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Researchers have examined representations of the body in the adult brain but relatively little attention has been paid to ontogenetic aspects of neural body maps in human infants. Novel applications of methods for recording brain activity in infants are delineating cortical body maps in the first months of life. Body maps may facilitate infants' registration of similarities between self and other – an ability that is foundational to developing social cognition. Alterations in interpersonal aspects of body representations might also contribute to social deficits in certain neurodevelopmental disorders.

Connecting self and other through neural body representations

The past decade has seen sustained interest in the neural processes involved in the perception of the human body. Studies in adults have illuminated the brain networks contributing to the sense of body ownership [1,2] and have documented cortical regions associated with perceiving the bodies of other people [3–5].

Historically, the representation of one's own body and the perception of the bodies of others have often been studied independently. Growing attention is now being paid to the interconnections between them [6–8], including the role of neural representations of the body in adult social cognition. There is evidence that the brain systems mediating the perceptual and sensory experience of one's own body are involved in social and emotional processes [9–14].

Although research with adults is providing insights into interpersonal aspects of body representations, developmental studies are lacking. One line of relevant behavioral research has examined infants' visual recognition of human forms, but much of this work has not considered infants' representation of their own body or how this might influence the perception and representation of the bodies of others (Box 1). Here we focus on somatotopic maps (see Glossary) in the infant brain as a foundational aspect of how the body is represented in early human development. Novel applications of methods for recording infant brain activity can foster an understanding of how cortical body maps emerge and develop and can illuminate their role in facilitating connections between self and other in the first weeks and months of life.

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Alongside research programs using infant magnetoencephalography (MEG) [15,16] and functional near-infrared spectroscopy (fNIRS) [17,18], refinements in electroencephalography (EEG) are stimulating new investigations of the neural processes involved in early social engagement [19–24]. One set of EEG findings highlighting social implications of body maps comes from studies showing that the sensorimotor mu rhythm displays a somatotopic response pattern during both action observation and action production in 14-month-old infants [25,26] (Figure 1). This provides neuroscience evidence that infants can register correspondences between their own body parts and the body parts of others. It also invites further studies of somatotopic organization in the infant brain and how it relates to key aspects of human development, including imitation [24,27].

Research on the mu rhythm continues to shed light on how infants perceive the actions of others in relation to their own capacities for action [24,28,29]. Here we outline a new direction for infant cognitive neuroscience that brings attention to aspects of neural organization that have been missed or underemphasized by the focus on the motor cortex and mirror neurons in past developmental work (Box 2). We describe ideas and research that are employing methods for recording cortical responses to somatosensory stimulation to probe the development of body maps in the brain. These methods for investigating body maps in human infancy provide connections to fertile areas of

Glossary

Body schema: in humans the body maps of preverbal children can be viewed as one building block of the complex psychological construct of the body schema, which refers to sensorimotor representations of the body that guide actions without awareness or the necessity of conscious monitoring [75]. The body schema is distinct from the concept of the body image, which is a later-occurring psychological achievement and refers to more conceptual, consciously accessible aspects of bodily awareness, including culturally appropriate appearances [76,77].

Mu rhythm: a brain oscillation in the alpha frequency range (8–13 Hz in adults, slightly lower frequencies in infants and children; e.g., 6–9 Hz) that can be detected over sensorimotor regions using EEG and MEG methods. The mu rhythm is desynchronized (reduced in amplitude) during action observation and action production in infants, children, and adults [24,28,78].

Somatosensory evoked potential (SEP): an averaged, time-locked response in the EEG signal at central electrode sites that is elicited by somatosensory stimulation. The SEP response can be elicited by various means including median nerve stimulation and tactile stimulation of the skin. The analogous response in the MEG signal is the somatosensory evoked field (SEF).

Somatotopic map: a spatial arrangement of neurons reflecting the topography of body parts. One well-studied example of a somatotopic map in the brain of humans and nonhuman primates is the homuncular representation of the body surface in SI [79]. The representation of the body surface in SI represents the end point of sensory pathways carrying information about touch (from the skin) and proprioception (from the joints of the body). These projections retain an orderly somatotopic organization as they ascend to SI from the periphery.

