DEVELOPMENTAL MEDICINE & CHILD NEUROLOGY INVITED REVIEW

Body maps in the infant brain: implications for neurodevelopmental disabilities

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ABBREVIATIONS

ASD	Autism spectrum disorder
MEG	Magnetoencephalography
MMN	Mismatch negativity
SEP	Somatosensory evoked potential
sMMN	Somatosensory mismatch negativity

This review and synthesis discusses recent work that has utilized brain imaging methods, such as the electroencephalogram (EEG) and magnetoencephalogram, to provide insights into the ways that the body is represented in the infant brain. One aspect of body representation concerns somatotopic maps of the body surface in somatosensory cortex. A good deal is known about the properties of these maps in adults, but there has been relatively little developmental work. Recent studies have provided new insights into the organization of infant neural body maps and have laid the foundations for examining their plasticity in relation to behavioral development. Other work has suggested that neural body maps may be involved in the registration of correspondences between self and other, with implications for early social development. Here, body representations are discussed in the context of preterm birth and autism spectrum disorder, providing novel perspectives relevant to developmental medicine and child neurology.

BODY MAPS IN THE INFANT BRAIN

Potential implications for developmental neurodisabilities

Rapid advances have been made in understanding how the body is represented in the developing brain.[1] Although much of the research in this area has been conducted with typically developing populations, the study of neural body representations has the potential to inform the understanding of developmental disabilities. Here, we first consider how studying infant brain responses to tactile stimulation can shed light on the representation of the body in the developing brain. We then present our proposal that body maps play a role in early psychosocial development by facilitating the detection of correspondences between self and other. These approaches lay the groundwork for designing novel research on developmental neurodisabilities, with the potential for illuminating both theoretical and applied issues.

Studies examining responses to touch in adult humans and animals present useful information about representations of the body in the brain. These studies have provided insights into the properties of somatotopic maps of the body in the somatosensory cortex, building on classic findings of the homuncular representation of the body in the adult human brain.[2] The homunculus is characterized by a somatotopic organization in which the feet, legs, and trunk are represented closer to the midline on the primary somatosensory and motor cortical strips, with the areas devoted to the hands, face, and mouth being more laterally positioned. A further property of the homunculus is that certain parts of the body (e.g. the hands and the mouth) are overrepresented in terms of the size of their cortical representations relative to the size of the body parts themselves. A good deal is understood about the neuroplasticity of somatosensory body maps in adults,[3] including activity-dependent effects on the size of the cortical representation of body parts.[4] However, less is known about the development of neural body maps and the various influences that shape the representation of the body in the infant brain.

Studies of brain responses to hand and foot stimulation in neonates born preterm and at term have suggested that a somatotopic cortical pattern develops prenatally. A study employing functional magnetic resonance imaging used robotic devices to drive ankle- and wrist-joint movement and to stimulate the mouth region in infants born preterm[5] (gestational age at birth 26–36wks; postmenstrual age at the time of testing 33–36wks). The main finding was that functional activity within the sensorimotor cortices in infants born preterm is somatotopically organized in a pattern roughly similar to the classic homuncular representation. Another recent study used electroencephalographic (EEG) methods to document somatotopic responses to tactile stimulation in neonates born between 34 and 42 weeks postmenstrual age and tested at a median postnatal age of 3 days.[6] In addition to affirming a pattern of somatotopy that conformed to the classic homuncular configuration, this study showed different maturational trajectories of early versus late components in the somatosensory evoked potential (SEP) elicited by tactile stimulation of the hands and feet. The scalp distribution of short-latency SEP components (e.g. P1 and N2 that occur in the first 200ms after tactile stimulus) was relatively unchanged by the extent of preterm birth, whereas later components of the SEP (P2 and N3, between 200ms and 400ms after stimulus onset) showed a specific maturational pattern with gestational age. This suggests that although somatotopy appears early, there is also developmental change in the cortical processing of tactile stimulation over the perinatal period.

