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Cite this article: Marshall PJ, Meltzoff AN. 2014 Neural mirroring mechanisms and imitation in human infants. *Phil. Trans. R. Soc. B* **369**: 20130620. http://dx.doi.org/10.1098/rstb.2013.0620

One contribution of 19 to a Theme Issue 'Mirror neurons: fundamental discoveries, theoretical perspectives and clinical implications'.

Subject Areas:
neuroscience

Keywords:
infancy, imitation, neural mirroring, electroencephalogram, mu rhythm

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Neural mirroring mechanisms and imitation in human infants

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Studying human infants will increase our understanding of the nature, origins and function of neural mirroring mechanisms. Human infants are prolific imitators. Infant imitation indicates observation–execution linkages in the brain prior to language and protracted learning. Investigations of neural aspects of these linkages in human infants have focused on the sensorimotor mu rhythm in the electroencephalogram, which occurs in the alpha frequency range over central electrode sites. Recent results show that the infant mu rhythm is desynchronized during action execution as well as action observation. Current work is elucidating properties of the infant mu rhythm and how it may relate to prelinguistic action processing and social understanding. Here, we consider this neuroscience research in relation to developmental psychological theory, particularly the 'Like-Me' framework, which holds that one of the chief cognitive tasks of the human infant is to map the similarity between self and other. We elucidate the value of integrating neuroscience findings with behavioural studies of infant imitation, and the reciprocal benefit of examining mirroring mechanisms from an ontogenetic perspective.

1. Introduction

Behavioural studies of human infants show that the observation and execution of human acts are tightly linked. One striking example is imitation: human infants imitate a wide range of behaviours they observe carried out by others. Imitation indicates that infants can use the perceived acts of others to generate their own matching acts—action perception drives action production. Through the social context of imitation, children learn skills, tool-use techniques and cultural practices. To build their repertoire, human infants need not rely on their own individual discoveries or extrinsic reward and punishment following from their own actions. Rather, infants accelerate and amplify their knowledge of people, things and the causal effects of human action, by observing the acts of other social agents and using this as a basis for self-action [1].

Human infants are more prolific imitators than the young of any other species; they are imitative generalists and are motivated to imitate a wide range of motor, vocal and object-related acts without explicit reward. Infant imitation is not the manifestation of an uncontrollable impulse—infants do not imitate every act they see, no matter how familiar the motor pattern or interesting the effect [2]. Imitation is regulated by top-down factors, including infants' anticipation of the emotional reactions of other people to the infants' impending actions [3].

Imitation has attracted interest from diverse fields ranging from developmental science, experimental psychology, cognitive neuroscience, robotics, evolutionary biology and the philosophy of action [1,4–6]. Studying imitation holds the potential for prompting insights that span behavioural findings, cognitive models and neuroscience data. For this potential to be realized, however, one challenge is to elucidate the psychological and neural mechanisms that undergird the rapid imitative learning of human children. This paper focuses on human infants and the unique contributions that studying ontogenesis can make in understanding neural mirroring mechanisms and their relation to imitation.

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2. Ontogenesis: developing self–other maps at psychological and neural levels

Behavioural work on imitation has firmly established that preverbal infants have bidirectional maps between action perception and their own action production. A key question is how to characterize the ontogeny of the underlying neural processes [7]. How might such neural processes be measured in infants, and how do they relate to imitative learning and other key aspects of early human social cognition?

Developmental investigations can draw on neuroscience studies with non-human primates and adult humans, in which there has been intense interest in elucidating the nature and function of neural mirroring mechanisms [8–12]. However, relevant *ontogenetic* issues remain understudied—perhaps because of the difficulties in carrying out neuroscience studies in infants—despite the potential of such data for unlocking key puzzles in the field (see also [13]).

