

2

Importance of body representations in social-cognitive development: New insights from infant brain science

Andrew N. Meltzoff^{a,*}, Peter J. Marshall^b

^a*Institute for Learning & Brain Sciences, University of Washington, Seattle, WA, United States*

^b*Department of Psychology, Temple University, Philadelphia, PA, United States*

*Corresponding author: Tel.: +1-206-685-2045, e-mail address: meltzoff@uw.edu

Abstract

There is significant interest in the ways the human body, both one's own and that of others, is represented in the human brain. In this chapter we focus on body representations in infancy and synthesize relevant findings from both infant cognitive neuroscience and behavioral experiments. We review six experiments in infant neuroscience that have used novel EEG and MEG methods to explore infant neural body maps. We then consider results from behavioral studies of social imitation and examine what they contribute to our understanding of infant body representations at a psychological level. Finally, we interweave both neuroscience and behavioral lines of research to ground new theoretical claims about early infant social cognition. We propose, based on the evidence, that young infants can represent the bodily acts of others and their own bodily acts in commensurate terms. Infants initially recognize correspondences between self and other—they perceive that others are “like me” in terms of bodies and bodily actions. This capacity for registering and using self-other equivalence mappings has far-reaching implications for mechanisms of developmental change. Infants can learn about the affordances and powers of their own body by watching adults' actions and their causal consequences. Reciprocally, infants can enrich their understanding of other people's internal states by taking into account the way they themselves feel when they perform similar acts. The faces, bodies, and matching actions of people are imbued with unique meaning because they can be mapped to the infant's own body and behavior.

Keywords

Infant, Body representations, Neural body maps, EEG, MEG, Somatosensory cortex, Touch, Cross-modal, Imitation, Social cognition

1 Body representations and social-cognitive development: Insights from infant brain science

The overarching goals of developmental social-cognitive neuroscience are to: (i) enrich existing theories of child development, (ii) provide explanations for social and cognitive change, and (iii) stimulate new experiments and generate novel predictions beyond those deriving from behavioral studies alone. Neuroscience and behavioral studies of young children have often proceeded independently. We believe that the time is ripe for more thoroughly interweaving brain and behavioral measures to shed light on long-standing puzzles in child development. Our focus is on body representations in infancy, with the aim of showing how combining insights from brain science and behavioral science is leading to advances in theories of social-cognitive development.

Several areas of study in infancy have already profited from combining behavioral and neuroscience approaches. For example, classic behavioral experiments revealed precocious face and speech perception by young infants, and these domains have recently become hot topics for infant brain studies, which has, in turn, advanced theory (e.g., [Johnson et al., 2015](#); [Kuhl et al., 2014](#)). Here, we focus on a related but different topic—the building blocks for social cognition. Specifically, we focus on body representations in the infant brain and the importance of these representations for social imitation and interpersonal relations. We review and synthesize this burgeoning line of work and then draw broader theoretical inferences for the development of human social cognition.

2 Centrality of body representations

The ways that the body is represented in the brain have been the subject of investigation across multiple areas of neuroscience. A chief source of information derives from studies examining brain responses to touch, which have highlighted the presence of somatotopically organized representations of the body in somatosensory cortex in adult subjects (e.g., [Kaas, 1997](#); [Kaas et al., 2001](#)). An extensive literature using adult human and nonhuman primates has documented the properties of these body maps, including demonstrations of their plasticity ([Buonomano and Merzenich, 1998](#); [Elbert et al., 1995](#); [Kaas, 1991](#)). However, the existence and development of these neural body maps in human infants has been understudied.

Although developmental neuroscience approaches have not traditionally been applied to study the neural representations of the body in human infants, several exclusively behavioral approaches have been used to explore infants' perception of their own and other people's bodies. One prominent line of work using visual

stimuli has investigated infants' visual recognition of intact versus distorted body configurations (Jubran et al., 2019). Other work has explored infants' reaching to the parts of their bodies that are being tactilely stimulated (Leed et al., 2019; Somogyi et al., 2018) and infants' spontaneous self-touching (DiMercurio et al., 2018).

Additional knowledge about young infants' processing of the body derives from behavioral experiments on: (i) infant imitation, which bears on infants' perception of their own bodies in relation to those of other people (Meltzoff, 2007, 2013; Meltzoff and Moore, 1997), (ii) visual-tactile/proprioceptive contingency detection (Bahrick and Watson, 1985; Rochat and Morgan, 1995), and (iii) body-related multisensory integration (Filippetti et al., 2013, 2015; Zmyj et al., 2011). Alongside these behavioral approaches, new neuroscience techniques are beginning to be used to assess infants' neural representations of bodies (e.g., Marshall and Meltzoff, 2014, 2015; Meltzoff et al., 2018; Rigato et al., 2014, 2019).

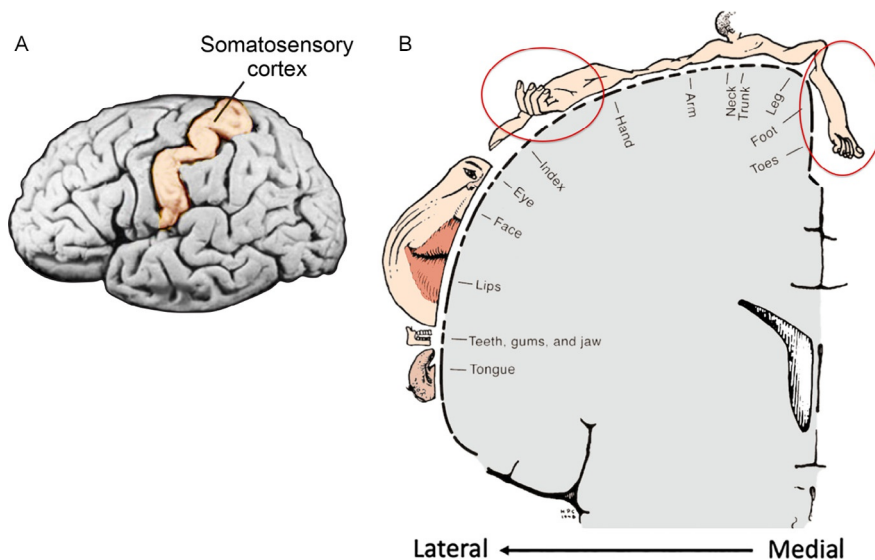
Our own interest in the neuroscience of body representations derives from the fact that work in this area can shed light on the origins and development of interpersonal connections and the feelings of affinity between self and other in infancy. We have advanced the novel idea that neural body representations play a role in the registration of self-other correspondences, and as such, may facilitate the earliest interpersonal relationships (Marshall and Meltzoff, 2015; Meltzoff and Marshall, 2018). This line of research is founded in a theoretical perspective that infants gain an initial foothold on the social world through the understanding that other people are "like me" in bodily structure and activity (Meltzoff, 2007, 2013).

We are further interested in the neuroscience of infant body representations because it provides a test case for enhancing knowledge about cortical plasticity and the interplay between brain development and experience (Marshall, 2015). Finally, we have argued that the exploration of body representations can inform research on developmental disabilities (Marshall and Meltzoff, 2020), particularly autism spectrum disorder, which is associated with impairments in somatosensory processing and the organization of cortical responses to tactile stimulation (Gaetz et al., 2017; Ropar et al., 2018), as well as with impairments in high-fidelity body imitation (Dawson et al., 1998; Edwards, 2014; Nadel, 2014; Toth et al., 2006).

In this chapter, we will articulate current progress and the future promise of integrating experiments on infant neural body representations with related behavioral studies of the body. We focus on various themes that we have addressed in our own empirical studies of brain and behavior to illustrate the added benefits of integrating work across these domains. Our overarching aim is to provide a more comprehensive picture of the development of social cognition than could be afforded by either neural or behavioral studies in isolation.

3 Neural body maps in human infants

The classical description of how the body is represented in the human brain derives from the work of Penfield and colleagues (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950) (Fig. 1). Penfield initially described the "homuncular"

**FIG. 1**

The primary somatosensory cortex processes touch and proprioceptive information, and is located in the central area of the brain, posterior to the central sulcus (A). Penfield showed that the primary somatosensory cortex is organized in a somatotopic fashion (B). To facilitate comparisons to the infant neuroscience work discussed in this chapter, we note that the foot region is situated at midline and that the hand and lip regions are progressively more lateral.