Related evidence suggests that somatotopic body maps emerge prenatally through a combination of intrinsic factors and activity-dependent processes. A role for intrinsic factors is indicated by findings from a study of primates in which somatotopic maps developed in the somatosensory cortex, even in the context of disordered sensory inputs.[7] Other work also points to a role for fetal activity and intrauterine somatosensory stimulation in the patterning of early body maps.[8,9]

POSTNATAL DEVELOPMENT OF NEURAL BODY MAPS

Although there is a growing knowledge base about the initial body maps in the newborn human brain, much is still to be learned about postnatal neuroplasticity in body maps. The period of infancy is of particular interest. One novel suggestion is that social experience may play a role in shaping infant body maps.[10] For instance, in reciprocal imitation, parents act as social mirrors, reflecting infants' behavior back to them. This experience may sharpen or change pre-existing body maps as infants gain experience in seeing what felt actions look like.[10,11] Other key questions concern how neural body maps change with motor experience. For instance, does grasping experience alter the neural representations of hands? Does the onset of babbling or spoken language change the neural representation of the lips? How such changes in body representations in typically developing infants compare to those with motor, speech and language, or other disabilities is an area of special interest. To this point, most research in this area involving atypically developing populations has involved older children. For instance, one line of research has used magnetoencephalography (MEG) methods to document abnormal patterns of somatotopy in children (mean age 12y) with hemiplegic cerebral palsy.[12] Studies of infants could provide further information on the development of these cortical response patterns.

In our own work, we have been examining SEP responses at strategically selected age points in infancy with a view to developing and refining experimental protocols to examine plasticity in body representations across the first year of life. In a study of term-born 60-day-old infants, we analyzed responses to tactile stimulation of the infants' hands, feet, and lips.[13] This age was chosen because it precedes when infants begin systematically using their hands to reach for external objects, and is before they use their feet for locomotion. The tactile stimulus elicited a prominent positivity in the SEP that peaked between 150ms and 200ms after onset of the stimulus. As predicted, for hand stimulation, this positive response was strongest at the contralateral central electrode, whereas the positivity in the SEP elicited by foot stimulation was largest over the midline. Lip stimulation was associated with a strong bilateral response that was significantly larger in amplitude than the response to hand or foot stimulation. It is possible that the strong infant SEP response to lip stimulation reflects cortical magnification of the oral region in the infant sensory homunculus, which would also be associated with increased tactile sensitivity of part of the body. Further examination of infant lip representations is worthwhile, because of the essential involvement of lips in sucking, speech and language development, and the production of emotional expressions.

What this paper adds

- Somatotopic body maps develop prenatally through intrinsic and activity-dependent mechanisms.
- There is increasing interest in understanding postnatal plasticity in body maps.
- Body representations may be involved in the registration of preverbal, interpersonal relationships.

In two further studies, we probed body maps at 7 months of age. This age point was chosen because all infants could be tested during a waking state, further allowing us to develop protocols for examining visual-tactile interaction in relation to SEP responses. The work completed at this age point also laid the foundation for new studies of body maps in relation to the emergence of novel sensorimotor abilities in the second half of the first year of life.

In one study, we documented a somatotopic distribution of the SEP in response to punctate tactile stimulation of hands and feet of 7-month-old infants.[14] In a further study, we tested whether SEP responses to tactile stimulation of the body at 7 months of age are influenced by the observation of touch of another person's body. The rationale for this study comes from our proposal (outlined below) that body maps may play a role in the registration of correspondences between self and other in infancy. We systematically varied whether infants felt and observed touch to a matching versus non-matching part of the body of another person.[15] Analyses compared responses from electrodes overlying the hand and foot regions when the observed limb matched the stimulated limb (congruent condition) and when it did not match (incongruent condition). Cross-modal influences, as indicated by significant differences between the congruent and incongruent conditions, were observed in the late potential of the SEP (400–600ms; Fig. 1), as well as in the infant beta rhythm response. This is in line with the idea that self–other correspondences may be registered at the level of body part representations, with implications for the study of social development.