In considering the potential role of neural mirroring mechanisms in imitation, it is immediately apparent that a simple notion of direct resonance between observation and execution is not sufficient to account for the range of imitative abilities documented in human infants and young children. Other cognitive mechanisms and social motives are necessary to explain the full scope of the behavioural findings. Consider the following examples. First, human infants perform deferred imitation based on their memory of a perceptually absent display after delays of one week or more [14,15]; there needs to be postulated some storage or representation of observed events that can be used to generate a matching response at a later time. Second, infants and young children selectively imitate, regulating who and what to imitate as well as when to perform the imitative act. Thus, much of human infant imitation is not an automatic, uncontrolled impulse but is under intentional control, modulated and governed in ways that have been quantified [3,16,17]. Third, if an adult strives to accomplish a goal but fails, the infant will not imitate what they actually observe but rather what the adult intended to do [18,19]. Fourth, studies of facial imitation show that young infants correct their imitative responses [16]. Such correction implies response guidance—a cross-modal (visual-proprioceptive) matching-to-target process.

A comprehensive, neurobiologically informed theory of imitation and its development will need to account for this panoply of behavioural data. At the present point in time, the relevant experiments with human infants using neuroscience measures have focused on a specific subset of the imitative capacities discovered by the behavioural work, namely immediate imitation of goal-directed acts. This paper analyses this work, which relies chiefly on the infant electroencephalogram (EEG). We believe that this work sheds light on the role of neural mirroring mechanisms in establishing and supporting a prelinguistic mapping between self and other at the level of bodily acts. The nature and extent of this self–other linkage would be influenced by, and would further influence, the interpersonal interactions that transpire between parent and child and by the cognitive processing of, and behavioural reactions to, those social interchanges.

Although the ontogenetic investigation of neural mirroring mechanisms is rather new, it can draw on well-established behavioural data and psychological theory. There is a psychological theory about the ontogenesis of self–other correspondence—the 'Like-Me' framework [20,21]—which proposes that the bedrock foundation for human social cognition is the infant's prelinguistic processing of other people as 'like-me'. According to this view, infants use self-generated experience—including prenatal motor activity—to form a supramodal act space that supports and enables postnatal mapping between their own bodily acts and those observed in others. This view draws on an 'active intermodal mapping' (AIM) model of imitation [16] that specifies at a psychological level the cross-modal 'metric of equivalence' between the perception and production of matching acts. In this paper, we suggest that infant neuroscience studies can complement and illuminate such theorizing from cognitive psychology.

In keeping with a developmental orientation, we believe that although infants, even newborns, can detect and use the cross-modal equivalence between their own acts and those of others, there are also developmental changes and enrichments of this system that play a role in developing a mature adult social cognition (sometimes called 'theory of mind' or 'mentalizing'). How the initial prelinguistic phase is transformed into the mature adult state is a topic of intense interest in developmental science both at the level of cognitive neuroscience [22–24] and psychological mechanisms [25].

3. The sensorimotor mu rhythm

Commonly used neuroimaging methods in adult work on neural mirroring, such as functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS), are not feasible for use with infants. However, developmental work has been accelerated by the realization that measures derived from the EEG can inform the study of overlaps between action execution and observation in preverbal humans. Investigators working in this area have been particularly interested in the developmental properties of the sensorimotor mu rhythm over central electrode sites.

Although the adult mu signal has two frequency components, one centred around 10 Hz and another occurring at around 20 Hz [26], experiments have tended to focus on the lower frequency component, which falls within the alpha frequency range (8–13 Hz in adults). This alpha-range component of mu is functionally distinct from the classical occipital alpha rhythm that occurs over posterior electrode sites [27]. Unlike the occipital rhythm, the adult mu rhythm over central regions is desynchronized (reduced in amplitude) by bodily movement and somatosensory stimulation and is minimally affected by light/dark changes [28,29].

While changes in the adult mu rhythm in response to self-movement were well documented [30], studies using magnetoencephalography [31,32] and EEG [33–41] further revealed that the adult mu rhythm is desynchronized during the observation of others' actions. Related effects were reported with older children [42,43], setting the stage for work with prelinguistic human infants using EEG.