Modified from Penfield, W., Rasmussen, T., 1950. The cerebral cortex of man: A clinical study of localization of function. Macmillan, New York.

organization of the post-central gyrus (primary somatosensory cortex, S1) and the pre-central gyrus (primary motor cortex, M1). Further work has since shown additional neural representations of the body in other brain areas. Until recently, most of this research involved adults, with few developmental investigations of neural body representations in human infants or children. Recent years have seen this area rapidly becoming a hotbed of activity in developmental social-cognitive neuroscience (for reviews, see [Marshall and Meltzoff, 2015, 2020](#); [Rigato et al., 2019](#)).

In one study designed to explore infant neural body representations, we tested 7-month-old infants using electroencephalography (EEG) ([Saby et al., 2015](#)). We used a computer-controlled device that delivered brief, punctate taps to specific areas of the infants' left hand, left foot, right hand, and right foot ([Fig. 2](#)). We hypothesized that the topography of the infant somatosensory evoked potential (SEP) would reflect a broad somatotopic pattern as described in Penfield's homuncular map. Following Penfield's map, we predicted that when the infant's body was touched, there would



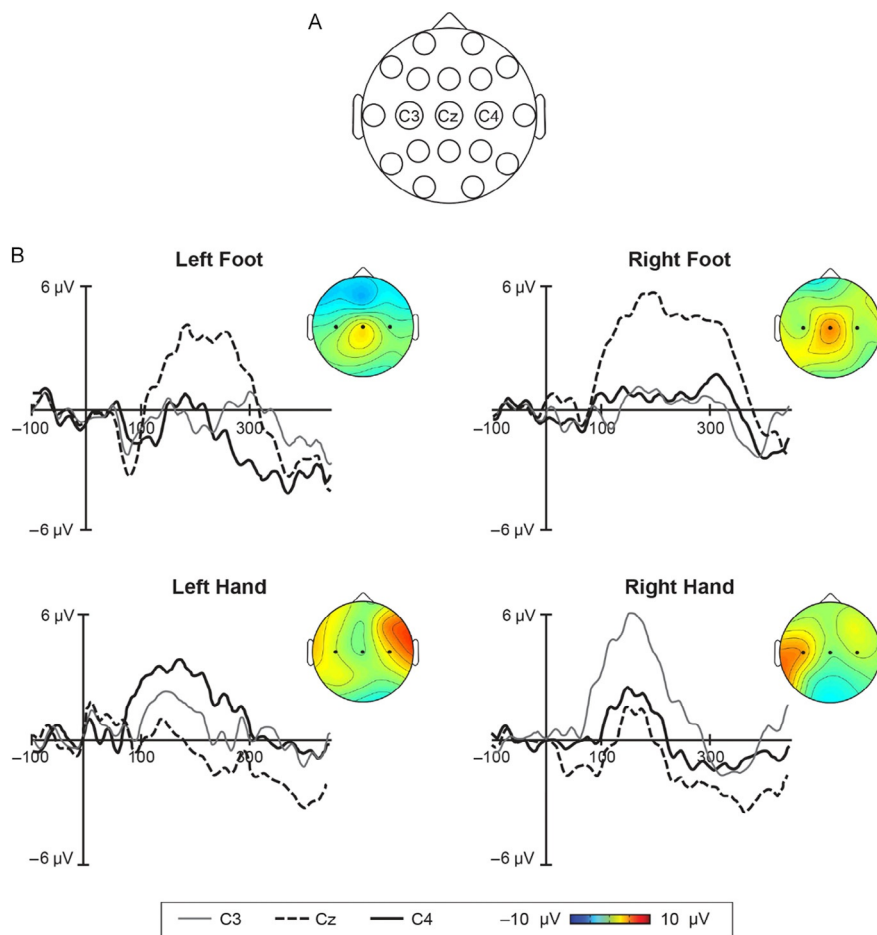
FIG. 2

Computer-controlled device for administering punctate tactile stimulus to infant body parts (in this case, the foot). A burst of compressed air delivered through the tubing inflates the membrane. The compressed air delivery is controlled by stimulus presentation software in combination with a pneumatic stimulator unit and an adjustable regulator that controls airflow.

*Reproduced with permission from 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.*

be increased activity at central electrodes that overlie primary somatosensory cortex. The more fine-grained prediction was that stimulation of infants' feet would be associated with a prominent response at the midline central electrode (Cz), which overlies the foot region, whereas tactile stimulation of the hands would yield a response at more lateral central electrodes (C3 and C4), which overlie the regions for the right and left hand respectively. The results were in line with this hypothesis.

Analyses focused on the magnitude of a prominent positivity in the evoked potential that peaked around 175 ms following onset of the tactile stimulus (Fig. 3). In response to hand stimulation, the amplitude of this positive component was significantly larger over the lateral central electrodes (C3/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. Furthermore, it has been established from work with adults that the anatomical wiring is such that when, for example, the left hand receives tactile stimulation, the contralateral hemisphere (right) is activated. This pattern of contralateral activation was obtained in the infant data (Fig. 3). Taken together, the indication of somatotopy in the infant SEP response demonstrated that measuring event-related scalp responses to discrete tactile stimulation using EEG provides a practical and informative method for beginning to explore neural body maps in infancy.

**FIG. 3**

7-month-old infant somatosensory evoked potentials in response to touch to four body parts. The location of the central electrodes (C3, Cz, C4) included in the analysis is shown (A). The tactile stimulus elicited a large positive component that was organized somatotopically. For the left and right foot stimulation the amplitude of the peak was greatest at midline (Cz). For the left and right hand, the peak was greatest at the lateral central electrodes (C3 and C4). Scalp maps of mean amplitude between 100 and 200ms are shown, with central electrodes indicated by black dots (B).

Reproduced with permission from 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.

4 Lips on the brain: A test in 60-day-old infants

What about younger infants and other body parts? Meltzoff et al. (2019) modified the methods used by Saby et al. (2015) to examine neural body maps in 60-day-olds, prior to the age that infants begin to systematically use their hands to reach or their feet for locomotion. We also extended our previous studies by assessing a new body part—infant lips. Lips are an important organ to infants for survival (sucking), language (speech articulations), affective behavior (emotional expressions), and pre-verbal social-communication (imitation of facial acts in parent-child gestural interactions). The representation of infant lips is also of relevance for developmental theory, because although 60-day-olds will have seen their hands and feet, their own lips remain *invisible* to them. The inclusion of lip stimulation therefore allowed an evaluation of whether body representations are in place prior to visual experience with one's own relevant body part.

Participants were 25 infants tested in a narrow age range to reduce inter-subject variance (range 52–64 days old) (Meltzoff et al., 2019). A repeated-measures design was used such that each infant received stimulation on the lip (center of the top lip), left hand, and left foot. Punctate taps were delivered in blocks of 40 trials to a single body part, with blocks randomized across participants. Results revealed a pattern (Fig. 4) that was consistent with the hypothesis of somatotopy. When the infant's left hand was touched, the amplitude of this response was greatest over lateral central electrodes in the right hemisphere (C4/C6). For stimulation of the foot, the response

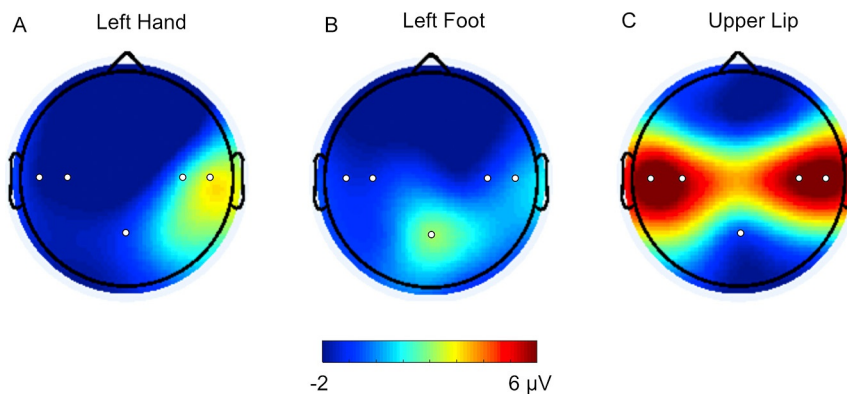


FIG. 4

Cortical signatures of touch to three body parts in 60-day-old infants. Scalp maps show the spatial distribution of mean amplitude of the somatosensory evoked potential following touch to the (A) hand, (B) foot, and (C) midline upper lip. 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.

