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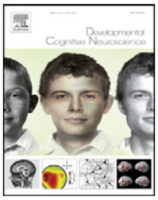

Review

Neural mirroring systems: Exploring the EEG mu rhythm in human infancy

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ABSTRACT

How do human children come to understand the actions of other people? What neural systems are associated with the processing of others' actions and how do these systems develop, starting in infancy? These questions span cognitive psychology and developmental cognitive neuroscience, and addressing them has important implications for the study of social cognition. A large amount of research has used behavioral measures to investigate infants' imitation of the actions of other people; a related but smaller literature has begun to use neurobiological measures to study infants' action representation. Here we focus on experiments employing electroencephalographic (EEG) techniques for assessing mu rhythm desynchronization in infancy, and analyze how this work illuminates the links between action perception and production prior to the onset of language.

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1. Introduction

Behavioral studies document that the observation and execution of human acts are closely linked in human infancy. For example, infants imitate actions they observe others perform. The existence of successful imitation indicates that infants can use the acts they perceive to generate their own matching acts: perception drives production. The human infant is a more prolific and skilled imitator than the young of any other species. Although passerine birds learn to sing like their conspecifics and certain nonhuman primates imitate particular acts (chiefly to obtain food), human infants are motivated to imitate a wide range of acts even without explicit rewards for doing so. Infant imitation serves a social-emotional function of communication and bonding. It also serves a cognitive function, as a mechanism for acquiring motor skills, causal information, and tool-use techniques. Human children do not rely exclusively on their own individual discoveries or on reward/punishment contingencies. Before language emerges, imitation is one of the chief mechanisms for early learning in *Homo sapiens* (Meltzoff et al., 2009).

A crucial question concerns the neural processes involved in such everyday human behavior, a topic of increasing interest as the gap is bridged between neuroscience and the study of human social interaction (Blakemore et al., 2004; Frith and Frith, 2010). The intricacy of the behavioral findings suggests that formulating a comprehensive developmental neuroscience of social learning and imitation will ultimately involve examining interactions among multiple brain systems. However, one starting point concerns basic mechanisms by which neural activation during action observation may overlap with the patterns of activation during action execution. Although this highlights just one aspect of the neural processes likely involved in human imitation, it focuses on the fundamental link between perception and production, which is pivotal to successful imitation and which is at the center of our inquiry here.

Interest among neuroscientists in perception–action coordination and imitation has long historical roots, but its visibility was boosted by the discovery of “mirror neurons,” using single-cell recording techniques, in the ventral premotor cortex (F5) of macaque monkeys (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). These neurons respond not only when a monkey carries out a particular goal-directed action on an object (e.g., grasping a peanut), but also when the monkey observes the same action being carried out by another individual. It is not well established that individual mirror neurons exist in the human brain, because single-cell recording is not possible in typically functioning people (although for a study of adult epileptic patients see Mukamel et al., 2010). Nonetheless, there is a great deal of evidence for overlaps in activation of certain brain systems during action execution and action observation in humans (e.g., Decety and Grèzes, 2006; Frith and Frith, 2010; Hari and Kujala, 2009; Rizzolatti and Craighero, 2004).

In adults, evidence for shared neural circuits for action observation and execution has derived from a variety of neuroimaging techniques including functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), and electroencephalography (EEG), as well as the transient disruption of cortical networks through the use of transcranial magnetic stimulation (TMS). The fact that there is shared circuitry – at some level of description – is not contentious. However, there is a vigorous debate about the inferences that can be drawn from the existence of such circuitry. Some investigators argue that a human “mirror neuron system” (MNS) plays an essential role in the understanding of others' actions and adults' inferences about others' mental states (Iacoboni, 2009; Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001; Rizzolatti and Sinigaglia, 2010). In contrast, others suggest that many of the broad inferences that have been drawn from MNS research are poorly characterized and depend on speculations that reach too far beyond the empirical findings (Dinstein et al., 2008; Hickok, 2009; Turella et al., 2009).