Recent work on the infant mu rhythm has built on a prior literature of applying EEG methods to social and cognitive development [44–46]. Studies of the development of the EEG signal indicated that the mu rhythm is present in infancy [47,48] and that it occupies a lower frequency range in infants

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compared with older children and adults, as do other brain rhythms [47,49]. The last few years have seen a rapid growth of studies using the mu rhythm to examine action processing in human infants (for reviews see [7,50,51]). Although outside our focus on human work, relevant EEG work has also been carried out in infant rhesus monkeys [52,53].

Table 1 presents the extant studies of the EEG mu rhythm in human infants according to several key dimensions: (i) the kinds of actions used (e.g. grasping versus pressing), (ii) whether both action execution and action observation conditions were included and contrasted, (iii) whether the experimental protocol involved live humans or video (two dimensional) actions, and (iv) whether the protocol involved face-to-face social interaction or not. These procedural variations accompany differences in theoretical orientation and in the interpretation of mu rhythm desynchronization. Such differences notwithstanding, the accumulated body of literature clearly shows that measures derived from the infant EEG are useful for investigating how infants perceive, process, compare and interpret the actions of self and others.

In the remainder of this paper, we focus on recent work in which we have taken up the challenge of studying changes in the infant mu rhythm as recorded during live social interactions with an adult partner. One motivation for our developmental neuroscience work is the theory, based on behavioural data, that young infants gain an initial foothold on the social world through the recognition that other people are 'like-me' in their morphology and bodily actions [20,21]. We believe that studies of the infant mu rhythm, when taken together with developmental theory and extant behavioural data, can serve as a useful tool for illuminating the origins, nature and scope of human social cognition and interpersonal emotions.

4. Examining self–other mappings in early human development

We conducted a series of converging studies examining imitation and self–other mapping using infant EEG. These are briefly sketched in this section to give a flavour of the nature of the work. A detailed analysis of the findings and the inferences they license then follows in §5.

In one study, we used a social-interactive task to examine infants' EEG responses during both action perception and action production conditions [54]. Following a strict experimental protocol, 14-month-old infants took turns with an adult executing and observing a goal-directed act (pressing a button on a novel box). Previous behavioural work had established that infants at this age would quietly watch such an act and also imitate it [15]. Reactivity of the infant mu rhythm over central sites was examined to both observation and execution of the target act relative to baseline epochs preceding each trial. As predicted, infants' own actions on the button box as well as their observation of the experimenter's acts were associated with significant mu rhythm desynchronization.

We next investigated three fundamental aspects of self–other mapping that are important in the social development of human infants. One study examined the neural correlates of being imitated. We tested whether infants treat being imitated by an adult in a special fashion and whether seeing an adult act like a 'biological mirror' is associated with changes in the mu rhythm. This question was guided by behavioural work showing that infants are attracted to people who match the form of their actions. In a two-choice perceptual test, infants preferred to look at people who matched their actions versus those who mismatched them [20], with infants also showing more positive emotion towards the matching adult (indicating an affective-reward component). In the infant EEG work, we examined the neural correlates of being imitated by systematically manipulating whether the adult matched or mismatched the behaviour of the infant. This allowed us to examine whether the mu rhythm is sensitive to congruence in the form of executed and observed actions.

In another study, we evaluated the effect of infants' self-experience on neural processing during the observation of other people's acts. We tested whether infants could use their own hands-on practice with particular objects to extract expectations about how other people would act on those objects. Infants were given experience of manipulating objects that differed in weight, and we then examined the mu rhythm response during observation of another person acting on similar objects.

Another application of infant EEG described below concerns the somatotopic organization of the mu rhythm. In this work, infants saw an adult perform goal-directed acts that led to the same effect as they had themselves produced (i.e. the goal/outcome was controlled). We systematically varied whether the adult accomplished that end using one body part (hand) or another (foot). This experiment assessed whether the infant mu rhythm response is mainly sensitive to goals, outcomes or effects, or whether it also reflects details of *how* an outcome was achieved, in particular which effector is used. In this study, we also directly examined the neural underpinnings of the correspondence between the body of self and other—a key component of infant imitation.