Reproduced with permission from Meltzoff, A.N., Saby, J.N., Marshall, P.J., 2019. Neural representations of the body in 60-day-old human infants. Develop. Sci. 22, e12698.

was largest over the midline parietal electrode (Pz), which approximately overlies the foot region but was displaced in the posterior direction, possibly due to immature features of the skull of 60-day-olds, including an open anterior fontanelle that may obscure or distort activity at the midline central site (Cz). For stimulation of the lip, the response was observed bilaterally over the central region, a pattern consistent with the literature on lip stimulation in adults (Disbrow et al., 2003; Hashimoto, 1988; Hoshiyama et al., 1996; Tamura et al., 2008). It was also striking that the response amplitude to lip touch was greater than that to hand or foot touch (Fig. 4), perhaps reflecting the tactile sensitivity of lips and/or pre- and postnatal sensorimotor experience. Further work has pursued the youngest age at which human somatotopic organization can be documented, and has provided evidence for a structured neural body map in the somatosensory cortex of newborns, including healthy preterm participants (Dall’Orso et al., 2018), underscoring the early emergence of basic neural body maps.

5 Toward an infant body schema: Carving the body at the joints

To this point, we have been referring to specific body parts, such as the hand or foot. However, the skin surface is one continuous sheet. Linguistic labels chunk the skin surface into units, but without regard to language, where does the hand end and the forearm begin? Does the human infant already chunk the body into categorized segments as demarcated by adult language? Or is the acquisition of a semantic label needed to carve the body schema into segmented units?

Behavioral research with adults shows that tactile perception is modulated by a high-level representation of the body, often referred to as the body schema. The chief methodology used in this research involves participants reporting on the distance between two points of tactile stimulation on the body. Using adult subjects, de Vignemont et al. (2009) showed that the perceived distance between two equally spaced points on the skin is greater when these points go across body-part boundaries than when both points are within body-part boundaries. For instance, there is enhanced discrimination of two points on either side of the wrist joint compared to two points of metrically equivalent distances located within the hand or within the forearm. Other research indicates that this is not reducible to differences in tactile receptor density differences (Le Cornu Knight et al., 2014). This suggests that the representation of the body may be structured with joints acting as categorical boundaries between body parts. Although this behavioral effect has also been demonstrated in 5- to 7-year-old children (Le Cornu Knight et al., 2017), the preverbal origins of this categorical effect—thought to be due to the top-down effect of a central body schema on tactile perception—had not been studied in infants.

To address this issue, we made novel use of infant EEG responses to tactile stimulation by employing a mismatch negativity (MMN) paradigm. In adults, the MMN has been used to examine categorical effects in the auditory (Dehaene-Lambertz, 1997),

visual (Mo et al., 2011), and somatosensory (Shen et al., 2018b) modalities. In infants, the MMN work has principally been on speech and language development (e.g., Ferjan Ramírez et al., 2017; Friedrich et al., 2009). These studies have consistently found an enhanced MMN response to cross-category deviants compared to within-category deviants with equal physical differences.

Our infant study adapted a somatosensory mismatch negativity (sMMN) paradigm that has successfully been used to probe categorical aspects of body perception in adults (Shen et al., 2018b) and infants (Shen et al., 2018a). We tested 6- to 7-month-old infants by providing tactile stimulation to the body within and across the potential category boundary of the wrist (Fig. 5). The results showed that the amplitude of the sMMN elicited by tactile stimuli across the wrist boundary was significantly greater than for stimuli of equal distance within the boundary, suggesting a categorical effect in infant body processing (Shen et al., 2020). The early-appearing, structured representation of the body into segmented parts, such as “hand” or “foot,” developmentally predates infants’ learning of linguistic labels for these categories (see also, Le Cornu Knight et al., 2020). We suggest that such structured representations may support later learning of linguistic labels as well as scaffolding a mapping of equivalence between self and other (see below).

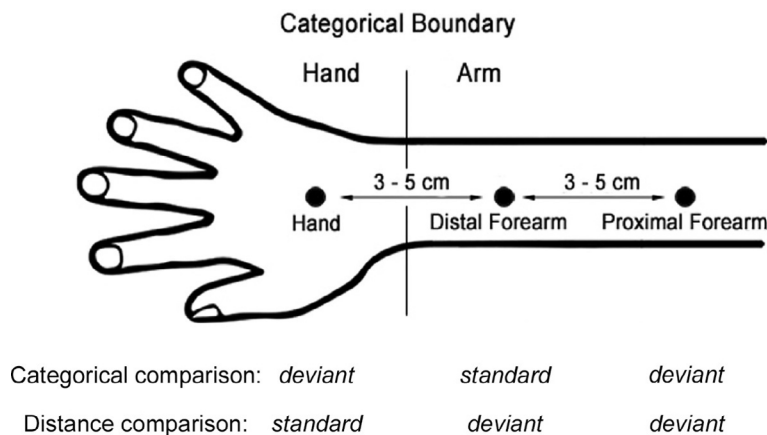


FIG. 5

Placement of tactile stimulators (indicated by black dots) on the upper limb of 6- to 7-month-old infants. Physical distances between each stimulator were equal. Results showed a categorical effect in body perception in infants. The contrast involving tactile stimulation across the forearm-hand boundary (distal forearm/hand) elicited significantly larger sMMN responses than the contrast of tactile stimuli within the forearm (distal forearm/proximal forearm).

Reproduced with permission from Shen, G., Meltzoff, A.N., Weiss, S.M., Marshall, P.J., 2020. Body representation in infants: categorical boundaries of body parts as assessed by somatosensory mismatch negativity. Develop. Cogn. Neurosci. 44, 100795.

6 Cross-modal effects for body representations

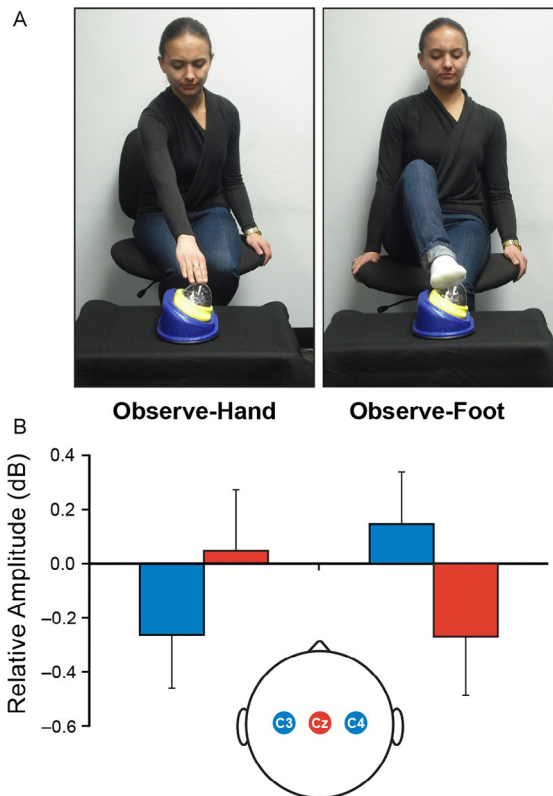
In the mature adult representation of the body, there are not only identifiable body parts, but these parts can be recognized as “the same” across perceptual modalities. My hand is the same as your hand; my foot is the same as your foot. Our bodies are comparable, a point that has far-reaching implications for social-cognitive development. Our initial foray into more social aspects of body perception tapped into the sensorimotor mu rhythm. The mu rhythm occurs over central electrode sites in the alpha band (8–13 Hz in adults, 6–9 Hz in infancy; Cuevas et al., 2014; Marshall and Meltzoff, 2011; Marshall et al., 2002). Previous work utilizing hand actions alone showed that the infant mu rhythm over central sites is desynchronized (reduced in amplitude) during infant motor production (Southgate et al., 2009) and also while observing another person carry out a similar action (Marshall et al., 2011; Nyström et al., 2011; Southgate et al., 2009).

We designed a test situation that allowed us to examine the topography of the infant mu rhythm response during the observation of actions that had an identical goal (to press a button) (Marshall et al., 2013; Saby et al., 2013). The crucial experimental manipulation was that the same button pushing could be carried out using different effectors (hands vs feet) (Fig. 6A). Any difference in the mu rhythm response could not be due to the goal, which was controlled, but to the *body part used* by the actor to achieve the goal.

