

Neural representations of the body in 60-day-old human infants

Andrew N. Meltzoff^{1*}  | Joni N. Saby^{2*} | Peter J. Marshall³

¹Institute for Learning & Brain Sciences, University of Washington, Seattle, Washington

²Department of Radiology, Children's Hospital of Philadelphia, Philadelphia, Pennsylvania

³Department of Psychology, Temple University, Philadelphia, Pennsylvania

Correspondence

Andrew N. Meltzoff, Institute for Learning & Brain Sciences, University of Washington (Box 357988), Seattle, WA 98195, USA.
Email: Meltzoff@uw.edu

Funding information

Supported by NSF grants SMA-1540619 (ANM) and BCS-1460889 (PJM).

Abstract

The organization of body representations in the adult brain has been well documented. Little is understood about this aspect of brain organization in human infancy. The current study employed electroencephalography (EEG) with 60-day-old infants to test the distribution of brain responses to tactile stimulation of three different body parts: hand, foot, and lip. Analyses focused on a prominent positive response occurring at 150–200 ms in the somatosensory evoked potential at central and parietal electrode sites. The results show differential electrophysiological signatures for touch of these three body parts. Stimulation of the left hand was associated with greater positive amplitude over the lateral central region contralateral to the side stimulated. Left foot stimulation was associated with greater positivity over the midline parietal site. Stimulation of the midline of the upper lip was associated with a strong bilateral response over the central region. These findings provide new insights into the neural representation of the body in infancy and shed light on research and theories about the involvement of somatosensory cortex in infant imitation and social perception.

1 | INTRODUCTION

The way in which the human body is represented in the adult brain is well documented and has been the source of key findings in cognitive neuroscience. Much of the work in this area has focused on neural representations in primary somatosensory cortex (S1), in which the body surface is represented in an orderly fashion along the postcentral gyrus. This somatotopic organization was initially identified using intracranial electrical stimulation in patients undergoing neurosurgery (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950), which provided data for the classic 'homuncular' maps in human sensorimotor cortex. Subsequent work has continued to elucidate the representation of the body in the adult brain using noninvasive methods such as functional magnetic resonance imaging (fMRI; Keysers, Kaas, & Gazzola, 2010; Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014), magnetoencephalography (MEG; Hari et al., 1993; Nakamura et al., 1998; Yang, Gallen, Schwartz, & Bloom, 1993), and electroencephalography (EEG; Heed & Röder, 2010; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997).

Taken together, the findings from adult participants have established that the feet are represented medially (within the longitudinal fissure), followed (in a medial to lateral direction) by the trunk, upper limbs, hands, lips, and tongue in primary somatosensory (S1) and motor (M1) cortices. Although much research has focused on these somatotopic maps (see Kaas, Jain, & Qi, 2002, for work with nonhuman animals), neural body maps have also been identified in other areas of the adult human brain (e.g. Cunningham, Machado, Yue, Carey, & Plow, 2013; Forna et al., 2018; Hari et al., 1993).

The neural body maps in S1 and M1 have long been known to be involved in one's own body awareness and actions. More recent work has suggested that they may also be involved in social perception. Neuroimaging studies with adults have reported somatotopic activation in premotor cortex during the observation of actions produced by other people (Buccino et al., 2001; Wheaton, Thompson, Syngienotis, Abbott, & Puce, 2004). Other studies with adults have shown that observing another person being touched is associated with activation of the observer's own somatosensory cortex (Bolognini, Rossetti, Fusaro, Vallar, & Miniussi, 2014; Gillmeister, Bowling, Rigato, & Banissy, 2017; Keysers et al., 2010; Kuehn, Mueller, Turner, & Schutz-Bosbach, 2014; Meyer, Kaplan, Essex, Damasio, & Damasio, 2011;

*Authors contributed equally.

Pihko, Nangini, Jousmäki, & Hari, 2010; Schaefer, Heinze, & Rotte, 2012). Such vicarious activation has been hypothesized to facilitate social cognition by enabling observers to relate to the bodily experiences of others (e.g. Hari & Kujala, 2009; Keysers et al., 2010; Meltzoff, Ramírez, Saby, Larson, Taulu, & Marshall, 2018).

1.1 | Human infant social-cognitive neuroscience

Despite an extensive literature on adults, surprisingly little attention has been given to the development of representations of the body in the human infant brain (Marshall & Meltzoff, 2015). Work with infants at about 1 year of age has suggested that they possess at least grossly organized neural body maps and, moreover, that these maps may have interpersonal properties akin to those in adults. These studies have mainly focused on the spatial distribution of mu rhythm desynchronization while infants performed (and observed) actions carried out with different body parts. Consistent with adult work, desynchronization of the mu rhythm in the central region was greater over lateral electrode sites (e.g. C3 and C4) in the contralateral hemisphere when infants performed right or left hand actions, and was greater over more medial sites (e.g. Cz) when they performed foot actions (de Klerk, Johnson, & Southgate, 2015; Marshall, Saby, & Meltzoff, 2013). The mu rhythm was also found to show this response pattern when 14-month-old infants simply observed an experimenter performing hand and foot actions (Marshall et al., 2013; Saby, Meltzoff, & Marshall, 2013).

This line of work on actions has been extended to examine infants' neural responses to observing another person's body being touched. In an MEG study with 7-month-old infants, Meltzoff et al. (2018) showed that watching another person's hand or foot being touched, even in the absence of infants being touched themselves, activated the infant's own somatosensory cortex. Taken together with the infant mu rhythm findings, this work motivates future studies examining the development of neural body representations and their potential role in early social-cognitive development. It also complements an emerging literature using behavioral measures (Bhatt, Hock, White, Jubran, & Galati, 2016; Somogy et al., 2017) that, together with the developmental neuroscience work, can inform our understanding of the infant body schema—a construct that refers to sensorimotor representations of the body that guide actions (Gallagher, 2005).