5. Infant responses to being imitated: brain and behaviour

Human infant imitation is fundamentally social and provides infants with valuable information about the psychological attributes of other people. The mechanisms underlying imitation are hypothesized to be bidirectional: the process that takes visual input and generates a matching response can also run in reverse, which allows the recognition of when the self's own actions are being mirrored [20]. Through such reciprocal imitation, infants are hypothesized to exercise and elaborate their grasp that others are 'like-me', which is instrumental in building human social cognition [25].

Behavioural studies have demonstrated that preverbal infants show particular interest in watching an adult who acts like them [73–76]. This interest also manifests in everyday social interactions between infants and caretakers. Many human parent–child games are reciprocal in nature, and mirroring games are a favourite with human infants. The sensitivity to being imitated is not only apparent in infancy, but adults also have positive reactions to behavioural mirroring [77] and often unconsciously copy the postures, expressions and mannerisms of their social partners [78].

What is so engaging for human infants about seeing their own actions mirrored back to them? We believe that temporal contingency is important but so is the similarity of the form

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Table 1. Infant EEG studies using the mu rhythm response to investigate action processing. Studies are categorized by primary research question (in subheadings).

references	mean age (months)	conditions	nature of protocol	major findings using mu rhythm
(a) object-directed hand actions				
Marshall *et al.* [54]	14	execution and observation	live; interactive	significant desynchronization for both execution and observation of button press
Nyström [55]	6	observation only	video; non-interactive	action observation condition did not differ from baseline (viewing moving dot)
Nyström *et al.* [56]	8	observation only	live; non-interactive	greater during observation of object-directed grasp versus hand movement
Southgate *et al.* [57]	9	execution and observation	live; non-interactive	significant desynchronization during execution and observation of grasp
Southgate *et al.* [58]	9	execution and observation	live; non-interactive	greater during observation of grasp act than flat hand movement
Warreyn *et al.* [59]	24	execution and observation	live; non-interactive	responses for object-directed actions and for observing intransitive hand movements
(b) variations in experience with actions/objects				
Marshall *et al.* [60]	14	execution and observation	live; interactive	mu response varied with actual (execution) or expected (observation) object weights
Paulus *et al.* [61]	8	observation only	audio only; non-interactive	greater during perception of sound associated with S's experience of carrying out that action
Paulus *et al.* [62]	8	observation only	audio only; non-interactive	greater during perception of sound previously paired with S's observing that action
Southgate & Begus [63]	9	observation only	video; non-interactive	greater in context suggesting impending action (even impossible acts for S to execute)
Stapel *et al.* [64]	12	observation only	video; non-interactive	greater for unusual versus more usual actions
van Elk *et al.* [65]	15	observation only	video; non-interactive	response to viewing walking versus crawling depended on crawling experience
Virji-Babul *et al.* [66]	7	observation only	video; non-interactive	responses during observation of grasping, walking and object movement
(c) social influences				
Reid *et al.* [67]	14	observation only	live; interactive and non-interactive	greater during observation of actions carried out in interactive than non-interactive context
Ruysschaert *et al.* [68]	26	execution and observation	live and video; interactive and non-interactive	greater for observation of live versus video; significant response during execution
Saby *et al.* [69]	14	execution and observation	live; interactive	greater during observation of actions that the infant had just carried out
Southgate & Vernetti [70]	six	observation only	video; non-interactive	greater when infants were presumed to be anticipating a reach by an actor
(d) somatotopy				
Saby *et al.* [71]	14	execution and observation	live; interactive	somatotopic pattern during execution and observation of hand and foot actions
Marshall *et al.* [72]	14	observation only	live; non-interactive	somatotopic pattern during observation of hand and foot actions

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of the participants' acts. The relevant behavioural tests with infants [20,76] revealed that they do not simply prefer people who are acting 'just when they act' (temporal contingency) but are attuned to people who are acting 'just like they act' (structural congruence). In these studies, infants faced two adults who sat passively until the infant performed a target act. This triggered both adults to act in unison; with one matching the infant and the other performing a mismatching response. Results revealed that infants looked longer and smiled more at the imitator.