SOMATOSENSORY MISMATCH NEGATIVITY AS A NOVEL MEASURE OF BODY MAPS

Studies of SEP responses to stimulation of different body parts typically rely on a blocked design in which one part

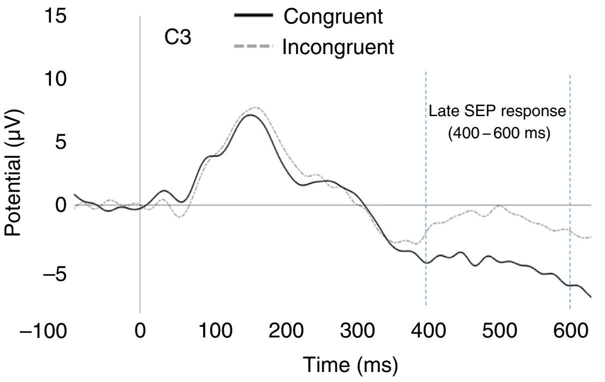

Figure 1: Somatosensory evoked potential (SEP) responses of 7-month-old infants from the left central electrode (C3) to tactile stimulation of the infants right hand viewing of touch to congruent (hand) and incongruent (foot) stimuli. Differences between conditions in the amplitude of the late SEP response (400–600ms) are indicated. Reprinted from Drew et al.[15] via Creative Commons license. [Colour figure can be viewed at wileyonlinelibrary.com]

of the body is repeatedly stimulated. In recent work, we took a different approach by employing a design in which frequent stimulation of one body part was interspersed with infrequent stimulation of another body part. This 'oddball' design allowed us to probe the utility of the mismatch negativity (MMN) response in the study of body representations. The MMN is most commonly used to explore responses to auditory stimuli, including in studies of music, phonetic perception, and infants' discrimination of native versus foreign speech sounds.[16] We adapted this technique to somatosensory stimulation in order to assess aspects of body representations in infants. Like the auditory MMN, the somatosensory MMN (sMMN) reflects fundamental change-detection responses that are elicited via oddball paradigms employing infrequent 'deviant' stimuli embedded in a stream of frequent standard stimuli.

In an EEG study of 6- to 7-month-old infants, we elicited sMMN responses to tactile stimulation of particular pairs of body parts that differed in their (postulated) separation in the neural body map in primary somatosensory cortex versus how separated they are on the body surface itself.[17] In adults, there is a discontinuity in the cortical representation of body parts regarding the location of the hand, face, and neck areas in primary somatosensory cortex. Specifically, the representations of the hands and the face are adjacent to each other in the neural homunculus, while the face and the neck are measurably further apart. This contrasts with the layout on the 3D body surface in which the face and neck are adjacent to one another and the hands are further away. We investigated whether, as in adults,[18] the infant sMMN is more sensitive to the distances between the body parts on the neural map, or whether this measure is more reflective of their degree of separation on the body surface. Two oddball contrasts were employed by delivering frequent tactile stimuli to the face (standard stimulus) and infrequent (deviant) tactile stimuli to either the hand or the neck. We employed a particular experimental design (the 'identity MMN' method) that controls for possible differences in tactile sensitivity between the different sites. Previous results from a range of studies indicate that the amplitude of the MMN is positively related to the extent of discrepancy between the standard and deviant stimuli. The amplitude of the infant sMMN response was greater for the contrast between face and neck stimulation than for the contrast between face and hand stimulation. One interpretation of this finding is that sMMN amplitude elicited by stimulation of two different body parts is more influenced by the degree of separation of the cortical representations of these body parts in somatosensory cortex than by the degree of separation on the 3D body surface. While further studies are needed to examine this question, this work suggests that the sMMN may be useful for informing developmental questions about body representations.