This essay is not primarily aimed at the debate over a putative human MNS, and indeed, as will become evident, the analysis we provide is largely orthogonal to the debate as it is currently framed. Instead, our focus lies squarely on *developmental* issues. In an attempt to get important new developmental issues on the table – and to avoid being drowned out by the existing controversy over the nature and correct characterization of an adult MNS – we use the rhetorical strategy of largely avoiding the phrases “mirror neurons” or “MNS” with respect to humans. Instead, we prefer the phrase “neural mirroring systems” and seek to use it in a theoretically neutral way that is not wedded to single-cell mirror neurons of the type reported in the monkey work. Echoing the approach of Hari and Kujala (2009), we use this phrase as a theoretical pointer to the fact that some (as yet unspecified) neural circuitry obviously supports human behaviors involving observation–execution coordination. A pressing question is how to best characterize this neural machinery in terms of its origins and development.

A *developmental* focus on the neural processes connecting action observation and execution has received less empirical attention than it deserves. The fact that human infants imitate establishes that action observation and execution are already closely bound in the human preverbal period. Cognitive models of infant imitation have proposed the idea that infants have a “supramodal representation of human acts” that unites into one common framework their own acts and those they see others perform (Meltzoff and Moore, 1997). However, despite a great deal of behavioral work on infant imitation and related constructs in social–cognitive development, until recently there was very little infant neuroscience data relevant to this proposal. Although some speculations about the neuroscience of infant action processing have been offered (Del Giudice et al., 2009; Gallese et al., 2009; Heyes, 2010; Kilner and Blakemore, 2007; Lepage and Théoret, 2007), over the past few years a number of new empirical studies of infants using neuroscience techniques have appeared.

Here we focus on the newly emerging literature from developmental cognitive neuroscience that has used EEG measures to characterize overlaps in patterns of neural activity between action perception and action production in infants and young children. The approach taken in this review involves firstly grounding the developmental neuroscience work by considering related studies done with adults, and secondly analyzing the extant EEG studies that have assessed the mu rhythm as an index of action processing in infants and young children. This review and analysis provides the groundwork for a section of the essay that articulates five open theoretical questions which will hopefully serve to guide future work in this relatively new but growing area of developmental cognitive neuroscience.

2. The EEG mu rhythm as an index of perception–production overlaps in adults

Part of the reason for the dearth of data in human infancy concerning the neural correlates of imitation and action representation stems from the fact that the most frequently used methods for studying these in adults (fMRI and TMS) are not feasible with infants. A breakthrough came when researchers began to apply measures derived from the EEG. EEG methods have been used extensively to investigate infant cognitive and emotional development (Bell and Wolfe, 2007; de Haan, 2007; Johnson, 2010a; Nelson and Luciana, 2008). The newly emerging infant neuroscience work on action processing has capitalized both on this work and also on well-established EEG paradigms that have been used to study action representation in adults. Our focus is on the mu rhythm, which has been the primary measure of interest in the developmental and adult EEG studies of action representation. For infant work on action processing using EEG measures other than the mu rhythm, see e.g., Reid et al. (2009).

The adult EEG mu rhythm occurs in the alpha frequency range (8–13 Hz) and is typically recorded from central electrode sites (e.g., C3, Cz and C4 in the international 10–20 system of EEG electrode placement). It has long been known that the mu rhythm in adults is reduced in amplitude by movement (Gastaut et al., 1954), with more recent work clarifying the specific dynamics of mu rhythm activity prior to, during, and after voluntary movement (Pfurtscheller, 2003). The reduction in mu amplitude at central sites associated with movement onset is thought to be due to a desynchronization – a decrease in neuronal synchrony – associated with the cortical processing of movement-related information (Pfurtscheller and Lopes da Silva, 1999).

The adult mu rhythm over central sites in adults is considered to be separate from the classical posterior alpha rhythm which occurs in the same frequency band (8–13 Hz) but which tends to be strongest at occipital electrode sites and is strongly synchronized (increased in amplitude) by a reduction in ambient illumination or through eye closing. Niedermeyer (1997) summarized the contemporary view that the occipital alpha rhythm and the central mu rhythm are functionally and topographically distinct oscillations within the same "alpha-range" frequency band in adults. Unlike the occipital alpha rhythm, the mu rhythm at central regions in adults is attenuated by voluntary movement and somatosensory stimulation and is minimally affected by light/dark changes or eye closing (Kuhlman, 1978).