In a recent study [69], we examined the neural correlates of reciprocal imitation (see also [67,79]). We measured 14-month-old infants' brain responses to observing an experimenter's button press act, and systematically varied the act that the infants executed immediately before they observed the adult. Specifically, in the initial part of each trial, infants either had executed a button press or they had grasped a small toy. They then immediately saw an adult execute a button press (i.e. the visual stimulus was controlled). Thus, the mu rhythm was measured during the observation of an act presented in two contexts—one in which the adult was mirroring the infant's act and the other where she was not.

Desynchronization of the mu rhythm at central sites was greater when infants observed an act that matched their own executed one than when they observed a mismatched act. This makes theoretical sense: given that both the observation and execution of an act elicit mu rhythm desynchronization, their co-occurrence in mutual imitation episodes elicits a particularly strong neural response. Mutual imitation is a kind of super-mirroring: the infant's neural response to it is highly distinctive and significant.

6. Heavy lifting: sensitivity of the infant mu rhythm to self-experience

Also tested was whether infants' self-experience with objects changed their mu rhythm response when they observed another person manipulate similar objects [60]. We examined patterns of mu rhythm desynchronization when infants observed another person reaching for objects that the infant believed to be heavy or light, based on their own prior experience.

Studies with adults have shown increased facilitation of sensorimotor cortex during the observation of grasping and lifting of objects expected to be heavier rather than lighter [80–82]. In our infant study, infants first learned particular colour-weight correspondences for two objects. They learned that an invisible property of the objects—the weight—could be predicted by the visible property of colour. We then analysed infants' mu rhythm responses when they observed an experimenter reach towards the objects, testing for differences based on the 'expected weight' that the other person would encounter.

Results revealed effects of infants' prior self-experience on the EEG response during observation of the experimenter's reach. Specifically, the effects of object weight were manifested in hemispheric differences in the mu rhythm response to actions on the (expected) heavier and lighter objects. These hemispheric differences were specific to central electrode sites, with similar effects not seen over other regions. Although there was between-subjects variability in the data, the patterning of means showed that when adults approached the objects that infants thought were heavier, this was associated with greater mu desynchronization over the right central site, with an opposing effect being seen for the left central site.

The pattern of effects suggests that the infant mu rhythm is sensitive to infants' predictions and anticipations about adult acts. Infants' neural reactions to seeing another person reaching towards objects is conditioned by the infants' beliefs about these objects, as derived from their prior first-person 'hefting' of them. Such neuroscience results are compatible with behavioural studies that infants' self-experience changes their expectancies about others' engagement with the same objects [2,83,84].

7. Somatotopic organization of self and other: the body in the infant brain

Behavioural work shows that infant imitation is influenced by the specific means by which an observed action is carried out. One striking example is that 14-month-old infants imitate the novel act of using their heads to touch an object to activate it [15]. This suggests that the specific effector used to accomplish a goal is preserved in infants' action representations. Here, we examined the neural correlates of which body effector is used.

The representation of the body is integral to Meltzoff & Moore's [16] cognitive theorizing about how infant imitation is accomplished. According to their AIM model, imitative acts of infants and adults can be differentiated into three interlocking subcomponents: the body part used, the movement carried out and the goal or end-state achieved. Concerning the first, Meltzoff and Moore argue that accurate infant imitation necessitates infants identifying which body part on their own body corresponds to that of the other person's—a process they call *organ identification*.