We found that the infant mu rhythm displayed a somatotopic response pattern not only during action execution but also during action perception. As shown in Fig. 6B, the pattern of activation over hand (electrodes C3/C4) and foot (electrode Cz) regions of the sensorimotor cortex differed according to whether infants saw a hand or a foot used. For hand acts, there was a greater reduction in mu amplitude at lateral electrode sites (C3/C4); conversely, for foot actions there was a greater reduction in mu amplitude at midline (Cz). This suggests that perceiving *someone else* using a specific body part (hand vs foot) is associated with activation of the corresponding area of the sensory and/or motor strip in the observer’s brain.

6.1 Infant MEG: Cross-modal effects for felt and observed touch

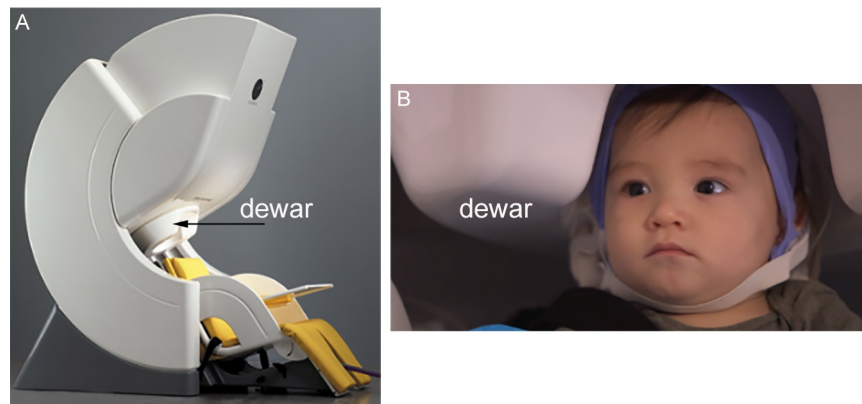
The foregoing experiments used EEG to explore infant body representations. In order to provide a more sensitive estimate of the sources of activity inside the brain, we have also conducted experiments using infant magnetoencephalography (MEG) brain imaging (Fig. 7). Sensors in the MEG dewar can detect minute changes in magnetic fields (extending outside of the skull) that are due to electrical signals (neural sources) inside the brain (Hämäläinen and Hari, 2002). Source-level analysis routines use inverse methods to estimate the location of neural sources in the brain (Lew et al., 2013). MEG technology is ideally suited to explore body representations because body maps in sensorimotor/somatosensory cortex are close to the surface of the brain; and MEG has proven to be extremely helpful to making discoveries about body representations in adult participants (e.g., Pihko et al., 2010).

**FIG. 6**

14-month-old infants observed visual events using the hand or foot (A). Negative values reflect a reduction in mu rhythm amplitude (desynchronization) relative to a pre-stimulus baseline. Desynchronization significantly varied as a function of experimental group (B). There was greater reduction in amplitude over the hand regions (C3/C4) for infants who observed hand actions; and greater reduction in amplitude over the foot regions (Cz) for infants who observed foot actions. Error bars represent 1 SEM.

Modified from 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.

For studying cortical body representations in infants, MEG has several desirable features compared to other infant neuroscience technologies. First, compared to EEG, MEG has about the same temporal resolution (millisecond level) but has superior spatial resolution (~ 2 mm). EEG is more vulnerable than MEG to distortions due to the structural immaturities of the infant skull (e.g., open fontanels and sutures) and variability in skull connectivity (Lew et al., 2013). Second, compared to fMRI, MEG has superior temporal resolution, and infants can be awake and sitting upright in a chair, whereas infant fMRI typically involves infants who are asleep in a supine

**FIG. 7**

MEG brain-imaging device (A). The MEG (Elekta Oy, Helsinki, Finland) has 306 sensors (204 planar gradiometers and 102 magnetometers), which are housed inside the dewar. The baby is positioned wearing a nylon cap containing five head positioning coils that emit signals throughout the recording session (B). This allows continuous tracking of the infant's head position, which is used for head-movement compensation in data analysis. See [Meltzoff et al. \(2018a\)](#) for details.

Modified and reproduced with permission of the University of Washington Institute for Learning & Brain Sciences (I-LABS) and D. Alpert (No Small Matter).

position in order to avoid head movements (which introduce too much noise for fMRI analyses). To examine infant neural responses to visual perception of other people's bodies, infants have to be awake and alert (and therefore will move their heads), ruling out infant fMRI. Third, although fNIRS allows testing of awake infants with head movements, the temporal and spatial resolution afforded by infant MEG is superior.

This does not mean that infant MEG is to be preferred in all applications. MEG is expensive (similar to MRI) and not portable. Therefore, MEG cannot be used in the field or at home, for which EEG and fNIRS technologies are more suitable. Also, infant MEG is fairly new, and the head-movement tracking and compensation algorithms and source-level analysis routines are not readily available in off-the-shelf packages. For our MEG studies of infant body representations, we were able to capitalize on the University of Washington's MEG Center at the Institute for Learning & Brain Sciences (I-LABS), directed by Samu Taulu (creator of the most widely used MEG head-movement compensation methods, which allow one to correct for subject head movements relative to the fixed sensor array, see [Fig. 7: Taulu and Hari, 2009; Taulu et al., 2005](#)). His work and that of others at I-LABS is focused on optimizing MEG for infants ([Clarke et al., 2020; Ferjan Ramírez et al., 2017; Larson and Taulu, 2017](#)).

We used MEG whole-brain imaging and advanced source-localization techniques to probe the representation of the body in the infant brain ([Meltzoff et al., 2018a](#)). In two experiments using 7-month-old infants, our work built upon

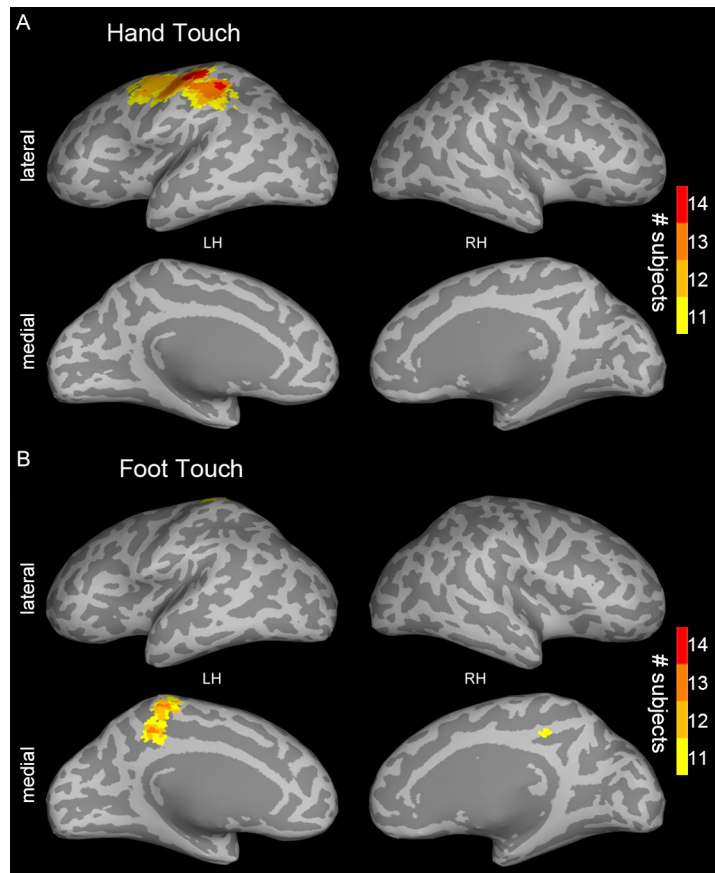
and sought to extend prior findings (Nevalainen et al., 2014; Saby et al., 2015). Experiment 1 evaluated the spatiotemporal organization of infants' brain responses to being touched on their hands and feet. We found significant activation in the hand and foot regions of contralateral primary somatosensory cortex as well as increased activity in other parietal and frontal areas. According to the source estimates, the most salient neural activity when the foot was touched was at the midline along the inter-hemisphere wall (see Penfield's map, Fig. 1B), and the activity when the infant's hand was touched was, on average, 19mm more lateral. Our MEG source-level results were more detailed than could be obtained from our EEG scalp-level recordings with infants (Fig. 8), but are consonant with them. The main pattern of results suggested a somatotopic organization in infant cortex resembling that in adults.

