatotopic organization of infant somatosensory evoked responses, the present study focused on a single age group (7-month-olds) and employed a low-density electrode array in combination with stimulation of four body parts (both hands and both feet) that were expected to be far apart in the neural body map. Future work could employ high-density EEG arrays or MEG methods in combination with findings from structural neuroimaging to build a more detailed and spatially precise picture of the wider infant body map in relation to the morphology of the developing brain. The use of such methods with infants of different ages promises to inform our understanding of developmental concomitants of changes in body maps, including changes associated with specific milestones in motor development.

Relevant studies with adults have demonstrated that particular aspects of motor experience can influence the fine-grained somatotopic organization of somatosensory cortex (Butefisch et al., 2000; Candia et al., 2003; Elbert et al., 1995). Given the extensive changes in motor skills that occur in infancy—including developments in grasping, crawling, and walking—infancy is an ideal period in which to explore questions about neuroplasticity and the effects of experience on the ontogenesis of the neural body map. Indeed, there is already some evidence that developmental changes in neural responses to hand stimulation correlate with developments in infants' reaching and grasping abilities (Gondo et al., 2001; Rigato et al., 2014). Relating aspects of motor development to changes in the neural representation of the body in infancy is also relevant to the study of developmental disorders of motor coordination, in which the organization of body maps may be altered (Papadelis et al., 2014; Wittenberg, 2009).

In prior EEG work we found evidence for a somatotopic pattern of mu rhythm (6-9 Hz) responses while infants carried out actions with their hands and their feet (Marshall et al., 2013). Although mu rhythm desynchronization during action production has different origins and functional correlates than the SEP, the somatotopic response of the infant mu rhythm is relevant to the current work in two specific ways. First, while the mu rhythm likely reflects the combination of activity from various sources across the sensorimotor region, one likely salient contribution is activity in primary somatosensory cortex (Arnstein et al., 2011; Hari and Salmelin, 1997; Ritter et al., 2009). Second, in prior work we found that infants' *visual observation* of hand and foot actions was also associated with a somatotopic pattern of mu rhythm desynchronization (Saby et al., 2013), which is consistent with theories proposing that body representations may be involved in infants' registration of cross-modal correspondences between self and other (Marshall and Meltzoff, 2014; Meltzoff, 2007). The present finding of an effector-specific response to somatosensory stimulation suggests that SEPs may be another useful tool (in addition to the mu rhythm) for studying self-other mapping in young infants. Relevant to this is the finding that EEG responses to somatosensory stimulation are affected by the simultaneous observation of matching or mismatching body parts in adults (Voisin et al., 2011); and similar research has been carried out with preschool-age children (Remijn et al., 2014).

Another interesting future extension will be to explore links between neuroscience measures of body representation in infancy, such

as reported here, and social behavioral measures. Human infants are prolific imitators, which entails selecting and activating the corresponding body parts of one's own body based on visual observation of the other person's body (Meltzoff, 1988; Meltzoff and Moore, 1997). The neural foundations of imitation in human infancy remain an open question.

Conclusions

The SEP response to brief, punctate tactile stimulation delivered to 7-month-old infants' hands and feet shows a somatotopic organization across central electrode sites. This suggests that infant neural body maps can be studied using readily available EEG methods in awake infants. Taken together with other relevant work, the current findings about the neural body map in human infants provide a foundation for a new line of research on the ontogenesis and plasticity of body maps and their relation to aspects of motor and social-cognitive development.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.05.097.

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