The established finding from adults of mu rhythm desynchronization during overt movement is, in itself, only one piece of the puzzle. Extending the initial observations by Gastaut and Bert (1954), recent findings from the adult EEG literature have shown that the mu rhythm at central sites is also desynchronized during the observation of others' actions (Babiloni et al., 2002; Bernier et al., 2007; Calmels et al., 2006; Cochin et al., 1999; Fan et al., 2010; Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy et al., 2004; Oberman et al., 2007; Perry and Bentin, 2009; Pineda et al., 2000; Streltsova et al., 2010). This recent work also builds on earlier research using MEG which demonstrated the activation of motor cortex – without concurrent muscle contractions – during the observation of another person's action (Hari et al., 1998; see also Hari, 2006). This finding sparked further investigation of the mu EEG rhythm and other related oscillations, such as the higher frequency beta rhythm. Pineda (2005, 2008) has summarized the recent literature on the adult EEG mu rhythm, including a discussion of its physiological origins as well as the role that it might play in the study of social interactions and action processing.

The findings concerning the relation of the adult mu rhythm to action processing, combined with the relative ease of collecting EEG data from infants, leads to the question of whether a mu-like rhythm is present in infancy. Emerging evidence suggests that a rhythm indeed exists in the infant EEG signal which has similar properties to the mu rhythm in adults. Although there are a number of key questions that need to be addressed (see Section 6), exploring the properties of this infant EEG rhythm may provide a useful window into the linkages between action perception and production in early human development.

3. The infant central rhythm as an analog to the adult mu rhythm

One starting point in the search for an infant analog of the adult mu rhythm has been to examine the development of the EEG signal across infancy, with a particular focus on unique rhythmic activity around central electrode sites, from where the adult mu rhythm is typically recorded. A second, related consideration has been to examine the functional properties of such rhythmic activity and compare them with the properties of the mu rhythm in adults. We consider both strands of research.

3.1. *Alpha-range rhythmic EEG activity in infancy*

There is a rich history of examining the development of the EEG signal in infants and its relation to psychological development (Bell, 1998; Johnson, 2010a,b; Schmidt and Fox, 1998). This work has established the existence of infant rhythms that are functionally and topographically similar to the classical EEG rhythms in adults, such as the posterior alpha rhythm.

Early studies employed visual examination of the EEG trace to suggest that an occipital alpha-like rhythm is present in infants at a lower frequency range than in adults (Henry, 1944; Lindsley, 1938; Smith, 1941). More recent work using updated analysis techniques has solidified these observations: as in adults, the posterior infant rhythm varies as predicted with manipulations in ambient lighting, but it occurs in the frequency range of 6–9 Hz in the first two years of life (Stroganova et al., 1999), compared with the 8–13 Hz range that characterizes this rhythm in adults.

In addition to an alpha-like oscillation over occipital sites which is prominent during conditions of reduced illumination, studies of the developing EEG have documented a rhythm over central sites which occurs in the same frequency range in infancy (around 6–9 Hz) but which appears to have different functional properties. In his classic work, Smith (1938, 1941) employed visual examination methods to document a distinct oscillation at a frequency of 7 Hz over central sites which could be seen in the waking EEG signal at 4 months of age. The mean frequency of this rhythm, which Smith labeled "central alpha," remained at 7 Hz until around 18 months of age, when it was present at a slightly higher frequency (8 Hz). Hagne et al. (1973) also noted a central rhythm in the EEG which was clearly visible in power spectra at a peak frequency of 6 Hz at 6 months of age.

More recent findings have further illuminated developmental changes in the infant central rhythm. One systematic investigation was carried out by Marshall et al. (2002) who examined the development of the EEG signal from infancy to early childhood in a longitudinal sample during periods of quiet attention to an abstract visual stimulus. During periods of quiet visual attention at the age points of 10, 14 and 24 months, a prominent central rhythm was clearly present in the EEG power spectra with a peak frequency of 7–8 Hz. By 51 months of age, the peak frequency of the central rhythm had shifted to 9 Hz. It is notable that at all ages a similar peak in the power spectra was not clearly discernible over the other scalp regions that were examined in this study (frontal, parietal, and occipital).