BODY MAPS AND SOCIAL PERCEPTION

We have advanced the novel idea that as one aspect of the developing body schema, body maps in the infant brain are involved in the registration of self–other correspondences, and as such may facilitate the earliest relationships and feelings of connectedness to others.[1] This line of research is founded in a broader psychological theory that infants gain an initial foothold into the social world through the understanding that other people are 'like me'.[19,20] It also builds on the proposal of a supramodal bodily act space that allows infants to match observed acts onto their own acts.[11] There has been great interest in the neural processes involved in such a matching process in adults,[21] with studies of infants revealing the complexities of how connections between action production and action perception might develop.[22]

The mechanisms through which body representations may be involved in connecting self and other in infancy are of burgeoning interest in developmental cognitive neuroscience. One relevant line of research has focused on the sensorimotor mu rhythm that occurs over central electrode sites in the alpha band (8–13Hz in adults, 6–9Hz in infancy). Work utilizing hand actions showed that the infant mu rhythm is desynchronized (reduced in amplitude) during the infant's own production of actions, and also while observing another person carry out a similar action.[23] We extended these findings by examining the topography of the infant mu rhythm response during the execution and observation of actions that had an identical goal (to press a button) but were carried out using different effectors (hands vs feet). This work showed that the infant mu rhythm displays a somatotopic response pattern during both action observation and action production.[24,25] Consistent with a prediction of somatotopy, we found that for infant hand actions, mu rhythm desynchronization was greater over lateral central electrodes (C3 and C4, which overlie the hand region in the homunculus), compared with the midline central electrode (Cz). For foot actions, there was greater mu desynchronization over the midline central site (which overlies the foot region) than over the lateral central electrodes. We found the same pattern not only for action execution by infants,[25] but also while infants observed an adult carry out hand or foot actions (Fig. 2).[24]

This finding of a somatotopically organized response of the mu rhythm during action observation can be interpreted in the context of theorizing about psychosocial development, particularly regarding social learning and imitation. Meltzoff and Moore[11] proposed that one key step towards successful imitation is 'organ identification', i.e. the identification of the body part used by that person to carry out the act. If infants are shown a hand gesture, they must localize their own hand in order to imitate correctly; if they are shown a lip or tongue movement and choose to imitate it, they must activate their own lips or tongue. We have described how studying infants' neural body representations can help to explain how infants solve the correspondence problem between self and other in order to accomplish such preverbal imitation.[10] In turn, the capacity for high-fidelity imitation is a powerful channel for social learning and for therapeutic interventions based on watching the performances of others. This connection between neuroscience findings and behavioral studies is an example of ongoing efforts to integrate basic neuroscience with the literature on cognitive and social development.[10]