How early in development can we measure infant brain activity in response to tactile stimulation? A study with preterm infants (Milh et al., 2007) suggested that touching infants' hands and feet was associated with increased oscillatory activity in the EEG signal over lateral and midline central electrodes, respectively. This work had a number of limitations, including a small sample size, relatively uncontrolled tactile stimulation, and interpretations based on visible responses in the EEG record without conventional averaging and statistical analyses. Other studies of neural responses to tactile stimulation in the first half-year of life, while employing more rigorous designs and analyses, have relied on tactile stimulation of a single body part, typically the infant's hand (Nevalainen,

RESEARCH HIGHLIGHTS

- The neural correlates of the sense of touch have been understudied in infancy.
- We used tactile stimulation of three body parts to investigate the representation of the body in 60-day-old human infants.
- Tactile stimulation of infant lips, hands, and feet elicited distinguishable signatures in the infant EEG.
- Neural body representations are hypothesized to be a key component of infant imitation.
- Examining infant neural body representations sheds light on the earliest sense of self and foundations for social cognition.

Lauronen, & Pihko, 2014; Pihko et al., 2004; Rigato, Begum Ali, van Velzen, & Bremner, 2014). These studies have consistently found responses at central sites contralateral to the hand stimulated, which fits with the results from experiments with adults (Hari et al., 1993; Hari & Forss, 1999). A fuller understanding of the development of neural body maps in infancy requires experiments testing the spatial distribution of neural responses to tactile stimulation of multiple body parts.

Saby, Meltzoff, and Marshall (2015) carried out one such experiment by comparing evoked responses to punctate tactile taps to left and right hands and feet in 7-month-old infants. Statistical analyses of the somatosensory evoked potential (SEP) waveforms focused on a prominent positive component that peaked around 175 ms and was strongest over central electrode sites. As expected, the amplitude of this response to hand stimulation was greater at central sites contralateral to the side of stimulation (C3 or C4) than at the midline electrode (Cz). For stimulation of the feet, the amplitude was greater over the midline site than at the lateral sites. This suggests that measuring neural responses elicited by punctate touches of body parts may be a useful technique for exploring the development of infant neural body representations.

1.2 | Rationale for current experiment

In the current study, we modified the methods used by Saby et al. (2015) to examine neural representations of multiple body parts in a much younger age group, 60-day-old infants. This age was chosen because it is prior to the time that infants begin to systematically use their hands to reach for external objects, which begins at around 20 weeks of age, and is prior to the time they use their feet for locomotion. We also extended previous studies by assessing a body part that has heretofore not been explored—infants' lips. Representations of the lips are important given the centrality of lips to infant survival (sucking), language (speech articulations), affective behavior (emotional expressions), and preverbal social-communication (imitation of



facial acts in parent-child gestural interactions). The neural representation of infant lips is also interesting because although 60-day-olds will have seen their hands and feet as they contact objects, their own lips remain invisible to them. The current experiment provides the first assessment of multiple body parts including lips, hands, and feet, in a within-subjects design, in human infants as young as 60 days old.

Tactile stimulation was delivered to the left hand, left foot, and midline of the upper lip of the infant participants. Based on the organization of the somatosensory cortex in adults, and prior work with older infants, we expected that neural responses to left hand stimulation would be maximal over lateral central electrode sites in the contralateral (right) hemisphere, and that responses to left foot stimulation would be maximal over midline electrode sites. In contrast, responses to midline lip stimulation were expected to be bilaterally represented across the central region, in line with adult studies (Hashimoto, 1988; Hoshiyama et al., 1996; Tamura, Shibukawa, Shintani, Kaneko, & Ichinohe, 2008). We further hypothesized that stimulation of infants' lips would be associated with a particularly prominent response in the infant SEP.

A complete design would include stimulation of left and right hands, left and right feet, as well as lips; however, due to time constraints in working with 60-day-old infants, we stimulated only one hand and one foot in addition to the infants' lips. As noted above, prior infant studies have consistently indicated that evoked responses to hand stimulation are contralateral to the hand touched (Nevalainen et al., 2014; Pihko et al., 2004; Rigato et al., 2014; Saby et al., 2015). Considering this and the expectation that stimulation of both feet would be associated with activation of the same midline electrode sites (see results in Saby et al., 2015), we chose to stimulate only one side of the body in order to maximize the likelihood of obtaining sufficient trial numbers for all three body parts tested (hand, foot, and lip) within one session using the within-subjects design.

2 | MATERIALS AND METHODS

2.1 | Participants

Infants were recruited through a central subject pool at the university. Soon after birth, parents were sent a postcard inviting them to participate in infant studies. Parents who returned the card were entered into a computerized list and contacted later to solicit participation. Families received a nominal gift for participating. Predetermined criteria used for recruiting infants into the study were: normal gestational age (± 3 weeks of due date), typical birth weight (2.5–4.5 kg), and no medical or developmental problems according to parental report. Recruitment and experimental procedures were approved by the University Institutional Review Board and parental informed consent was obtained prior to data collection.