In two recent studies, we used infant EEG to investigate infants' neural representation of their own and others' bodies [71,72]. The orderly mapping of specific body parts onto motor and somatosensory cortex—a somatotopic organization—has been documented in both adult humans and non-human primates [85]. In adults, this organization is also reflected in the mu rhythm response, such that executed (and imagined) hand movements are associated with greater mu desynchronization at central electrodes overlying hand regions of sensorimotor cortex (electrodes C3 and C4) than over the foot area (electrode Cz); conversely, for foot actions mu desynchronization is greater over the foot area than over hand areas [30,86,87]. In adults, somatotopic patterns of cortical activation during action observation have also been shown using other techniques beyond EEG, including fMRI [88–91] and TMS [92].

Studies of sleeping infants suggest a pattern of somatotopic brain activity in response to direct tactile stimulation of different body parts and infants' spontaneous movements [93,94], but no prior study had examined the possibility of infants' somatotopic responses to the mere *observation* of another's action.

In an EEG study of infant somatotopy, we tested two randomly assigned groups of 14-month-olds [71]. Infants in both groups saw the same experimenter achieve the same goal (pushing a button to trigger an effect), but one group observed the experimenter use her hand to act on the object

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and the other group observed her use her foot. We predicted that infants observing hand actions would exhibit greater desynchronization at electrodes overlying hand areas of sensorimotor cortex (C3, C4) than at the electrode overlying the foot area (Cz). For infants observing foot actions, the opposite pattern was predicted.

Consistent with the prediction of somatotopy, we found a significant difference in the spatial distribution of the infant mu rhythm response as a function of experimental group. Desynchronization of the mu rhythm over the foot area of sensorimotor cortex was greater in the group of infants who observed foot actions than in the group who observed hand actions. Conversely, desynchronization over the hand area was greater for the infants who watched hand actions relative to those who observed foot actions. Such an effect was not seen over the parietal region, suggesting that the somatotopic response of the infant mu rhythm was specific to central sites.

In a further study [72], we extended this work by including both action observation and execution conditions and using a more socially interactive test paradigm while collecting infant EEG. The infant and adult shared a goal of pressing a button to activate an interesting effect, with protocol being designed such that the button could be pushed by using either hands or feet, yielding four experimental conditions: (i) infant execution of a hand act to achieve the goal, (ii) infant execution of a foot act to achieve the goal, (iii) infant observation of the adult using her hand to achieve the goal and (iv) infant observation of the adult using her foot to achieve the goal.

When infants executed hand versus foot acts, the pattern of mu rhythm activity overlying the hand and foot areas showed the predicted changes. Importantly, we also replicated and extended our finding of a somatotopic distribution of mu rhythm desynchronization during action observation.

These findings show that watching a person act using a particular body part is associated with activation of the corresponding area of the infant's own sensorimotor cortex. This constitutes the first evidence for the somatotopic organization of infants' neural responses to the mere observation of human acts. Our findings are consistent with the literature on infant imitation showing that infants maintain a representation of the specific effector used by an adult model to fulfil a goal [15]. They are also compatible with the body part specificity in neonatal behavioural imitation—tongue protrusion to tongue protrusion, and mouth opening and lip protrusion to those observed gestures [16].

8. Unpacking the origins and meaning of mu rhythm desynchronization

We have presented evidence from infant studies relating both to the literature on neural mirroring in adults (human and non-human) and also to data and theorizing about human imitation in infancy. The studies suggest that developmental neuroscience methods using the sensorimotor mu rhythm can provide information about prelinguistic action processing, and more specifically, can illuminate the neural correlates of infant imitation. In order for progress to continue, it will be important to place the work on mu rhythm desynchronization within a developmentally oriented framework that connects, and is coherent across, the behavioural, cognitive and neurophysiological levels of analysis. With this goal in mind, we suggest two signposts that are grounded in the adult cognitive neuroscience literature and that suggest key topics for future developmental work.

(a) The nature and origins of the mu rhythm

While much of the relevant literature on the mu rhythm in adults has focused on the alpha (8–13 Hz) range, some studies have also included a consideration of oscillations in the beta (15–30 Hz) range [95–97]. This consideration follows in part from qualitative observations of the distinct appearance of mu as an arch-shaped or 'wicket' rhythm [98], which hinted that it might be composed of two different cortical rhythms. This was indeed confirmed by quantitative studies in adults showing the presence of two related rhythms over sensorimotor areas: one at around 10 Hz and the other cycling around 20 Hz, which falls in the beta frequency range [26].