Having shown that infant MEG is an effective technology for exploring neural body representations, we next conducted a more ambitious study. Experiment 2 explored infant brain responses to visually perceiving another person's body being touched. To conduct this experiment, we made video recordings of a rod gently touching an adult's hand or foot. Infants watched the videos, but they were not touched themselves. Consistent with the results of Experiment 1, significant activation occurred in the infant's own somatosensory cortex in response to seeing a hand or foot being touched. This supports the idea that shared anatomical regions in human infants are activated whether touch of the body is tactilely or visually perceived, which fits with cognitive neuroscience work in human adults (Keysers et al., 2010; Pihko et al., 2010), as well as with newer infant EEG work on tactile-visual interactions (Drew et al., 2018). At the same time, we found that the activation for observed touch (Experiment 2) occurred in fewer infants than for felt touch (Experiment 1). It is noteworthy that a weaker somatosensory response to observed touch has also been reported in adult subjects (Pihko et al., 2010), for whom the source strength for observing someone else being touched was around 10 times weaker than that to felt touch.

Finally, it is of significant interest that in Experiment 2 we also found activity in brain areas involved in multisensory body and self-other processing. Specifically, observation of another person's hand being touched was associated with activation in areas corresponding to the extrastriate body area (EBA), fusiform body area (FBA), and the temporal-parietal junction (TPJ). Previous infant work has used fNIRS to broadly examine temporal cortex responses to observed biological motion (Lloyd-Fox et al., 2011), but to our knowledge, our results are the first to suggest EBA and FBA responses to seen body parts in infants.

7 Neural responses to reciprocal imitation social games

In the real world, outside of the neuroscience laboratory, reciprocal imitative games are a common form of parent-child interaction. The baby shakes a rattle. The mother mimics the baby. The baby repeats the game. We believe that one of the reasons that

**FIG. 8**

Results of infant MEG experiment involving tactile stimulation of hand (A) and foot (B) in 7-month-old infants. Source localization analysis methods were used. The resulting consistency maps show, at each voxel, the number of infants (out of 14) meeting a conservative $P < 10^{-6}$ threshold at any time point within the 400 ms window following tactile stimulus. The maps are visualized with a lower bound of 11 subjects.

*Reproduced with permission from Meltzoff, A.N., Ramírez, 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. *Develop. Sci.* 21, e12651.*

parents and infants find this interpersonal game, so alluring is that both partners recognize that they are matching the bodily movements of the other. We thought that infant brain studies could shed light on these interpersonal matching activities.

The neuroscience work was built on a series of behavioral studies of reciprocal imitation conducted by Meltzoff (1990, 2007). In one study, 14-month-old infants sat across the table from two adults who were side-by-side (a paired comparison

setup similar to infant looking-time studies). Two television monitors were situated behind the infant and in view of the adults. One screen displayed the current infant, and the other a recording of the immediately preceding infant from the same study. Each adult mimicked one of the infants on the screens. Behavioral measures showed that infants looked longer and smiled more at the person who was imitating them, indicating preferential attention and emotional reactions at being “matched.” This pattern was replicated and extended in 9- to 18-month-olds by [Agnetta and Rochat \(2004\)](#); and additional studies using behavioral measures have also verified infant preferences for people who match the infants’ own behavior ([Carpenter et al., 2013](#); [Nadel, 2014](#)).

The novelty of the neuroscience experiment was that we recreated a reciprocal imitation situation while recording infant EEG ([Saby et al., 2012](#)). EEG signals were recorded from 14-month-old infants while they observed an adult who, by experimental design, either matched or mismatched the actions the infant had just executed. We hypothesized that mu rhythm desynchronization over central sites would differentiate between these two conditions, in part based on our own previous neuroscience work (discussed above) and in part based on brain studies in adults ([Kourtis et al., 2010](#)) and 3-year-olds ([Meyer et al., 2011](#)), which showed that the extent of mu rhythm desynchronization is greater when an observed action takes place in the context of joint action. We also analyzed the time course of EEG desynchronization immediately before and after the culmination of the adult’s goal-directed matching act in order to explore the idea of a predictive component in infant social interactions: Infants may not simply respond to what the adult does in mutual imitation games but may be able to predict it ahead of time.

Results indicated that desynchronization of the EEG mu rhythm was greater when infants were imitated than when they were not. Moreover, we found that this effect was strongest in the 500ms time period immediately prior to the culmination of the observed imitative act. This temporal pattern is consistent with theory ([Csibra, 2007](#); [Weiss et al., 2018](#)) and infant data ([Filippi et al., 2016](#); [Köster et al., 2020](#); [Southgate et al., 2009, 2010](#); [Stapel et al., 2010](#)) showing that infant neural responses during action observation have an anticipatory element. We believe that predictive coding comes strongly into play in interactions involving reciprocal imitation. We think that infants’ ability to anticipate the adult’s behavior and to recognize that the observed act by the adult is “like me” (matching a self-generated act) makes this type of social interaction particularly salient and enjoyable to infants (see also below).

8 What infant imitation tells us about body representations

To this point, we have primarily taken a neuroscience perspective on body representation in infancy. In this section, we examine behavioral studies of social imitation that inform us, at a psychological level, about the representation of bodies.

One early study of imitation illuminating body representations was conducted by [Meltzoff \(1988\)](#). Fourteen-month-old infants observed an adult press the top panel of

an object with his *head*, which made the panel illuminate. The object was out of reach from the infants, and the infants were not allowed to touch or handle it during the adult demonstration. After a delay, infants were presented with the object. Results showed that infants imitated by using their *head* to press the panel, with 67% of the infants in the experimental group doing so. Two control groups were used, one was a baseline control to assess spontaneous production of this behavior, and the other was an end-state control (the adult pressed the object with his hands to make the panel illuminate). None of the infants in either of the control conditions touched the panel with their heads. This experiment provided the first demonstration of infant imitation using a novel body part, and it has now been widely replicated and extended (e.g., Beisert et al., 2012; Buttelmann et al., 2013; Gergely et al., 2002; Király et al., 2013; Zmyj et al., 2009; see also Gleissner et al., 2000).

One reason that this imitation using the head is informative is that it is an unusual act. Infants would more naturally use a different effector (the hand) to press the panel and turn on the light. Control groups demonstrated that the head-touch act was not performed by infants unless they saw the adult use his head to turn on the light. We can conclude that infants were not simply re-creating the end-state of “light on,” but were recognizing and imitating the use of *a particular body part* per se. A reasonable inference from the pattern of results is that infants can map the similarity between their head and the head of another person.

This brings us to imitation of facial gestures. Meltzoff and Moore (1977, 1994) designed studies of early facial imitation not only to assess the nature and scope of the phenomenon but also to uncover information about body representations. In the 1977 study, the three facial acts used (lip protrusion, mouth opening, and tongue protrusion) were selected to evaluate the specificity of infants’ matching behaviors. Results showed that infants could use *the same body part* to imitate two different acts (lip pursing vs. lip opening) and could use two *different body parts* to perform the same general action (lip protrusion vs. tongue protrusion). In the absence of infant neuroscience data, the hypothesis put forward was that young infants were capable of representing at least a small set of body parts: “Infants seem to have a primitive body scheme that allows them to map a delimited set of body parts: tongue to tongue, lips to lips. We have not observed young infants confusing tongue protrusion with finger protrusion, for example. When tongue protrusion is presented, infants activate the tongue quite quickly, as if the first level of analysis is a kind of organ identification” (Meltzoff and Moore, 1994, p. 95).

The broader theoretical point is that generative imitation at any age—whether in neonates or in 14-month-olds—cannot exist without an internal representation of the body and recognition of the correspondence between one’s own body and the bodies of others. When a 14-month-old sees the head-touch act, they are manifesting an ability to map the other person’s head to a specific body part of their own. When a neonate imitates mouth opening, they likewise map the other person’s lips to their own lips. One reason that facial imitation is so interesting for theory is that infants cannot see their own face, and so facial imitation reveals *cross-modal* mapping.

However, this is not unique. The imitation of head-touch also involves a body part that is invisible: The child cannot see their own head any more than they can see their own lips or tongue. And yet they imitate.