Box 1. Human infants' responses to depictions of the human body

There is increasing interest in studying developmental aspects of body representations [80]. Initial studies suggested that sensitivity to body structure in static images was not apparent until the second year of life [81]. However, recent behavioral work suggests that infants may be sensitive to disruptions in the configuration of the human body at significantly younger ages [82–84]. Accompanying these behavioral investigations is a small number of studies examining infant neural responses to experimentally manipulated disruptions in bodily representations in static and dynamic displays [85–88]. In terms of how infants represent their own bodies in relation to the bodies of others, recent behavioral work shows that newborns detect temporal and spatial correspondences between a video display of an infant's face being stroked and tactile stimulation of their own face [89,90]. An investigation using fNIRS suggests that temporal lobe activity differs in 5-month-old infants who viewed video displays of their body that were temporally contingent with their movements versus delayed [17].

neuroscience research in adults on somatotopy, plasticity, and cortical representations of the body. Although much is known about neural somatotopy in adults, developmental work in this area is virtually nonexistent. The novel idea being advanced here is that, as one aspect of the developing body schema, body maps in the infant brain are involved in the basic registration of self–other correspondences and thus may facilitate the earliest relationships and feelings of connectedness with others. We articulate a developmental position that addresses questions of neural plasticity and provides a fresh view on crucial aspects of social–cognitive development.

Neuroscience approaches to investigating body maps

Research on the representation of the body in the mammalian brain has often focused on the properties of somatotopic maps in the primary somatosensory cortex (SI). Extensive research with human adults as well as with nonhuman primates has examined questions concerning change in body maps in SI in response to changes in afferent input [30,31] and learning [32,33]. However, despite a large literature on somatotopic body maps in adults, little attention has been paid to how these maps are established and refined. Some developmental insights may be gleaned from neuroscience research with nonhuman species (Box 3) as well as from computational approaches. Although these existing lines of research can provide guideposts, advancing our understanding of the ontogenesis of body maps in the human brain requires the application of noninvasive brain imaging methods with young infants.

One promising approach for delineating cortical body maps in infants involves examining the topography of event-related responses to tactile stimulation applied to different parts of the body. The analysis of EEG and MEG responses to somatosensory stimulation has been useful for investigating neural body maps in adults [34–37] and is proving valuable for ontogenetic work. Several studies with infants have examined responses that are evoked by stimulation of one or both hands [38–41]. These responses are typically strongest at central electrode sites in the contralateral hemisphere, which echoes findings in

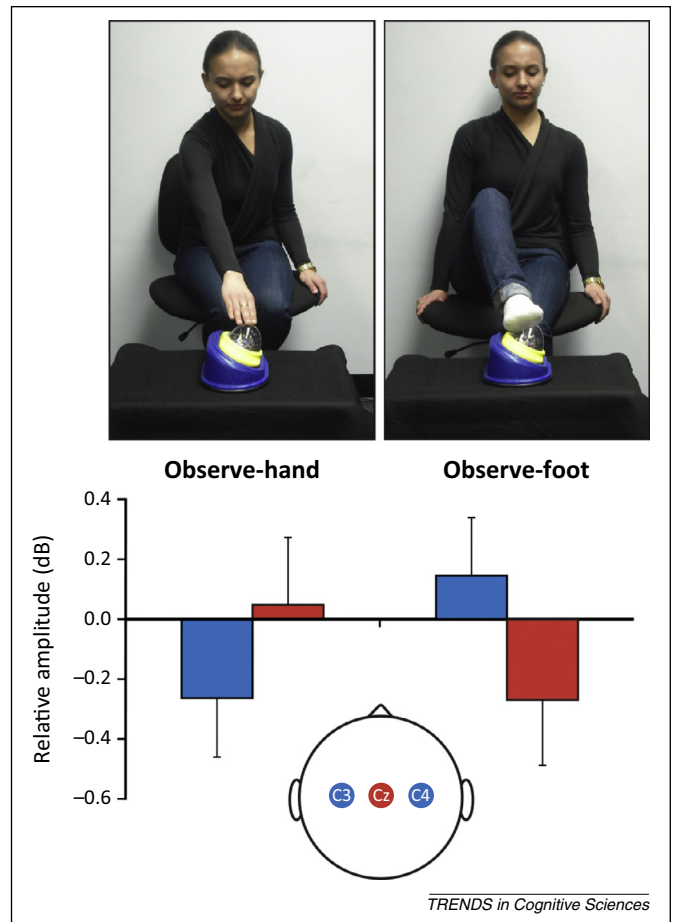


Figure 1. Somatotopic mu rhythm responses to action observation in 14-month-olds. Infants watched an adult reach toward and touch an object using either her hand or her foot. The goal of touching the domed surface was the same but the body part used was different. The pattern of activation over hand (electrodes C3/C4) and foot (electrode Cz) regions of the 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 at C3/C4 (left blue bar); conversely, for foot actions there was a greater reduction in mu amplitude at Cz (right red bar). Adapted from [26].

adults and is suggestive of a somatotopic organization of responses to tactile stimulation.