Data analyses are based on 25 8-week-old infants tested in a narrow age range to reduce intersubject variance ($M_{\text{age}} = 58.48$ days, $SD = 3.31$, range 52–64 days; 9 males). An additional 16 infants

participated, but did not provide a sufficient number of trials (at least 30) in one or more conditions due to early termination of the protocol/fussiness ($n = 7$) or excessive EEG artifact ($n = 9$). The criterion for the minimum number of accepted trials was set prior to the start of the study, based on pilot work showing that approximately 30 trials yielded an acceptable signal-to-noise ratio in the infant SEP using the current methods. The use of 30 trials also comports with the number of accepted trials reported in previous EEG literature on somatosensory responses in infants (Saby et al., 2015). The rate of attrition in this study is consistent with existing electrophysiology studies in the age range tested here (e.g. He, Hotson, & Trainor, 2009; Mai et al., 2012; van den Heuvel et al., 2015).

2.2 | Tactile stimulation

A hand-held wand was used to deliver tactile stimulation through light taps to the infant's upper lip, left hand, and left foot. The tip of the wand consisted of a bundle of optical fibers (~1.5 mm diameter) that were connected to a photoelectric switch. Half of the fibers emitted light; the other half detected the reflection of light. When the tip of the wand made contact with the skin surface, the changes in reflectance triggered an event mark in the EEG recording, allowing for accurate quantification of touch-related brain responses (Jousmäki, Nishitani, & Hari, 2007). The use of this specialized wand is preferable to other means of tactile stimulation, because: (a) it provides a more ecologically valid infant touch than electrical or vibrotactile stimulation, (b) it is more feasible than clipping inflatable diaphragms to infant lips, and (c) air-jet tactile stimulators used with adults are noisy and not practical with young infants.

A single trained experimenter delivered the tactile stimuli for all sessions. The stimuli were delivered to the midpoint of the dorsal surface of the hand and foot (comparable with published work; e.g. Saby et al., 2015) and to the midline of the upper lip, immediately below the philtrum and aligned vertically with the nose. Infants received up to 360 tactile stimuli, 120 stimuli to each of the three body parts, with an interstimulus interval of approximately 2 s. Stimuli were delivered in blocks of 40 trials to a single body part with the order of the blocks randomized across participants. Offline analyses of the digitized event marks showed that the interstimulus interval was around 2 s with some natural jitter ($M = 2.35$ s; range = 1.94–2.87). The protocol lasted approximately 15 minutes (not including cap placement) or until the infant became overly fussy. During the session, infants were held by their caregivers ($n = 23$) or were lying on an infant lounger ($n = 2$).

2.3 | Video recording and behavioral annotation

All sessions were videotaped for purposes of offline coding of infant movements. During the session, a vertical interval time code (VITC) was automatically inserted on the video recording, which was aligned with the EEG record to the precision of one video frame (33 ms). The video record from each session was reviewed using coding software (James Long Company, Caroga Lake, NY),

and trials in which the infant produced discernible body movements or there was poor contact between the wand and skin were marked and excluded from further analysis (see Section 2.4 for number of rejected trials).

2.4 | EEG methods

EEG was recorded using a stretch cap (EasyCap GmbH, Herrsching, Germany) with 25 electrode sites placed according to the international 10–20 system (Fp1, Fp2, F3, F4, F7, F8, Fz, C1, C2, C3, C4, C5, C6, Cz, T7, T8, P3, P4, P7, P8, Pz, O1, O2, M1, M2). Scalp electrode impedances were accepted if they were below 30 k Ω . The signal from each electrode was amplified using optically isolated, custom bioamplifiers with high input impedance (~1 G Ω ; SA Instrumentation, San Diego, CA) and was digitized using a 16-bit A/D converter (\pm 5 V input range). Bioamplifier gain was 5000 and the hardware filter (12 dB/octave rolloff) settings were 0.1 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 & Makeig, 2004). Continuous EEG data were low-pass filtered at 40 Hz and re-referenced to the average of the left and right mastoids. In a few cases ($n = 5$), a single mastoid served as the reference because the other contained excessive artifact. The preprocessed data were then segmented into epochs extending from -70 to 700 ms relative to stimulus onset. Epochs were visually inspected and excluded if they contained eye or muscle artifacts or if the amplitude exceeded $\pm 250 \mu\text{V}$ at one or more central (C1, C2, C3, Cz, C4, C5, C6), temporal (T7, T8), or parietal (P3, Pz, P4) electrodes. SEPs were computed for each participant and condition relative to a 70 ms prestimulus baseline. The mean number of trials included in the analyses were 70.32 for the left hand ($SD = 18.94$; range: 30–106), 71.28 for the left

foot ($SD = 20.82$; range: 30–118), and 67.20 for the lip ($SD = 22.55$; range: 31–103).

3 | RESULTS

Results are based on data from 25 60-day-old infants. A number of the participants were sleeping when they arrived at the laboratory or fell asleep prior to the start of the EEG session. Preliminary analyses of infants' EEG responses to tactile stimulation revealed similar responses in terms of the timing and location of the responses across the scalp in both states, see Supporting Information (SI). Therefore, all 25 infants were used in the main analysis, with supplemental analyses carried out separately for waking versus sleeping infants (see SI).

The SEP waveforms to stimulation of the three body locations were characterized by a positive deflection over central-parietal sites that peaked between 150 and 200 ms after stimulus onset (Figure 1). As predicted, visual inspection showed that lip stimulation elicited a bilateral response at central sites (C3/C5 in the left hemisphere and C4/C6 in the right hemisphere). For left hand stimulation, the positive deflection was most pronounced over central sites in the contralateral hemisphere (C4 and C6). For foot stimulation, the response was concentrated over the midline, and was slightly more posterior (Pz) compared to the responses for hand and lip (see Figure 2).