Meltzoff and Moore (1997) advanced a theory termed “Active Intermodal Mapping” (AIM) to explain the mechanisms involved in infant imitation. AIM provides a detailed account of the metric of equivalence used by infants to map bodily acts they see onto matching acts of their own. Of most relevance to the current chapter, Meltzoff and Moore (1997): (i) proposed that the representation of the body is integral to how infants solve the correspondence problem for imitation (pp. 183–184, 186), (ii) described the role of prior motor experience including prenatal experience in imitation (p. 184), and (iii) highlighted social games involving reciprocal imitation in the development of children’s imitation (pp. 189–190). Although the findings on early imitation have generated debate (see Meltzoff et al., 2018b), much of the recent empirical work (Coulon et al., 2013; Heimann and Tjus, 2019; Nagy et al., 2020) has replicated and extended the findings by showing neonatal imitation of tongue protrusion, lip movements, and finger movements. Beyond imitative behavior per se, studies using other behavioral techniques (looking-time measures) have successfully documented cross-modal body representations in neonates (Filippetti et al., 2015), which aligns well with the AIM model.

9 Theory: Body representations as building blocks in social cognition

What are the broader implications of the foregoing work for theories of social-cognitive development? Classical developmental theory has at times struggled to explain the rapid onset and development of human social cognition. According to Piaget’s (1954, 1962) classical stage-developmental theory, infants are “egocentric”—unable to discern equivalences between the self and other. Young infants may be visually attracted to faces, or auditorily attentive to speech, but these are thought to be solely perceptual biases, according to classical theory.

In contrast, modern research using a combination of neuroscience and behavioral approaches suggests that young infants can represent the bodily acts of others and their own bodily acts in *commensurate terms*. According to the “Like-Me” social-developmental framework (Meltzoff, 2007, 2013), self and other are linked, which allows for bidirectional learning. Infants can learn about the affordances and powers of their *own* body by watching adults’ actions and their causal consequences in the world. Reciprocally, infants enrich their understanding of *other people’s* internal states by taking into account the way they themselves feel when they perform similar acts.

We thus conjecture that the “first connection” to other people derives from a perceived similarity between the bodies and actions of self and other. Your hand is like my hand. Your foot is like my foot. This action I take is like the action you take.

You are a proxy for me, and I can learn about the world by observing your dynamic interactions with people and things and the causal consequences that follow.

In typical development, this construal of others in relation to self is not born through language, complex cognitive development, or associative learning. Rather, the perception that others are “like me” may be a foundation from which more complex levels of social cognition emerge. Infants interpret social interaction and reciprocal imitative games through “priors” that allow infants to interpret these events in particularly meaningful ways. Moving objects may generally attract infants’ attention based on perceptual biases and salience, but people and their actions are special to infants. Alongside perceptual biases, the faces, bodies, and matching actions of people are imbued with unique meaning because they can be mapped to the infant’s own body and behavior.

This “like-me” construal of other people’s bodily actions may also shed light on social-cognitive development in later infancy. Between 1 and 2 years of age, infants exhibit robust empathy and altruistic helping directed toward other people (Barragan and Dweck, 2014; Barragan et al., 2020; Newton et al., 2016; Schuhmacher et al., 2019; Svetlova et al., 2010; Warneken and Tomasello, 2006). The origins of such sociality are not fully understood, but one possible component is infants’ capacity to interpret social agents as being “like me”—with internal wants, needs, and intentions that require fulfillment—just like the infants’ own when they themselves display the same bodily actions (e.g., begging for an out-of-reach object). We hypothesize that infants’ experience with their own bodies, bodily actions and internal states, may be one pathway for coming to understand the internal states of others (Meltzoff, 1995, 2013; Meltzoff and Brooks, 2008).

The neuroscience work described in this chapter plays a role in elucidating infant social cognition by shedding light on the neurobiological bases of infants’ processing of bodies, both their own body and the body of others. Converging brain and behavioral studies on body representations provide a rich database for advancing scientific understanding of infants’ initial state and the mechanisms of change in social-cognitive development. Our thesis is this: As infants’ understanding of their own bodies and intentional actions change with experience, so too does their understanding of other people who are interpreted as “like me.” The behavioral and neuroscientific studies presented here suggested that young infants recognize the correspondence between self and other in terms of bodily representations, which provides a key bridge for coming to understand other minds.

Acknowledgments

Writing of this chapter was supported by grants from NSF (BCS-1460889), the Bezos Family Foundation, and the Overdeck Family Foundation. We thank J. Saby, R. Ramírez, G. Shen, A. Drew, and S. Weiss for longtime collaboration on the studies that are discussed here and R. Brooks for help on production.

References

- Agnetta, B., Rochat, P., 2004. Imitative games by 9-, 14-, and 18-month-old infants. *Infancy* 6, 1–36.
- Bahrack, L.E., Watson, J.S., 1985. Detection of intermodal proprioceptive-visual contingency as a potential basis of self-perception in infancy. *Dev. Psychol.* 21, 963–973.
- Barragan, R.C., Dweck, C.S., 2014. Rethinking natural altruism: simple reciprocal interactions trigger children’s benevolence. *Proc. Natl. Acad. Sci. U. S. A.* 111, 17071–17074.
- Barragan, R.C., Brooks, R., Meltzoff, A.N., 2020. Altruistic food sharing behavior by human infants after a hunger manipulation. *Sci. Rep.* 10, 1785.
- Beisert, M., Zmyj, N., Liepelt, R., Jung, F., Prinz, W., Daum, M.M., 2012. Rethinking ‘rational imitation’ in 14-month-old infants: a perceptual distraction approach. *PLoS One* 7, e32563.
- Buonomano, D.V., Merzenich, M.M., 1998. Cortical plasticity: from synapses to maps. *Annu. Rev. Neurosci.* 21, 149–186.
- Buttelmann, D., Zmyj, N., Daum, M.M., Carpenter, M., 2013. Selective imitation of in-group over out-group members in 14-month-old infants. *Child Dev.* 84, 422–428.
- Carpenter, M., Uebel, J., Tomasello, M., 2013. Being mimicked increases prosocial behavior in 18-month-old infants. *Child Dev.* 84, 1511–1518.
- Clarke, M., Larson, E., Tavabi, K., Taulu, S., 2020. Effectively combining temporal projection noise suppression methods in magnetoencephalography. *J. Neurosci. Methods* 341, 108700.
- Coulon, M., Hemimou, C., Streri, A., 2013. Effects of seeing and hearing vowels on neonatal facial imitation. *Infancy* 18, 782–796.
- Csibra, G., 2007. Action mirroring and action understanding: an alternative account. In: Haggard, P., Rosetti, Y., Kawato, M. (Eds.), *Sensorimotor Foundations of Higher Cognition: Attention and Performance XXII*. Oxford University Press, Oxford, pp. 435–459.
- Cuevas, K., Cannon, E.N., Yoo, K., Fox, N.A., 2014. The infant EEG mu rhythm: methodological considerations and best practices. *Dev. Rev.* 34, 26–43.
- Dall’Orso, S., Steinweg, J., Allievi, A.G., Edwards, A.D., Burdet, E., Arichi, T., 2018. Somatotopic mapping of the developing sensorimotor cortex in the preterm human brain. *Cereb. Cortex* 28, 2507–2515.
- Dawson, G., Meltzoff, A.N., Osterling, J., Rinaldi, J., 1998. Neuropsychological correlates of early symptoms of autism. *Child Dev.* 69, 1276–1285.
- de Vignemont, F., Majid, A., Jola, C., Haggard, P., 2009. Segmenting the body into parts: evidence from biases in tactile perception. *Q. J. Exp. Psychol.* 62, 500–512.
- Dehaene-Lambertz, G., 1997. Electrophysiological correlates of categorical phoneme perception in adults. *Neuroreport* 8, 919–924.
- DiMercurio, A., Connell, J.P., Clark, M., Corbetta, D., 2018. A naturalistic observation of spontaneous touches to the body and environment in the first 2 months of life. *Front. Psychol.* 9, 2613.
- Disbrow, E.A., Hinkley, L.B.N., Roberts, T.P.L., 2003. Ipsilateral representation of oral structures in human anterior parietal somatosensory cortex and integration of inputs across the midline. *J. Comp. Neurol.* 467, 487–495.
- Drew, A.R., Meltzoff, A.N., Marshall, P.J., 2018. Interpersonal influences on body representations in the infant brain. *Front. Psychol.* 9, 2601.
- Edwards, L.A., 2014. A meta-analysis of imitation abilities in individuals with autism spectrum disorders. *Autism Res.* 7, 363–380.