Further work with adults suggested different cortical origins for these two oscillations, with the alpha-range mu rhythm being localized to postcentral somatosensory cortex and the higher frequency beta-range component originating in precentral motor cortex [99]. This suggests the provocative possibility that these components of the mu rhythm may be responsive to different aspects of observed acts [87,100]. Related work in adults has found that changes in beta power may be particularly related to the kinematic aspects of observed actions [101].

Localization studies in adults suggest that the alpha-range component of the mu rhythm is mainly generated in primary somatosensory cortex [102–104]. Furthermore, the adult EEG mu response varies with changes in somatosensory aspects of observed actions [105–107], a finding that connects with other work at the intersection of somatosensory processing and social neuroscience [108], including affective aspects [109].

Taken together, the foregoing work raises the intriguing theoretical point that the extant work on the infant mu rhythm should not necessarily be interpreted with an exclusively 'motor' emphasis. Interestingly, cognitive models of early imitation highlight infants' use of proprioceptive and tactile-kinesthetic feedback in formulating imitative responses [16], which fits well with the somatosensory origins of the alpha-range mu rhythm. Further developmental neuroscience work may shed light on this suggestion and can also test whether alpha- and beta-range rhythms are differentially related to aspects of action processing in infants. At this point, only a small number of infant studies of the mu rhythm have included a consideration of a higher frequency (beta) range, and findings have been inconsistent [50].

(b) Attentional processes and sensorimotor engagement

In the discussion of why the infant mu rhythm is particularly responsive during episodes of mutual imitation [69], we speculated that infants' perception of an intercorporeal match between the acts of self and other may prompt an enhancement of attention, which also enhances the engagement of sensorimotor processes.

In tasks that do not involve social interaction, the adult mu rhythm shows greater responsivity during the observation of actions that are 'more relevant' to ongoing task requirements, compared with observing less relevant actions

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[110,111]. This increased responsivity to relevant actions may be amplified in a socially interactive context in which the actions of others are connected to one's previous (and impending) actions. Indeed, work with children and adults shows that mu rhythm desynchronization is greater when an observed act occurs in the context of joint action with another person [112,113]. The neural correlates of such 'social attention' deserve further investigation, particularly given the new developmental neuroscience work on social interaction, attention and reward in typically developing children [114,115] and children with autism [116,117].

There is also increasing recognition of the connection between attentional and sensorimotor processes. According to one contemporary perspective, the neural manifestation of attention can be framed as increased activation of cortical networks related to task-relevant sensorimotor processing [118]. Studies in adults have examined the role of alpha-range rhythms in the facilitation of attention towards upcoming sensory events, with implications for the way in which these events are perceived [119]. Related research has shown that fine-grained temporal and spatial changes in the alpha rhythm at posterior sites during anticipatory visuospatial attention can predict aspects of the perception of subsequent visual stimuli [120]. Intriguingly, a role for the mu rhythm in perceptual processes has also been reported, with changes during the anticipation of tactile stimulation being related to subsequent stimulus perception [96,121].

This foregoing work is relevant for the current discussion of infant neural mirroring in two ways. First, it invites consideration of whether changes in mu rhythm activity during human social interaction can be found during the anticipation of sensory stimulation delivered to others. Second, it suggests that the study of oscillatory brain activity (particularly alpha-range rhythms) provides a tool for exploring the interconnections among attention, perception and action [122], not only in adults but also developmentally. The emerging technology of infant magnetoencephalography (MEG) also has particular promise in this respect, as it allows a finer parsing of both the temporal and spatial aspects of oscillatory activity in the developing brain [123].