To capture this response pattern, mean amplitude in the 100–250 ms time window was computed for C3, C4, C5, C6, and Pz for each participant and each condition (lip, hand, foot). The amplitude at left central electrodes C3 and C5 was averaged to represent activity over the central region of the left hemisphere, and the amplitude at right central electrodes C4 and C6 was averaged to represent activity over the central region of the right hemisphere. Mean amplitude was then compared as a function of the stimulus conditions and

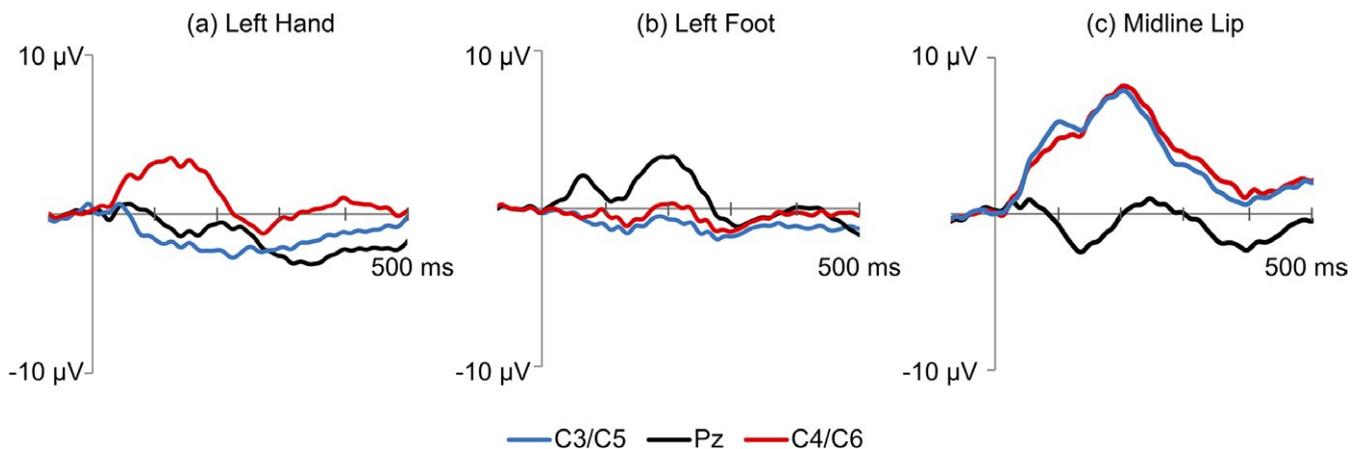


FIGURE 1 Grand average waveforms as a function of touch to (a) left hand, (b) left foot, and (c) midline of the upper lip. The waveforms are characterized by a positive deflection across central-parietal sites, peaking 150–200 ms from stimulus onset. For left hand stimulation, this deflection is observed in the central region at lateral electrode sites (C4/C6) contralateral to the hand touched. For left foot, it is observed at the midline (Pz). For the lip it is observed bilaterally, both at right (C4/C6) and left (C3/C5) central electrode sites

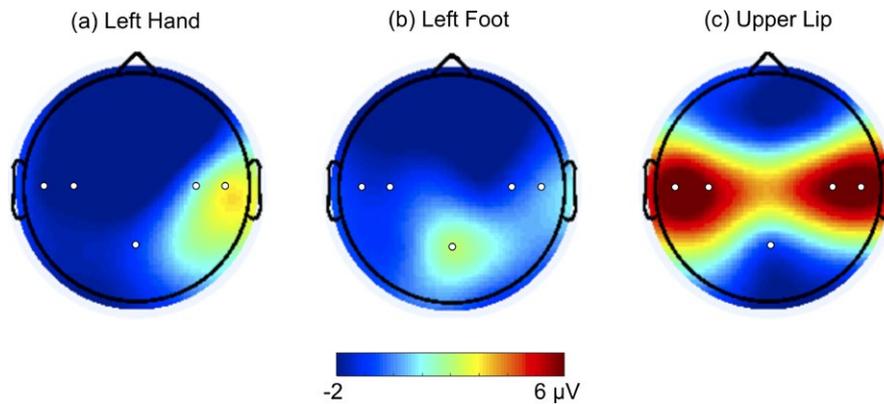


FIGURE 2 Scalp maps showing the spatial distribution of mean SEP amplitude over the 100–250 ms window following touch to the: (a) left hand, (b) left foot, and (c) midline of the upper lip. The locations of the electrodes included in the statistical analyses (C3, C4, C5, C6, and Pz) are indicated by white dots. The signature of touch to each body part is visually apparent: Contralateral activity for the touch to the hand, midline activity for the foot, and strong bilateral activity for the lip

regions using a repeated-measures analysis of variance (ANOVA) using within-subject factors of body part stimulated (lip, hand, foot) and scalp region (left, right, midline). In the results below, the Greenhouse-Geisser correction for non-sphericity has been used to adjust degrees of freedom as appropriate.

As expected, there was a significant main effect for the body part stimulated, $F(1.78, 42.75) = 9.57$, $p = 0.0006$, $\eta_p^2 = 0.28$, with greater mean amplitude in response to tactile stimulation of the lip than of the hand or foot. There was also a main effect for scalp region, $F(1.82, 43.67) = 8.45$, $p = 0.0011$, $\eta_p^2 = 0.26$, with greater mean amplitude over the right hemisphere than the left or midline. This was expected because left hand and foot were predicted to show activation over the contralateral (right) hemisphere, whereas the midline lip touch was expected to yield bilateral effects. Also as expected, there was a highly significant interaction between body part and scalp region, $F(3.04, 72.94) = 20.26$, $p = 1.0 \times 10^{-9}$, $\eta_p^2 = 0.46$. The results of post-hoc tests were in line with the hypothesis of neural somatotopy. Specifically, mean amplitude for tactile stimulation of the hand was significantly greater over the contralateral (right) than the ipsilateral (left) hemisphere, $t(24) = 4.70$, $p = 0.00009$, $d = 0.94$, or the midline, $t(24) = 2.98$, $p = 0.0066$, $d = 0.60$. For the tactile stimulation of the foot, amplitude was significantly greater for the midline than for the left, $t(24) = 4.30$, $p = 0.0003$, $d = 0.86$, or right, $t(24) = 2.35$, $p = 0.0275$, $d = 0.47$, hemispheres. As predicted, stimulation of the midline of the lip yielded a strong bilateral activation pattern, with greater amplitude over the left, $t(24) = 4.74$, $p = 0.00008$, $d = 0.95$, and right, $t(24) = 5.23$, $p = 0.00002$, $d = 1.05$, hemispheres than the midline.