Although studies involving hand stimulation have been informative, a fuller delineation of infant body maps depends on the collection of brain responses to stimulation of a wider range of body parts. In two EEG studies of preterm newborns, tactile stimulation of the hands was associated with visibly increased oscillatory activity at lateral central electrodes while stimulation of the feet was associated with increased activity at the midline central electrode [42,43]. The stimuli used in these studies were relatively uncontrolled in terms of their precise location, intensity, and duration and the unusual profile of the preterm EEG signal [44] precludes comparisons with the brain responses of older children and adults.

In recent work we recorded the somatosensory evoked potential (SEP) elicited in response to brief (60 ms) tactile stimuli that were applied to specific areas on the hands and feet of 7-month-old infants using precisely controlled delivery methods [45]. Analyses focused on the magnitude of a prominent positivity in the SEP that peaked around 175 ms following onset of the tactile stimulus (Figure 2).

Box 2. Multiple body maps in the brain

Neural maps have been found in multiple areas of the mammalian brain, including the motor and somatosensory cortices [91]. Classical work on these maps in humans and other species focused on responses to tactile stimulation and execution of motor actions. Researchers have increasingly investigated the activation of motor areas during action observation, including somatotopically organized neural responses in adults during the viewing of the bodily movements of other people [92]. Alongside this line of research, a newer literature is emerging that highlights the role of the somatosensory cortex in social perception in adults, including somatotopic representations [9]. Most neuroscience studies of human infants have not caught up with the idea that the bodily representation in the somatosensory cortex may play a role in processing social signals about others. For instance, much of the extant research on the infant EEG mu rhythm has been interpreted within a motor framework. However, the mu rhythm is not solely (or even primarily) a motor rhythm [78,93,94]. The emphasis on motor influences may be unnecessarily limiting for work with human infants and broadening the view to include somatosensory processes in social perception promises to advance developmental theory [24,27]. Neuroscience investigations of infants will profit from considering multiple body maps (both somatosensory and motor) and their interactions (Box 4).

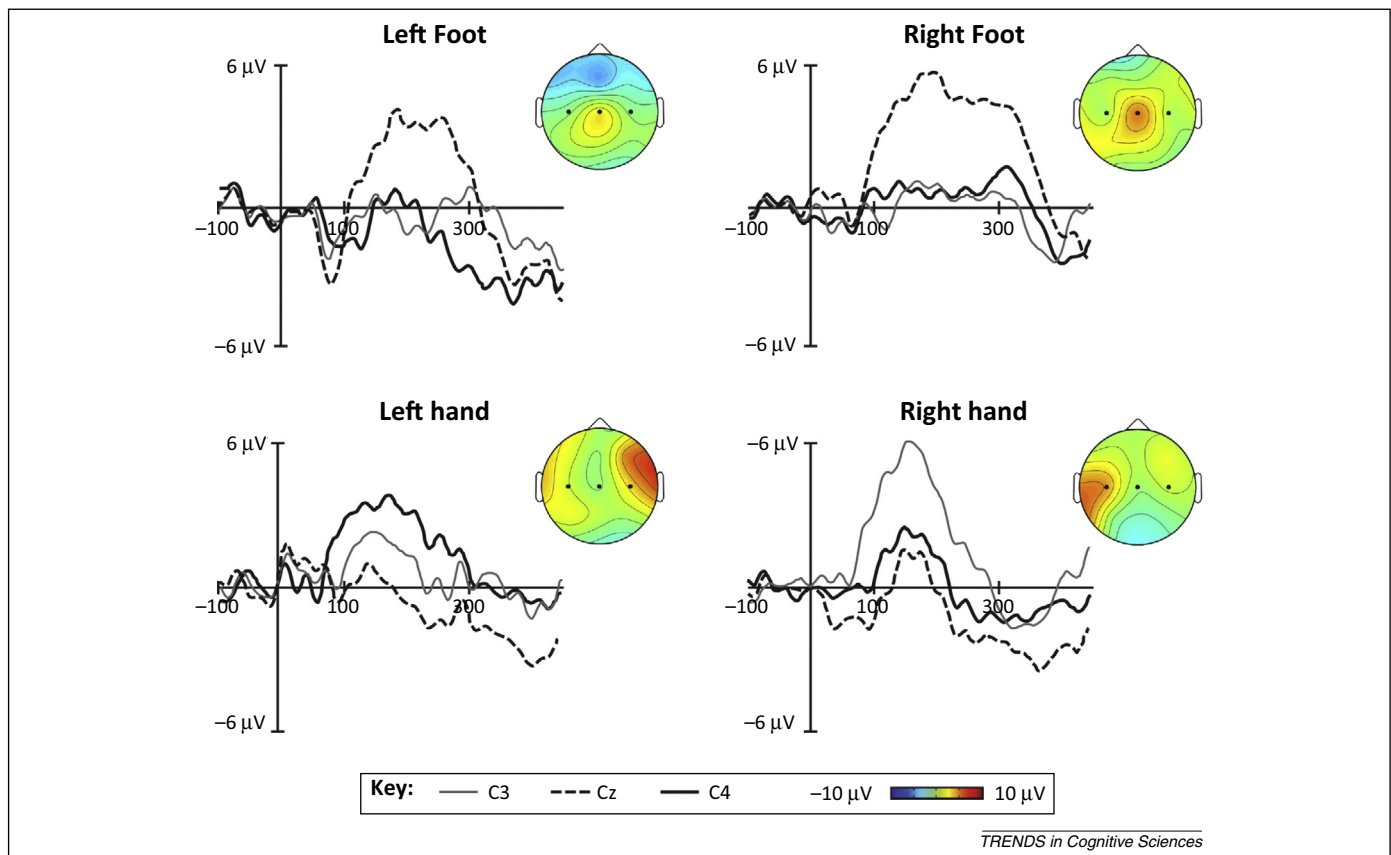
In response to hand stimulation, the amplitude of this positive component was significantly larger over the lateral central electrodes (C3 and C4) than over the midline central electrode (Cz). By contrast, stimulation of the foot elicited a significantly larger response at the midline site than at the lateral sites. This indication of somatotopy