9. A developmental perspective on neural mirroring mechanisms

One psychological task accomplished by the human infant is the recognition of similarities and differences between self and others, which forms the bedrock of human social cognition [20]. Adult humans experience the felt connection that other people are 'like-me', which has roots in infancy and gives rise to moral judgements and behaviour in the mature state [25]. As more powerful developmental neuroscience techniques become available, we can look forward to an increasingly more comprehensive rapprochement between the neural, psychological and behavioural levels of analysis in the development of such 'like-me' processes.

Data from existing studies, including those using the infant mu rhythm, already license some initial speculations. For instance, infant somatotopic EEG responses suggest that the specific body part used by self and other is tagged in the infant's action representation. This in turn has implications for understanding infant imitation. We can agree with the idea that goals, end-states and effects are important in action processing and imitation; however, there is a crucial additional point emerging from the neuroscience findings. The somatotopic pattern for both execution and observation indicates that the specific means used to accomplish a goal is also coded. This is highly relevant to characterizing human infants, because early work with non-human primates suggested that the majority of mirror neurons were activated via the goal of an act and by 'transitive' but not 'intransitive' actions (i.e. for goal-directed acts on objects and not empty miming). The infant somatotopy work suggests that *how* an act is accomplished, the specific effector used, is also coded by the human infant neural system—as it is in adults [89].

The somatotopy findings also invite links to developmental theory concerning social–emotional aspects of human social understanding—the feelings of intersubjectivity and shared communication experienced by two people as they interact. Prior to language, infants communicate through reciprocal actions and gestural turn-taking. One puzzle in developmental science is how infant intersubjectivity gets off the ground [124–126]. Based on our EEG findings, we speculate that the intercorporeal mapping for body parts of self and other is a building block for intersubjectivity: my hand and your hand are similar; my foot and your foot are similar; when I see you do something, I can imitate it in part because I can identify the corresponding body parts across self and other.

Given the findings of facial imitation by human newborns [16], two further issues are ripe for neuroscience exploration: (i) the origins and initial state of neural mirroring at birth and (ii) how it is transformed through social-interactive experience. Crucially, work in developmental psychology teaches us that these are not mutually exclusive propositions. The discovery that newborn humans have functional mappings between action observation and execution is not inconsistent with significant changes and elaborations though experience. Rather, it has been hypothesized that a rich set of human newborn competencies, coupled with a prolonged period of immaturity and elaborate adult caregiving and teaching of the young, engender and support the developmental trajectory towards mature adult social cognition [1,25].

Our own findings show that self-experience influences infants' neural responses when observing others [60], and there is good evidence at the psychological level showing that interactive experiences with social partners lead to developmental shifts in infant imitation and other aspects of early social understanding [16,25]. The application of neuroscience techniques to human newborns may help to uncover which aspects of human neural mirroring mechanisms are functional at birth, and how such mechanisms are altered through maturation, self-generated experiences, observational learning and social interchanges with others.

Developmental neuroscience can benefit from the prior neuroscience work in adult humans and non-human primates. Nonetheless, work on ontogenesis is essential for us to understand how the adult state comes to be. A developmental perspective adds an extra (and vital) level of complexity to how we typically conceive of the connections among cognition, behaviour and neural activity [127].

10. Conclusion

There is both novelty and value in exploring neural mirroring mechanisms in the *developing* organism and in examining

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neural mirroring in experimental protocols employing *live social interactions* between infants and adults. By studying human infants in a social context, we can isolate which basic aspects of human social understanding are accomplished without the support of protracted learning, complex adult mentation and language. The study of human infants allows us to discover the origins of human interpersonal beliefs, attitudes and emotions at a primitive, prelinguistic level and how they undergo change with age. The combination of neuroscience techniques and developmental science promises to provide new explanations for the complex social understanding and cultural learning that characterize human society.

Acknowledgements. The authors thank David Liu for comments on a previous draft of this manuscript.

Funding statement. The preparation of the paper was supported by grants from NIH (HD-68734) to P.J.M. and NSF (SMA-0835854) to A.N.M.

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