4 | DISCUSSION

The current experiment examined neural representations of the body in 60-day-old human infants. EEG was recorded while infants received tactile stimulation of the midline of their upper lip, their left hand, and their left foot. The findings advance our knowledge in

three ways: (a) this is the youngest age to compare evoked responses to tactile stimulation of three body parts; (b) we assessed the neural representation of infant lips—a body part that plays an important role in infant survival, speech development, and social-emotional communication; and (c) the tactile stimulation method utilized enables good temporal control while resembling naturalistic touch more closely than (for instance) electrical stimulation of the median nerve or vibrotactile stimulation.

The SEP waveforms elicited by the tactile stimulation were characterized by a prominent positive component peaking around 150–200 ms after stimulus onset. As predicted for stimulation of the hand, the amplitude of this response was greatest over lateral electrodes (C4/C6), which overlie the 'hand region' as identified in older infants (Meltzoff et al., 2018) and adults (Ulmer, 2013). For stimulation of the foot, the response was largest over the midline parietal electrode (Pz), which approximately overlies the foot region identified in older infants (Meltzoff et al., 2018) and adults (Hari et al., 1993; Nakamura et al., 1998). For stimulation of the midline of the lip, the response was observed bilaterally over the central region, a pattern consistent with the literature on lip stimulation in adults (Disbrow, Hinkley, & Roberts, 2003; Hashimoto, 1988; Hoshiyama et al., 1996; Tamura et al., 2008).

We chose to stimulate the midline of the lip both to assess the expected bilateral representation and also because it is easier to touch the same midline point, using the nose and philtrum as landmarks, than it is to touch a specific point to the side. We selected the upper lip because it is more stationary than the lower one, which is stretched and displaced by jaw movements. Future infant studies could attempt to stimulate the lower lip or one side of the lip to test for finer-grained differentiations within the oral region. Adult MEG studies have been able to differentiate cortical responses to various parts of the mouth including the upper lip, lower lip, and tongue (Disbrow et al., 2003; Hari et al., 1993; Nakamura et al., 1998). Recent advances in MEG hardware and software have established the utility of MEG for brain imaging studies of human infants (Ferjan Ramírez, Ramírez, Clarke, Taulu, & Kuhl, 2017; Meltzoff et al., 2018),



and such technology may be useful in future investigations of infant neural body representations including of the mouth region.

Based on prior studies with adults (Dowman & Schell, 1999; Pfurtscheller et al., 1997) and older infants (Saby et al., 2015), one might have expected responses to foot stimulation to be maximal at the midline central electrode (Cz), but we observed them at the midline parietal electrode (Pz). This finding of increased activity over the parietal region following foot stimulation is not surprising given that S1, at least in adults, is angled such that representations of the feet are consistently found to be posterior to those of the hands and face (Dowman & Schell, 1999; Hari et al., 1993; Nakamura et al., 1998). Indeed, EEG studies with adults have observed activation at midline electrodes over both central and parietal regions following foot touch or electrical stimulation of the tibial nerve (Heed & Röder, 2010; Kakigi & Shibasaki, 1983; Kany & Treed, 1997). Consistent with these findings, in prior EEG work with older infants, stimulation of the feet was also associated with increased activity over the midline parietal region (see Saby et al., 2015, Figure 2 scalp maps). However, in that study with 7-month-old infants, the response to foot stimulation was greatest at Cz, as it is in adults. The lack of comparable activity at Cz in the current study using 60-day-olds may be due to two factors: (a) the neural representation of the foot in infants of this young age may be more posterior than it is in older infants and adults, and/or (b) immature features of the skull in these young infants, such as the open anterior fontanelle, may obscure or distort activity at the vertex (Cz). Future research with MEG, which is less sensitive than EEG to the immature features of the infant skull (Lew et al., 2013), would be useful for disentangling these potential explanations.

The statistical analyses demonstrated that the mean amplitude of the SEP responses was significantly greater for the lip compared to the hand and foot (see Figures 1 and 2). Research with adults shows that neural responses to stimulation of the lips, tongue, and fingertips—body parts that are overrepresented in the brain ('cortical magnification')—are stronger than to stimulation of body parts that have less neural tissue devoted to them such as the chin or trunk (Nakamura et al., 1998; Nevalainen, Ramstad, Isotalo, Haapanen, & Lauronen, 2006; Nguyen, Tran, Hoshiyama, Inui, & Kakigi, 2004). We speculate that the strong infant SEP response to lip stimulation reflects cortical magnification of the oral region in the infant sensory homunculus. Such enlarged lip representations may be engendered both by experience-dependent (prenatal lip movements) and experience-expectant (evolutionary preparation for speech articulations) processes.

This raises questions about developmental change and neuroplasticity. Changes in somatotopic body representations following training (or injury) are foundational findings in human cognitive neuroscience (Buonomano & Merzenich, 1998; Bütefisch et al., 2000; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995) as well as in animal models (Kaas & Rothmund, 2006). The plasticity of neural body maps in human infants has not been systematically investigated. Longitudinal studies could profitably examine whether there is an expansion of the neural regions devoted to fingertips as infants gain experience with precision grips, toes as infants begin to walk, and oral articulators as infants begin to speak.