Box 3. Insights from animal models

Classic behavioral neuroscience work on whisker barrels highlighted the role of afferent input in the somatotopic organization of the rodent somatosensory cortex [95], with more recent research illuminating the specific mechanisms involved [96,97]. Other work with rodents suggests that the development of somatotopy depends on sensory feedback from muscle twitches that are spontaneously generated by the spinal cord and subcortical structures [98,99]. A similar mechanism has been suggested to play a role in sensorimotor development in humans [42].

Top-down influences have also been shown to be important [100]. In both juvenile and adult monkeys, severing the median nerve (which carries sensory information from the hand to the brain) results in a haphazard pattern of innervation of the skin surface. This disordered pattern is propagated through afferent pathways to SI, where a jumbled representation of the hand replaces the normal somatotopic arrangement [101]. However, if the median nerve is severed very early in development a considerable degree of somatotopy is retained in SI [102], suggesting that early in development an existing cortical body map can direct the reorganization of thalamo-cortical projections following a disruption in the orderly patterning at the periphery [103].

in the infant SEP response suggests that measuring event-related scalp responses to brief, discrete tactile stimulation using EEG provides a practical and informative method for mapping the representation of the body in the infant brain. The ability to successfully elicit SEP responses from multiple body parts in awake infants



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Figure 2. Somatosensory evoked potentials elicited by tactile stimulation of 7-month-old infants' hands and feet. Discrete, computer-controlled tactile stimulation elicited a large positive component peaking around 175 ms that was organized somatotopically over central electrode sites. For left- and right-hand stimulation, amplitudes were greatest at the lateral electrodes (C3/C4). For left- and right-foot stimulation, the peak amplitude was greatest at the midline central electrode (Cz). Topographic maps show amplitude distribution across the scalp. Adapted and reprinted from [45] with permission from Elsevier.

also opens novel possibilities for examining neural aspects of cross-modal interactions (e.g., visuotactile) in early development.

Developing body maps in the human brain

We suggest that continued research on neural somatotopic organization in infancy can illuminate the mechanisms of social engagement that are crucial for typical human development [46]. In particular, research on infant body maps promises to shed light on a fundamental question in developmental psychology: how human infants develop a sense of themselves as individuals who are both similar to and, at the same time, distinct from other people. One psychological model of young children's social development, the 'Like Me' framework [47,48], proposes that infants gain an initial foothold on the social world through a felt similarity between their own bodily acts and the bodily acts of others. The perception of this similarity depends on a primitive body schema that is influenced by self-generated bodily activity beginning prenatally [27]. Infants are hypothesized to use this experience to generate an act space that links the behavior of others to the behavior of self through shared representations [49]. Although this claim has been made at a theoretical level, and there are supportive behavioral data from the study of imitation, there has been little exploration of the neural processes involved in the social matching behavior that constitutes infant imitation.