Further work has clarified the functional properties of the central EEG rhythm in infancy. As in adults, one way in which this has been done is by contrasting changes in activity at central and occipital sites in response to qualitative changes in visual stimulation. In the early observations of Smith (1941), the amplitude of the infant central rhythm was not reduced by eye-opening, but the occipital rhythm was strongly affected. More recently, the experimental work of Stroganova et al. (1999) confirmed that in contrast to the occipital rhythm, the amplitude of the central rhythm in 7- to 12-month-olds was not increased during a condition of darkness (see also Galkina and Boravova, 1996). On the basis of this evidence, Stroganova et al. (1999) suggested that the infant central rhythm in the 6–9 Hz range is analogous to the adult mu rhythm (see also Stroganova and Orekhova, 2007). The developing trajectory of the peak of the early central rhythm suggests that, as with the posterior alpha rhythm, the frequency range of the infant mu band gradually increases over childhood until it reaches the adult frequency band (8–13 Hz).

Although the foregoing work suggests that the infant central rhythm is functionally distinct from the occipital alpha rhythm, and that it is likely related to the adult mu rhythm, it did not consider whether the infant mu rhythm was reactive to action execution and action observation.

3.2. *Logical considerations in using the infant mu rhythm in the study of action processing*

For studies exploring the relation of the putative mu rhythm in infants to action processing, we suggest two logical considerations. First, it is crucial to test for similarities in the infant EEG response to *both action observation and action execution*. In order to forge clearer connections between the reactivity of the adult mu rhythm and the infant central rhythm, one needs to assess whether the infant rhythm is desynchronized (relative to a baseline condition) for both the perception and production of action. Testing one of these conditions alone is insufficient. Second, it is important to explore the *scalp topography* of infant EEG responses to action observation and execution. Information on the regional patterning of effects would help tie infant work to the adult mu rhythm findings, in which an overlap in response to action execution and observation has been reported to be specific to the central region (Muthukumaraswamy and Johnson, 2004).

Reviewed next are the studies that have specifically attempted to examine the infant mu rhythm in relation to action processing. We begin with studies that reported EEG findings only from one condition–action observation. We distinguish these from studies in which both action observation and action execution conditions have been employed. For each study, we also consider whether the scalp topography of infants' EEG responses was examined in an attempt to look for regional specificity of effects.

4. Infant EEG responses to action observation

In an initial study of infant EEG responses to human actions, Nyström (2008) showed 6-month-old infants and adults videos of a person carrying out goal-directed actions (reaching for and grasping an object). The adults showed greater mu rhythm desynchronization to observing these stimuli compared with observing an inanimate stimulus (a moving dot), but there was no clear evidence of a similar differential response in the infant EEG signal. Based on the foregoing review of the development of EEG responses in infancy, one issue here is that there may be large individual differences in the presence and salience of the mu rhythm in the infant EEG at 6 months of age. It is also possible that the use of video versus live stimuli influenced the results; other studies using neuroscience measures have shown differences in infant responses to 2D versus 3D stimuli in young infants (Carver et al., 2006; Shimada and Hiraki, 2006).

In more recent work, Nyström et al. (2010) reported on EEG responses in 8-month-olds during the observation of a live experimenter performing a grasping action. Compared with the observation of a hand movement that was not directed toward a particular goal, there was a significant desynchronization in the 5–9 Hz frequency band which occurred around the time that the object was grasped. This effect was quite subtle, however, lasting approximately 100 ms, and unlike other recent findings (reported below) it was only apparent after independent component analysis (ICA) had been applied to the EEG data. In terms of scalp topography, the difference between the two conditions was apparent at various electrodes across the scalp but was concentrated around the mid-central electrode (C4) in the right hemisphere.