The current findings regarding infant lips are especially intriguing. An EEG study with adults showed that neural responses to a touch on the lips were enhanced when participants listened to bilabial stops (/p/) versus speech sounds that did not involve the lips as the place of articulation (/k/), or nonspeech sounds made by the hands (finger snaps) (Shen, Meltzoff, & Marshall, 2018). In infancy, cross-modal effects involving lips have been documented in studies of auditory-visual speech perception (infant 'lip reading') and vocal imitation (Kuhl & Meltzoff, 1982, 1996). The role of somatosensory cortex in infant speech perception and production is of deep interest to developmental theory. For example, infants cannot see their own lips and may use tactile information—registering 'lips touching together'—to guide their production of bilabial phonetic units, as in 'mama' or 'papa'.

The study of infant neural body maps also sheds light on social-cognitive development. Before spoken language, bodily imitation is one of the primary mechanisms for infant learning from and about people (Meltzoff, 2013; Meltzoff, Kuhl, Movellan, & Sejnowski, 2009; Tomasello, 1999). In order to imitate, infants need to identify what part of the body to move as well as how to move it. Recognizing the correspondence between my hand and your hand is crucial for manual imitation. Cognitive models of imitation have hypothesized that such 'organ identification' is a key first step in infant imitation (Meltzoff & Moore, 1997). Historically, the neural and perceptual underpinnings of organ identification have been unstudied in infancy with a few exceptions (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Jubran, White, Chroust, Heck, & Bhatt, 2018; Somogy et al., 2017). Further studies on how the infant body is represented in the infant brain will contribute to our understanding of the mechanisms underlying infant imitation and the development of the infant body schema.

In adults, the neural representation of one's own body is theorized to influence social perception (e.g. Keysers et al., 2010). Building on this, a study with 7-month-old infants found that neural regions activated when infants were touched on their own hands (or feet) overlapped with the neural regions activated when infants merely observed someone else's hands (or feet) being touched (Meltzoff et al., 2018). Infants who saw the touch of another person's hands or feet showed activation in their somatosensory cortex not simply their visual cortex. These findings document shared neural representations for 'felt' touch and 'observed' touch in infants. Related work using a different methodology reported that infants' EEG responses to tactile stimulation were modulated by observing touch (Rigato et al., 2017). It thus seems likely that infant neural body maps are not simply registering the infant's own body but also the bodies of others, which could thereby contribute to preverbal social perception.

The neural representation of the body in the infant's brain may be a building block not only for infant imitation but also for infants' 'felt' connectedness between themselves and other people. Further study of infant neural body representations promises to provide insights into long-standing questions about infants' primitive sense of self and their capacities for rapid social learning.



ACKNOWLEDGEMENTS

We thank A. Humphreys and R. Brooks for assistance.

CONFLICT OF INTEREST

There are no conflicts of interest.