- 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. *Dev. Sci.* 20, e12427.
- Filippetti, M.L., Johnson, M.H., Lloyd-Fox, S., Dragovic, D., Farroni, T., 2013. Body perception in newborns. *Curr. Biol.* 23, 2413–2416.
- Filippetti, M.L., Orioli, G., Johnson, M.H., Farroni, T., 2015. Newborn body perception: sensitivity to spatial congruency. *Infancy* 20, 455–465.
- Filippi, C.A., Cannon, E.N., Fox, N.A., Thorpe, S.G., Ferrari, P.F., Woodward, A.L., 2016. Motor system activation predicts goal imitation in 7-month-old infants. *Psychol. Sci.* 27, 675–684.
- Friedrich, M., Herold, B., Friederici, A.D., 2009. ERP correlates of processing native and non-native language word stress in infants with different language outcomes. *Cortex* 45, 662–676.
- Gaetz, W., Jurkiewicz, M.T., Kessler, S.K., Blaskey, L., Schwartz, E.S., Roberts, T.P., 2017. Neuromagnetic responses to tactile stimulation of the fingers: evidence for reduced cortical inhibition for children with autism spectrum disorder and children with epilepsy. *NeuroImage Clin.* 16, 624–633.
- Gergely, G., Bekkering, H., Király, I., 2002. Rational imitation in preverbal infants. *Nature* 415, 755.
- Gleissner, B., Meltzoff, A.N., Bekkering, H., 2000. Children's coding of human action: cognitive factors influencing imitation in 3-year-olds. *Dev. Sci.* 3, 405–414.
- Hämäläinen, M., Hari, R., 2002. Magnetoencephalographic characterization of dynamic brain activation: basic principles and methods of data collection and source analysis. In: Toga, A.W., Mazziotta, J.C. (Eds.), *Brain Mapping: The Methods*. Academic Press, San Diego, pp. 227–253.
- Hashimoto, I., 1988. Trigeminal evoked potentials following brief air puff: enhanced signal-to-noise ratio. *Ann. Neurol.* 23, 332–338.
- Heimann, M., Tjus, T., 2019. Neonatal imitation: temporal characteristics in imitative response patterns. *Infancy* 24, 674–692.
- Hoshiyama, M., Kakigi, R., Koyama, S., Kitamura, Y., Shimojo, M., Watanabe, S., 1996. Somatosensory evoked magnetic fields following stimulation of the lip in humans. *Electroencephalogr. Clin. Neurophysiol.* 100, 96–104.
- Johnson, M.H., Senju, A., Tomalski, T.P., 2015. The two-process theory of face processing: modifications based on two decades of data from infants and adults. *Neurosci. Biobehav. Rev.* 50, 169–179.
- Jubran, R., White, H., Chroust, A., Heck, A., Bhatt, R.S., 2019. Experimental evidence of structural representation of hands in early infancy. *Int. J. Behav. Dev.* 43, 35–42.
- Kaas, J.H., 1991. Somatosensory system, *Encyclopedia of Human Biology*. Academic Press, New York, 119–126.
- Kaas, J.H., 1997. Topographic maps are fundamental to sensory processing. *Brain Res. Bull.* 44, 107–112.
- Kaas, J.H., Jain, N., Qi, H.-X., 2001. The organization of the somatosensory system in primates. In: Nelson, R.J. (Ed.), *The Somatosensory System: Deciphering the Brain's Own Body Image*. CRC Press, Boca Raton, pp. 1–25.
- Keyzers, C., Kaas, J.H., Gazzola, V., 2010. Somatosensation in social perception. *Nat. Rev. Neurosci.* 11, 417–428.

- Király, I., Csibra, G., Gergely, G., 2013. Beyond rational imitation: learning arbitrary means actions from communicative demonstrations. *J. Exp. Child Psychol.* 116, 471–486.
- Köster, M., Langeloh, M., Kliesch, C., Kanngiesser, P., Hoehl, S., 2020. Motor cortex activity during action observation predicts subsequent action imitation in human infants. *Neuroimage* 218, 116958.
- Kourtis, D., Sebanz, N., Knoblich, G., 2010. Favouritism in the motor system: social interaction modulates action simulation. *Biol. Lett.* 6, 758–761.
- Kuhl, P.K., Ramírez, R.R., Bosseler, A., Lin, J.-F., Imada, T., 2014. Infants' brain responses to speech suggest analysis by synthesis. *Proc. Natl. Acad. Sci. U. S. A.* 111, 11238–11245.
- Larson, E., Taulu, S., 2017. The importance of properly compensating for head movements during MEG acquisition across different age groups. *Brain Topogr.* 30, 172–181.
- Le Cornu Knight, F., Longo, M.R., Bremner, A.J., 2014. Categorical perception of tactile distance. *Cognition* 131, 254–262.
- Le Cornu Knight, F., Cowie, D., Bremner, A.J., 2017. Part-based representations of the body in early childhood: evidence from perceived distortions of tactile space across limb boundaries. *Dev. Sci.* 20, e12439.
- Le Cornu Knight, F., Bremner, A.J., Cowie, D., 2020. Does the language we use to segment the body, shape the way we perceive it? A study of tactile perceptual distortions. *Cognition* 197, 104127.
- Leed, J.E., Chinn, L.K., Lockman, J.J., 2019. Reaching to the self: the development of infants' ability to localize targets on the body. *Psychol. Sci.* 30, 1063–1073.
- Lew, S., Sliva, D.D., Choe, M.-s., Grant, P.E., Okada, Y., Wolters, C.H., Hämäläinen, M.S., 2013. Effects of sutures and fontanels on MEG and EEG source analysis in a realistic infant head model. *Neuroimage* 76, 282–293.
- Lloyd-Fox, S., Blasi, A., Everdell, N., Elwell, C.E., Johnson, M.H., 2011. Selective cortical mapping of biological motion processing in young infants. *J. Cogn. Neurosci.* 23, 2521–2532.
- Marshall, P.J., 2015. Neuroscience, embodiment, and development. In: Overton, W.F., Molenaar, P.C. (Eds.), *Handbook of Child Psychology and Developmental Science*, seventh ed. Theory and Method, vol. 1. Wiley, New York, pp. 244–283.
- Marshall, P.J., Meltzoff, A.N., 2011. Neural mirroring systems: exploring the EEG mu rhythm in human infancy. *Dev. Cogn. Neurosci.* 1, 110–123.
- Marshall, P.J., Meltzoff, A.N., 2014. Neural mirroring mechanisms and imitation in human infants. *Philos. Trans. R. Soc. B. Biol. Sci.* 369, 20130620.
- Marshall, P.J., Meltzoff, A.N., 2015. Body maps in the infant brain. *Trends Cogn. Sci.* 19, 499–505.
- Marshall, P.J., Meltzoff, A.N., 2020. Body maps in the infant brain: implications for neurodevelopmental disabilities. *Dev. Med. Child Neurol.* 62, 778–783.
- Marshall, P.J., Bar-Haim, Y., Fox, N.A., 2002. Development of the EEG from 5 months to 4 years of age. *Clin. Neurophysiol.* 113, 1199–1208.
- Marshall, P.J., Young, T., Meltzoff, A.N., 2011. Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Dev. Sci.* 14, 474–480.
- 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. *Int. J. Psychol. Res.* 6, 22–29.
- Meltzoff, A.N., 1988. Infant imitation after a 1-week delay: long-term memory for novel acts and multiple stimuli. *Dev. Psychol.* 24, 470–476.