van Elk et al. (2008) took a different approach. Rather than using goal-directed hand actions, as in much of the prior work on the mu rhythm in adults, these authors showed 14-to-16-month-olds videos of infants who were crawling or walking. Spectral power in the 7–9 Hz band was more attenuated during the observation of crawling than walking. The authors suggested that this may be related to infants at this age having greater experience with crawling. Follow-up correlational analyses suggested that infants with greater crawling experience showed greater EEG desynchronization to the crawling versus the walking videos. The difference between the crawling versus walking conditions was not significant at left or right mid-central sites (C3 and C4), which are the typical electrode sites for detecting mu, and was only significant at frontal and central midline sites (FCz and Cz). This aspect of the findings is difficult to interpret, although it is possible that it relates to a suggestion in the adult literature (Pfurtscheller et al., 1997) that mu rhythm activity at C3 and C4 is primarily responsive to hand actions, rather than actions involving other parts of the body.

Stapel et al. (2010) computed alpha-range power while 12-month-olds watched sequences showing an adult carrying out two different kinds of actions. In one sequence type, the observed actions were ordinary (e.g., lifting a cup to the mouth), and in the other sequence type, the observed actions were unusual (e.g., lifting a mobile phone to the mouth, instead of placing it on the ear). Power in a narrow frequency band (7.5–8.3 Hz) was significantly lower at fronto-central and mid-frontal sites during the observation of unusual actions compared with ordinary actions. The authors interpreted this as showing a greater desynchronization of the mu rhythm in response to actions which have end-points that differ from what might normally be expected to happen. This inference raises a number of questions. First, it is not clear whether the frontal distribution of the observed effect reflects differences in mu rhythm activity, since an action execution condition was not included which could have clarified the characteristics of the mu response. Second, the notion that observing more unusual actions would be associated with greater desynchronization of the mu rhythm is not altogether consistent with the suggestion that the infant mu rhythm is more desynchronized when infants observe actions with which they have more extensive experience (van Elk et al., 2008).

The studies of Nyström (2008), Nyström et al. (2010), van Elk et al. (2008), and Stapel et al. (2010) provide useful insights into the reactivity of the infant EEG to action observation. However, returning to our logical considerations, it should be noted that although these studies included a consideration of scalp topography during action observation, they did not include an action execution condition. Without such a condition, it is difficult to firmly link the findings to arguments about developmental aspects of a neural overlap between action observation and action execution. We next consider the developmental EEG studies which tested both action observation and action execution conditions.

5. Infant EEG responses to both action observation and execution

5.1. Early childhood studies

Prior to the appearance of studies in infants, a small number of studies using older children examined mu rhythm suppression during both action observation and action execution conditions. In one of the first, Fecteau et al. (2004) used a subdural electrode grid to record EEG from a 36-month-old child with epilepsy who was awaiting neurosurgery. They examined two conditions; while the child drew with her right hand and while she watched an adult carry out a similar drawing action. The main finding was that alpha-range power at two electrodes over somatosensory cortex showed significant decreases in both conditions, relative to a resting baseline in which the child sat quietly with her eyes open.

This preliminary work was followed by a larger study of older children (mean age 8 years) by Lepage and Théoret (2006) who recorded scalp EEG during observation of repetitive hand actions which were either goal-directed (a grasp) or not (moving a flat hand). Observation of the grasping action was associated with greater mu rhythm desynchronization at central sites compared with observation of the flat hand movements. This study also included an action execution condition, with children's execution of hand grasps of an object being associated with a significant desynchronization of the mu rhythm over central sites, compared with the baseline epoch as well as compared with the two observation conditions (observing a grasp or observing a flat hand). Two points are noteworthy. First, the magnitude of mu desynchronization during action execution was much greater than during action observation. Second, analyses were only reported for central electrode sites and thus did not allow for a consideration of the scalp topography of the EEG response.

5.2. Infant studies

Southgate et al. (2009) reported significant desynchronization of what they called “sensorimotor alpha” (i.e., the mu rhythm) in the EEG of 9-month-old infants while they reached toward and grasped objects (small toys) that were presented through closed curtains. The desynchronization in the EEG response was present over a cluster of central–parietal sites during action execution, and reflected a reduction in amplitude during action execution relative to a 200 ms baseline epoch, which began 1000 ms prior to the onset of the infant's reaching action. The use of this temporally separate baseline was presumably meant to minimize the potential contamination of the baseline by EEG activity related to motor preparation.

