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Body maps in the infant brain

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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.

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.

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

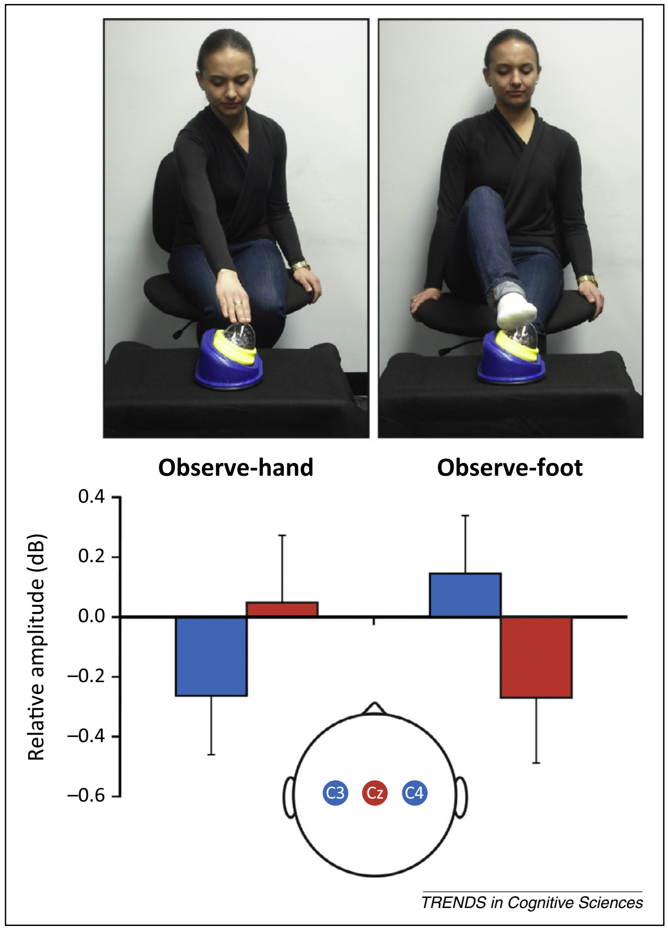

Figure 1. Somatotopic mu rhythm responses to action observation in 14-month-olds. Infants watched an adult reach toward and touch an object using either her hand or her foot. The goal of touching the domed surface was the same but the body part used was different. The pattern of activation over hand (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].

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).