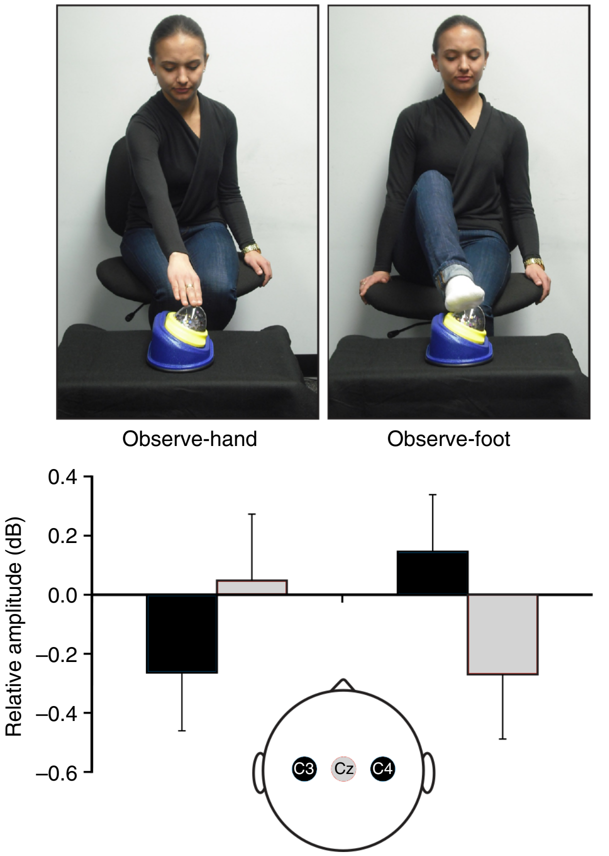

Figure 2: Somatotopic mu rhythm responses to action observation in 14-month-olds. Infants watched an adult reach towards and touch an object using either her hand or her foot. The goal of touching the domed surface was the same but the body part used was different. The pattern of activation over hand (electrodes C3/C4 black circles in head schematic) and foot (electrode Cz, gray circle) regions of sensorimotor cortex differed significantly according to whether infants saw a hand or a foot used. For hand actions, there was a greater reduction in mu amplitude over C3/C4 (black bars); conversely, for foot actions there was greater reduction in mu amplitude at Cz (gray bars). Figure is adapted from Saby et al.[24] via Creative Commons license. The model in the photograph gave written consent for the publication of this image. [Colour figure can be viewed at wileyonlinelibrary.com]

We recently employed MEG in combination with advanced source localization techniques to further probe the representation of the body in the infant brain, including interpersonal aspects. We mapped the spatiotemporal dynamics of cortical responses to tactile stimulation of hands and feet in 7-month-old infants.[26] This work provided evidence for effector-specific activation of the somatosensory cortex during infants' 'felt' touch of their own body and the 'observed' touch to other people's bodies. As expected, the response of the somatosensory cortex to observed touch to others was weaker than the response that was registered to direct touch to the infants' own skin. The MEG source-level analyses also provided information about other areas that were activated in the observed touch condition, including early visual areas and areas of the infant brain that may be associated with multisensory and self–other processing (e.g. extrastriate body area, fusiform body area, and the temporal-parietal junction). Taken together, these findings provide further support for the involvement of infant neural body representations in registering similarities between self and other, as postulated in Meltzoff's 'Like-me' theory that was based on behavioral data.[19,20] This line of work now opens the way to longitudinal investigations of the cortical basis of infant body perception and its relation to the emergence of more mature forms of interpersonal identification and social understanding during pediatric development.

The idea that body maps are involved in the early registration of correspondences between self and other[1,10] has potential implications for the early identification and clinical treatment of children with autism spectrum disorder (ASD). Studies have suggested differences in cortical processing of somatosensory stimulation[27,28] and in perceptual aspects of body representations in children with ASD,[29] although these findings have yet to be connected to theorizing about the role of body representations in self–other mapping.

An early disruption in self–other mapping would affect the ability to form and coordinate social representations, leading to a cascade of effects on social interaction, imitation, and communication. Drawing on a diverse set of neuroimaging and behavioral findings, Lombardo and Baron-Cohen have endorsed the idea that disruptions in

'Like-me' processing could result in an overly weak differentiation between self and other in children with ASD,[30] which may be a productive way of thinking about the disorder and the design of possible interventions.[31] Relevant behavioral findings have shown that older children with ASD display increased social affiliation and engagement towards an experimenter who is imitating them, compared with an experimenter who is acting contingently but carrying out a different action;[32] this replicates and extends similar work with typically developing infants.[10,33] Research has also uncovered a particular neural signature in the EEG when typically developing infants see someone else matching rather than mismatching their actions.[34] With increasing age, this preference for being closely imitated becomes less salient and appears to become a more subtle, implicit preference for others who are acting like the self. It is possible that in children with autism, this preference takes a different developmental course or does not naturally diminish to age-appropriate levels.

A deeper understanding of neural body representations and self–other connectivity in infants may help identify the key underlying mechanisms in successful interventions that emphasize the development of bodily and action coordination between children and adult therapists.[35] This kind of integration of neuroscience research and behavioral investigations across typically and atypically developing populations can both advance scientific theory and enrich clinical practice to help children.

CONCLUSION

A fertile new area of inquiry is beginning to focus on how body maps and other kinds of body representations are shaped through postnatal functional use, which may vary across individual infants due to disabilities or variation in opportunities to learn. Brain imaging methods such as EEG and MEG can be used to address such developmental issues in ways that have both theoretical and clinical significance.

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