ORCID

Andrew N Meltzoff  <http://orcid.org/0000-0001-8683-0547>

REFERENCES

- Bhatt, R.S., Hock, A., White, H., Jubran, R., & Galati, A. (2016). The development of body structure knowledge in infancy. *Child Development Perspectives*, *10*, 45–52.
- Bolognini, N., Rossetti, A., Fusaro, M., Vallar, G., & Miniussi, C. (2014). Sharing social touch in the primary somatosensory cortex. *Current Biology*, *24*, 1513–1517.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., ... Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buonomano, D.V., & Merzenich, M.M. (1998). Cortical plasticity: From synapses to maps. *Annual Review of Neuroscience*, *21*, 149–186.
- Bütefisch, C.M., Davis, B.C., Wise, S.P., Sawaki, L., Kopylev, L., Classen, J., & Cohen, L.G. (2000). Mechanisms of use-dependent plasticity in the human motor cortex. *Proceedings of the National Academy of Sciences, USA*, *97*, 3661–3665.
- Cunningham, D.A., Machado, A., Yue, G.H., Carey, J.R., & Plow, E.B. (2013). Functional somatotopy revealed across multiple cortical regions using a model of complex motor task. *Brain Research*, *1531*, 25–36.
- de Klerk, C.C.J.M., Johnson, M.H., & Southgate, V. (2015). An EEG study on the somatotopic organisation of sensorimotor cortex activation during action execution and observation in infancy. *Developmental Cognitive Neuroscience*, *15*, 1–10.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.
- Disbrow, E.A., Hinkley, L.B., & Roberts, T.P. (2003). Ipsilateral representation of oral structures in human anterior parietal somatosensory cortex and integration of inputs across the midline. *Journal of Comparative Neurology*, *467*, 487–495.
- Dowman, R., & Schell, S. (1999). Innocuous-related sural nerve-evoked and finger-evoked potentials generated in the primary somatosensory and supplementary motor cortices. *Clinical Neurophysiology*, *110*, 2104–2116.
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307.
- Ferjan Ramírez, N., Ramírez, R.R., Clarke, M., Taulu, S., & Kuhl, P.K. (2017). Speech discrimination in 11-month-old bilingual and monolingual infants: A magnetoencephalography study. *Developmental Science*, *20*, e12427.
- Filippetti, M.L., Johnson, M.H., Lloyd-Fox, S., Dragovic, D., & Farroni, T. (2013). Body perception in newborns. *Current Biology*, *23*, 2413–2416.
- Fornia, L., Ferpozzi, V., Montagna, M., Rossi, M., Riva, M., Pessina, F., ... Cerri, G. (2018). Functional characterization of the left ventrolateral premotor cortex in humans: A direct electrophysiological approach. *Cerebral Cortex*, *28*, 167–183.
- Gallagher, S. (2005). *How the body shapes the mind*. New York: Oxford University Press.
- Gillmeister, H., Bowling, N., Rigato, S., & Banissy, M.J. (2017). Inter-individual differences in vicarious tactile perception: A view across the lifespan in typical and atypical populations. *Multisensory Research*, *30*, 485–508.
- Hari, R., & Forss, N. (1999). Magnetoencephalography in the study of human somatosensory cortical processing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*, 1145–1154.
- Hari, R., Karhu, J., Hämäläinen, M., Knuutila, J., Salonen, O., Sams, M., & Vilkmann, V. (1993). Functional organization of the human first and second somatosensory cortices: A neuromagnetic study. *European Journal of Neuroscience*, *5*, 724–734.
- Hari, R., & Kujala, M.V. (2009). Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews*, *89*, 453–479.
- Hashimoto, I. (1988). Trigeminal evoked potentials following brief air puff: Enhanced signal-to-noise ratio. *Annals of Neurology*, *23*, 332–338.
- He, C., Hotson, L., & Trainor, L.J. (2009). Development of infant mismatch responses to auditory pattern changes between 2 and 4 months old. *European Journal of Neuroscience*, *29*, 861–867.
- Heed, T., & Röder, B. (2010). Common anatomical and external coding for hands and feet in tactile attention: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *22*, 184–202.
- Hoshiyama, M., Kakigi, R., Koyama, S., Kitamura, Y., Shimojo, M., & Watanabe, S. (1996). Somatosensory evoked magnetic fields following stimulation of the lip in humans. *Electroencephalography and Clinical Neurophysiology*, *100*, 96–104.
- Jousmäki, V., Nishitani, N., & Hari, R. (2007). A brush stimulator for functional brain imaging. *Clinical Neurophysiology*, *118*, 2620–2624.
- Jubran, R., White, H., Chroust, A., Heck, A., & Bhatt, R.S. (2018). Sensitivity to hand structure information in infancy. Manuscript submitted for publication.
- Kaas, J.H., Jain, N., & Qi, H.-X. (2002). The organization of the somatosensory system in primates. In R.J. Nelson (Ed.), *The somatosensory system: Deciphering the brain's own body image* (pp. 1–25). Boca Raton, FL: CRC Press.
- Kaas, J.H., & Rothmund, Y. (2006). Reorganization of somatosensory and motor cortex following peripheral nerve or spinal cord injury in primates. In S.G. Lomber & J.J. Eggermont (Eds.), *Reprogramming the cerebral cortex: Plasticity following central and peripheral lesions* (pp. 285–296). New York: Oxford University Press.
- Kakigi, R., & Shibasaki, H. (1983). Scalp topography of the short latency somatosensory evoked potentials following posterior tibial nerve stimulation in man. *Electroencephalography and Clinical Neurophysiology*, *56*, 430–437.
- Kany, C., & Treede, R.-D. (1997). Median and tibial nerve somatosensory evoked potentials: Middle-latency components from the vicinity of the secondary somatosensory cortex in humans. *Electroencephalography and Clinical Neurophysiology*, *104*, 402–410.
- Keysers, C., Kaas, J.H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience*, *11*, 417–428.
- Kuehn, E., Mueller, K., Turner, R., & Schütz-Bosbach, S. (2014). The functional architecture of S1 during touch observation described with 7T fMRI. *Brain Structure and Function*, *219*, 119–140.
- Kuhl, P.K., & Meltzoff, A.N. (1982). The bimodal perception of speech in infancy. *Science*, *218*, 1138–1141.
- Kuhl, P.K., & Meltzoff, A.N. (1996). Infant vocalizations in response to speech: Vocal imitation and developmental change. *Journal of the Acoustical Society of America*, *100*, 2425–2438.
- Lew, S., Sliva, D.D., Choe, M.-s., Grant, P.E., Okada, Y., Wolters, C.H., & Hämäläinen, M.S. (2013). Effects of sutures and fontanelles on MEG and EEG source analysis in a realistic infant head model. *NeuroImage*, *76*, 282–293.
- Mai, X., Xu, L., Li, M., Shao, J., Zhao, Z., deRegnier, R.-A., ... Lozoff, B. (2012). Auditory recognition memory in 2-month-old infants as