- Meltzoff, A.N., 1990. Foundations for developing a concept of self: the role of imitation in relating self to other and the value of social mirroring, social modeling, and self-practice in infancy. In: Cicchetti, D., Beeghly, M. (Eds.), *The Self in Transition: Infancy to Childhood*. University of Chicago Press, Chicago, pp. 139–164.
- Meltzoff, A.N., 1995. Understanding the intentions of others: re-enactment of intended acts by 18-month-old children. *Dev. Psychol.* 31, 838–850.
- Meltzoff, A.N., 2007. ‘Like me’: a foundation for social cognition. *Dev. Sci.* 10, 126–134.
- Meltzoff, A.N., 2013. Origins of social cognition: bidirectional self-other mapping and the “like-me” hypothesis. In: Banaji, M.R., Gelman, S.A. (Eds.), *Navigating the Social World: What Infants, Children, and Other Species Can Teach Us*. Oxford University Press, New York, pp. 139–144.
- Meltzoff, A.N., Brooks, R., 2008. Self-experience as a mechanism for learning about others: a training study in social cognition. *Dev. Psychol.* 44, 1257–1265.
- Meltzoff, A.N., Marshall, P.J., 2018. Human infant imitation as a social survival circuit. *Curr. Opin. Behav. Sci.* 24, 130–136.
- Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. *Science* 198, 75–78.
- Meltzoff, A.N., Moore, M.K., 1994. Imitation, memory, and the representation of persons. *Infant Behav. Dev.* 17, 83–99.
- Meltzoff, A.N., Moore, M.K., 1997. Explaining facial imitation: a theoretical model. *Early Dev. Parent.* 6, 179–192.
- Meltzoff, A.N., Ramírez, R.R., Saby, J.N., Larson, E., Taulu, S., Marshall, P.J., 2018a. Infant brain responses to felt and observed touch of hands and feet: an MEG study. *Dev. Sci.* 21, e12651.
- Meltzoff, A.N., Murray, L., Simpson, E., Heimann, M., Nagy, E., Nadel, J., Pedersen, E.J., Brooks, R., Messinger, D.S., De Pascalis, L., Subiaul, F., Paukner, A., Ferrari, P.F., 2018b. Re-examination of Oostenbroek et al. (2016): evidence for neonatal imitation of tongue protrusion. *Dev. Sci.* 21, e12609.
- Meltzoff, A.N., Saby, J.N., Marshall, P.J., 2019. Neural representations of the body in 60-day-old human infants. *Dev. Sci.* 22, e12698.
- Meyer, M., Hunnius, S., van Elk, M., van Ede, F., Bekkering, H., 2011. Joint action modulates motor system involvement during action observation in 3-year-olds. *Exp. Brain Res.* 211, 581–592.
- Mo, L., Xu, G., Kay, P., Tan, L.-H., 2011. Electrophysiological evidence for the left-lateralized effect of language on preattentive categorical perception of color. *Proc. Natl. Acad. Sci. U. S. A.* 108, 14026–14030.
- Nadel, J., 2014. *How Imitation Boosts Development: In Infancy and Autism Spectrum Disorder*. Oxford University Press, Oxford.
- Nagy, E., Pilling, K., Blake, V., Orvos, H., 2020. Positive evidence for neonatal imitation: a general response, adaptive engagement. *Dev. Sci.* 23, e12894.
- Nevalainen, P., Lauronen, L., Pihko, E., 2014. Development of human somatosensory cortical functions—what have we learned from magnetoencephalography: a review. *Front. Hum. Neurosci.* 8, 158.
- Newton, E.K., Thompson, R.A., Goodman, M., 2016. Individual differences in toddlers’ pro-sociality: experiences in early relationships explain variability in prosocial behavior. *Child Dev.* 87, 1715–1726.

- Nyström, P., Ljunghammar, T., Rosander, K., von Hofsten, C., 2011. Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Dev. Sci.* 14, 327–335.
- 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: A Clinical Study of Localization of Function*. Macmillan, New York.
- Piaget, J., 1954. *The Construction of Reality in the Child*. Basic Books, New York.
- Piaget, J., 1962. *Play, Dreams and Imitation in Childhood*. Norton, New York.
- Pihko, E., Nangini, C., Jousmäki, V., Hari, R., 2010. Observing touch activates human primary somatosensory cortex. *Eur. J. Neurosci.* 31, 1836–1843.
- Rigato, S., Begum Ali, J., van Velzen, J., Bremner, A.J., 2014. The neural basis of somatosensory remapping develops in human infancy. *Curr. Biol.* 24, 1222–1226.
- Rigato, S., Banissy, M.J., Romanska, A., Thomas, R., van Velzen, J., Bremner, A.J., 2019. Cortical signatures of vicarious tactile experience in four-month-old infants. *Dev. Cogn. Neurosci.* 35, 75–80.
- Rochat, P., Morgan, R., 1995. Spatial determinants in the perception of self-produced leg movements by 3- to 5-month-old infants. *Dev. Psychol.* 31, 626–636.
- Ropar, D., Greenfield, K., Smith, A.D., Carey, M., Newport, R., 2018. Body representation difficulties in children and adolescents with autism may be due to delayed development of visuo-tactile temporal binding. *Dev. Cogn. Neurosci.* 29, 78–85.
- Saby, J.N., Marshall, P.J., Meltzoff, A.N., 2012. Neural correlates of being imitated: an EEG study in preverbal infants. *Soc. Neurosci.* 7, 650–661.
- 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.
- Schuhmacher, N., Köster, M., Kärtner, J., 2019. Modeling prosocial behavior increases helping in 16-month-olds. *Child Dev.* 90, 1789–1801.
- Shen, G., Weiss, S.M., Meltzoff, A.N., Marshall, P.J., 2018a. The somatosensory mismatch negativity as a window into body representations in infancy. *Int. J. Psychophysiol.* 134, 144–150.
- Shen, G., Smyk, N.J., Meltzoff, A.N., Marshall, P.J., 2018b. Neuropsychology of human body parts: exploring categorical boundaries of tactile perception using somatosensory mismatch responses. *J. Cogn. Neurosci.* 30, 1858–1869.
- Shen, G., Meltzoff, A.N., Weiss, S.M., Marshall, P.J., 2020. Body representation in infants: categorical boundaries of body parts as assessed by somatosensory mismatch negativity. *Dev. Cogn. Neurosci.* 44, 100795.
- Somogyi, E., Jacquy, L., Heed, T., Hoffmann, M., Lockman, J.J., Granjon, L., Fagard, J., O'Regan, J.K., 2018. Which limb is it? Responses to vibrotactile stimulation in early infancy. *Br. J. Dev. Psychol.* 36, 384–401.
- Southgate, V., Johnson, M.H., Osborne, T., Csibra, G., 2009. Predictive motor activation during action observation in human infants. *Biol. Lett.* 5, 769–772.
- Southgate, V., Johnson, M.H., El Karoui, I., Csibra, G., 2010. Motor system activation reveals infants' on-line prediction of others' goals. *Psychol. Sci.* 21, 355–359.
- Stapel, J.C., Hunnius, S., van Elk, M., Bekkering, H., 2010. Motor activation during observation of unusual versus ordinary actions in infancy. *Soc. Neurosci.* 5, 451–460.

- Svetlova, M., Nichols, S.R., Brownell, C.A., 2010. Toddlers' prosocial behavior: from instrumental to empathic to altruistic helping. *Child Dev.* 81, 1814–1827.
- Tamura, Y., Shibukawa, Y., Shintani, M., Kaneko, Y., Ichinohe, T., 2008. Oral structure representation in human somatosensory cortex. *Neuroimage* 43, 128–135.
- Taulu, S., Hari, R., 2009. Removal of magnetoencephalographic artifacts with temporal signal-space separation: demonstration with single-trial auditory-evoked responses. *Hum. Brain Mapp.* 30, 1524–1534.
- Taulu, S., Simola, J., Kajola, M., 2005. Applications of the signal space separation method. *IEEE Trans. Signal Process.* 53, 3359–3372.
- Toth, K., Munson, J., Meltzoff, A.N., Dawson, G., 2006. Early predictors of communication development in young children with autism spectrum disorder: joint attention, imitation, and toy play. *J. Autism Dev. Disord.* 36, 993–1005.
- Warneken, F., Tomasello, M., 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301–1303.
- Weiss, S.M., Meltzoff, A.N., Marshall, P.J., 2018. Neural measures of anticipatory bodily attention in children: relations with executive function. *Dev. Cogn. Neurosci.* 34, 148–158.
- Zmyj, N., Daum, M.M., Aschersleben, G., 2009. The development of rational imitation in 9- and 12-month-old infants. *Infancy* 14, 131–141.
- Zmyj, N., Jank, J., Schütz-Bosbach, S., Daum, M.M., 2011. Detection of visual-tactile contingency in the first year after birth. *Cognition* 120, 82–89.