One way of advancing the understanding of connections between neural body maps and social processes is to examine whether cortical responses to tactile stimulation can be modulated by selective attention to the self or other. For adults, devoting attention to one's own hand modifies cortical responses to tactile stimulation [50], with effects at early stages of processing that are likely to reflect top-down modulation of SI [51]. Moreover, adult EEG responses to tactile stimulation are modulated according to the congruence between the stimulated body part and the observation of a matching or different body part of another person [52,53]. A MEG study with older children investigated responses to tactile stimulation of the index finger during the presentation of video clips showing another person being touched on either the hands or feet [54]. Activation over the hand areas of the somatosensory cortex was strongest when the tactile stimulation occurred during viewing of the hand-stimulation videos. This suggests possibilities for examining whether a similar modulation is present in infants.

It readily becomes apparent that there are a host of other novel questions about developing body maps in human infants (Box 4). One interesting issue concerns the spatial resolution at which body parts can be mapped in the infant brain. The extant developmental EEG research has used low-density scalp arrays and has involved body parts that are relatively distant from each other in cortical body maps. High-density EEG and MEG studies involving the stimulation of multiple body parts will prove useful for building a more detailed developmental picture of somatotopic neural organization.

Another question concerns how the organization of body maps may shift with changes in body morphology and

Box 4. Outstanding questions

- Can noninvasive neuroscience methods with high spatial resolution (e.g., MEG) be adapted to study the ontogenesis of fine-grained somatotopic organization of body maps in human infants? How many body parts can be clearly differentiated in infant neural body maps?
- Can advanced tools such as MEG differentiate between somatosensory and motor maps in human infants and illuminate the interactions between these maps?
- What are the neural temporal dynamics that occur when infants experience tactile stimulation?
- Do body maps show neuroplasticity in relation to changes in body growth and behavioral abilities, including developmental progressions in reaching, grasping, goal-directed acts, and expertise in tool use?
- How can neuroscience research on infant body maps be more deeply interwoven with psychological theorizing about the early development of the body schema and its role in social-emotional and cognitive development?

development. Given the transformations in behavioral skills that occur in infancy – including in grasping, crawling, and walking – infancy is an ideal period in which to explore questions about the effects of experience on neural body maps. There is some evidence that changes in the neural response to hand stimulation are correlated with developments in infants' reaching and grasping abilities [41,55]. A related topic concerns the effects of learning to use tools, a key part of infant development [56]. Expert tool use alters aspects of the body schema in both nonhuman primates [57] and human adults [58] and may do so in the developing infant brain. Another interesting question concerns how somatotopic representations combine with information about moment-to-moment changes in the positions of body parts as well as with representations of external (e.g., peripersonal) space [45].

Studying the ontogenetic aspects of body maps may also have implications for the study of atypical development, particularly autism spectrum disorder (ASD). It is clear that ASD is a heterogeneous, complex syndrome and that single-cause explanations will not suffice. At a broad level, however, it has been suggested that ASD involves a disruption in self–other processing that affects the ability to form and coordinate social representations, with cascading effects on imitation, communication, and interpersonal interaction [59]. Investigations of the role of neural body maps in facilitating self–other correspondences can complement ongoing lines of research on body representations in children with ASD [60–64]. Future exploratory work on the role of neural body maps in establishing interpersonal linkages has the potential to illuminate the mechanisms involved in interventions for ASD that emphasize bodily action coordination and mutual imitation between children and therapists [65–68].

Concluding remarks

Researchers across the rapidly growing field of developmental cognitive neuroscience are addressing various questions at the interface of brain, behavior, cognition, and developmental processes [69–71]. The inherent complexity of this interface necessitates integrative approaches in which findings from different domains can be leveraged to make

informed predictions about brain–behavior relations in human ontogenesis [72]. We suggest that developmentally oriented research on neural body maps holds particular promise for building bridges between literatures on the neural somatotopic organization in nonhuman species, adult cognitive neuroscience, and an emerging literature on body representations in human infancy. The study of infant body maps thus provides an ideal domain for examining developmental brain–behavior relations and neuroplasticity in humans.

We have highlighted a possible role of neural body maps in facilitating the registration of correspondences between self and other in early human development, before language. Further work in this area can advance the understanding of essential aspects of infant cognition such as the ability to imitate and learn from others via observation [73]. One important component of imitation involves visually identifying the part of the body used by another person to perform an action and then selecting the corresponding body part on one's own body to generate the imitative response [27,74]. The neural systems involved in the development of imitation remain under study. It is possible that body maps play a fundamental role in the processes that allow this powerful mechanism of social learning to unfold in human infancy.

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