- assessed by event-related potentials. *Developmental Neuropsychology*, 37, 400–414.
- Marshall, P.J., & Meltzoff, A.N. (2015). Body maps in the infant brain. *Trends in Cognitive Sciences*, 19, 499–505.
- Marshall, P.J., Saby, J.N., & Meltzoff, A.N. (2013). Imitation and the developing social brain: Infants' somatotopic EEG patterns for acts of self and other. *International Journal of Psychological Research*, 6, 22–29.
- Martuzzi, R., van der Zwaag, W., Farthouat, J., Gruetter, R., & Blanke, O. (2014). Human finger somatotopy in areas 3b, 1, and 2: A 7T fMRI study using a natural stimulus. *Human Brain Mapping*, 35, 213–226.
- Meltzoff, A.N. (2013). Origins of social cognition: Bidirectional self–other mapping and the 'Like-Me' hypothesis. In M.R. Banaji & S.A. Gelman (Eds.), *Navigating the social world: What infants, children, and other species can teach us* (pp. 139–144). New York: Oxford University Press.
- Meltzoff, A.N., Kuhl, P.K., Movellan, J., & Sejnowski, T.J. (2009). Foundations for a new science of learning. *Science*, 325, 284–288.
- Meltzoff, A.N., & Moore, M.K. (1997). Explaining facial imitation: A theoretical model. *Early Development and Parenting*, 6, 179–192.
- Meltzoff, A.N., Ramirez, R.R., Saby, J.N., Larson, E., Taulu, S., & Marshall, P.J. (2018). Infant brain responses to felt and observed touch of hands and feet: An MEG study. *Developmental Science*, <https://doi.org/10.1111/desc.12651>
- Meyer, K., Kaplan, J.T., Essex, R., Damasio, H., & Damasio, A. (2011). Seeing touch is correlated with content-specific activity in primary somatosensory cortex. *Cerebral Cortex*, 21, 2113–2121.
- Milh, M., Kaminska, A., Huon, C., Lapillonne, A., Ben-Ari, Y., & Khazipov, R. (2007). Rapid cortical oscillations and early motor activity in premature human neonate. *Cerebral Cortex*, 17, 1582–1594.
- Nakamura, A., Yamada, T., Goto, A., Kato, T., Ito, K., Abe, Y., ... Kakigi, R. (1998). Somatosensory homunculus as drawn by MEG. *NeuroImage*, 7, 377–386.
- Nevalainen, P., Lauronen, L., & Pihko, E. (2014). Development of human somatosensory cortical functions—What have we learned from magnetoencephalography: A review. *Frontiers in Human Neuroscience*, 8, 158.
- Nevalainen, P., Ramstad, R., Isotalo, E., Haapanen, M.-L., & Lauronen, L. (2006). Trigeminal somatosensory evoked magnetic fields to tactile stimulation. *Clinical Neurophysiology*, 117, 2007–2015.
- Nguyen, B.T., Tran, T.D., Hoshiyama, M., Inui, K., & Kakigi, R. (2004). Face representation in the human primary somatosensory cortex. *Neuroscience Research*, 50, 227–232.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, 60, 389–443.
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man*. New York: Macmillan.
- Pfurtscheller, G., Neuper, C., Andrew, C., & Edlinger, G. (1997). Foot and hand area mu rhythms. *International Journal of Psychophysiology*, 26, 121–135.
- Pihko, E., Lauronen, L., Wikström, H., Taulu, S., Nurminen, J., Kivitiel-Kallio, S., & Okada, Y. (2004). Somatosensory evoked potentials and magnetic fields elicited by tactile stimulation of the hand during active and quiet sleep in newborns. *Clinical Neurophysiology*, 115, 448–455.
- Pihko, E., Nangini, C., Jousmäki, V., & Hari, R. (2010). Observing touch activates human primary somatosensory cortex. *European Journal of Neuroscience*, 31, 1836–1843.
- Rigato, S., Banissy, M.J., Romanska, A., Thomas, R., van Velzen, J., & Bremner, A.J. (2017). Cortical signatures of vicarious tactile experience in four-month-old infants. *Developmental Cognitive Neuroscience*, <https://doi.org/10.1016/j.dcn.2017.09.003>
- Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A.J. (2014). The neural basis of somatosensory remapping develops in human infancy. *Current Biology*, 24, 1222–1226.
- Saby, J.N., Meltzoff, A.N., & Marshall, P.J. (2013). Infants' somatotopic neural responses to seeing human actions: I've got you under my skin. *PLoS ONE*, 8, e77905.
- Saby, J.N., Meltzoff, A.N., & Marshall, P.J. (2015). Neural body maps in human infants: Somatotopic responses to tactile stimulation in 7-month-olds. *NeuroImage*, 118, 74–78.
- Schaefer, M., Heinze, H.-J., & Rotte, M. (2012). Embodied empathy for tactile events: Interindividual differences and vicarious somatosensory responses during touch observation. *NeuroImage*, 60, 952–957.
- Shen, G., Meltzoff, A.N., & Marshall, P.J. (2018). Touching lips and hearing fingers: Effector-specific congruency between tactile and auditory stimulation modulates N1 amplitude and alpha desynchronization. *Experimental Brain Research*, 236, 13–29.
- Somogy, E., Jacquy, L., Heed, T., Hoffmann, M., Lockman, J.J., Granjon, L., ... O'Regan, J.K. (2017). Which limb is it? Responses to vibrotactile stimulation in early infancy. *British Journal of Developmental Psychology*. <https://doi.org/10.1111/bjdp.12224>
- Tamura, Y., Shibukawa, Y., Shintani, M., Kaneko, Y., & Ichinohe, T. (2008). Oral structure representation in human somatosensory cortex. *NeuroImage*, 43, 128–135.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Ulmer, S. (2013). Neuroanatomy and cortical landmarks. In S. Ulmer & O. Jansen (Eds.), *fMRI: Basics and clinical applications* (pp. 7–16). Berlin: Springer-Verlag.
- van den Heuvel, M.I., Otte, R.A., Braeken, M.A.K.A., Winkler, I., Kushnerenko, E., & Van den Bergh, B.R.H. (2015). Differences between human auditory event-related potentials (AERPs) measured at 2 and 4 months after birth. *International Journal of Psychophysiology*, 97, 75–83.
- Wheaton, K.J., Thompson, J.C., Syngienotis, A., Abbott, D.F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage*, 22, 277–288.
- Yang, T.T., Gallen, C.C., Schwartz, B.J., & Bloom, F.E. (1993). Noninvasive somatosensory homunculus mapping in humans by using a large-array biomagnetometer. *Proceedings of the National Academy of Sciences, USA*, 90, 3098–3102.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Meltzoff AN, Saby JN, Marshall PJ. Neural representations of the body in 60-day-old human infants. *Dev Sci*. 2018;e12698. <https://doi.org/10.1111/desc.12698>