For the analysis of infants' EEG responses to action observation, the specific frequency between 6 and 13 Hz which showed the maximum desynchronization during infant motor production (reaching) was identified for each infant. Individualized frequency bands were computed which extended 1 Hz above and below this peak frequency. These individual-specific bands were then used during the analysis of EEG from epochs in which infants observed actions being carried out. The use of individualized frequency bands helps compensate for potential individual differences in the frequency of the mu rhythm, although the actual variability between infants may be relatively limited. Although Southgate et al. (2009) did not report the frequency distribution of their mu bands, a second study using similar methods (Southgate et al., 2010) reported that the frequency band was either 6–8 Hz or 7–9 Hz for the majority (17/22) of infants, with the bands for the remaining participants being at slightly higher frequency ranges.

Southgate et al. (2009) analyzed changes in EEG responses during infants' observation of actions carried out by a hand which reached for and grasped an object lying on the stage floor. There were curtains around the stage which initially opened to reveal the object (prior to the hand's appearance) and then closed after the object had been grasped by the hand. Relative to a preceding baseline, there was a small but significant desynchronization during the action observation condition. Further analyses suggested that this decease began when the curtains were opening, prior to the onset of observed movement of the hand. This finding might complicate the interpretation of the results (since the response occurs *before infants observed* the relevant motor act), but Southgate et al. (2009) suggest that it reflected infants' learning to predict the impending action based on the curtain movement. This interpretation was supported by supplementary analyses suggesting that the desynchronization to the curtain opening was not present in the first three trials of the observation protocol, but appeared after that point.

Southgate et al. (2010) used similar methods in a second study of 9-month-olds that manipulated the stimulus in a fine-tuned way. They reported that compared with the movement of a flat, turned-up hand, EEG desynchronization was greater during observation of a reaching hand in a grasping posture, even when the outcome of the hand action was not seen. Consistent with the interpretation of their prior study, and in line with Csibra (2007), this finding was seen as reflecting infants' prediction of the motor program that would be needed to achieve the goal or end-state of the action (i.e., grasping). In order to control for familiarity effects, two other conditions were also contrasted for which the occluder was not present and in which the hand (either as a flat hand or a mimed grasp) moved toward the stage and came to rest on it. No significant difference in EEG desynchronization was observed between these conditions.

Returning to the two logical considerations specified earlier, the first concerned the need to include both action observation and execution conditions. By including both conditions, the studies of Southgate et al. (2009, 2010) advance our understanding beyond the prior work with infants. The second logical consideration concerned the need for analyzing the scalp distribution of EEG responses. In this respect it is notable that their statistical results in these studies were reported only for one cluster of electrodes straddling central and parietal scalp regions and thus detailed scalp topography information is not available.

Marshall et al. (2010) attempted to satisfy both logical considerations simultaneously by examining infants' EEG responses across a range of scalp regions during both action execution and action observation conditions. In formulating a suitable task we capitalized on paradigms and stimuli that have proven useful in assessing infant action imitation. The action was a punctate goal-directed act, specifically a button press on a custom-made button box which triggered a short electronic melody (see Fig. 1). Previous work had shown that 14-month-olds would quietly watch such an act and also imitate it themselves (Meltzoff, 1988), thus demonstrating an observation–execution network at the behavioral level. The experimental question was whether infant mu rhythm desynchronization could be detected during the observation as well as the execution of this action.

We examined EEG reactivity to both perception and production, relative to baseline epochs preceding each trial in which infants viewed simple visual patterns. The reactivity of the EEG rhythm in the 6–9 Hz range over central electrode sites (Marshall et al., 2002) was the focus of the study, although in line with our emphasis on elucidating the scalp topography of the infant EEG response, we also analyzed activity in the same band over frontal, parietal, and occipital scalp regions. The analyses were time-locked to the culmination of the goal-directed action, with the analysis epoch extending 500 ms before and after the button press.

As predicted from the adult work, there was a significant desynchronization over the central region (electrodes

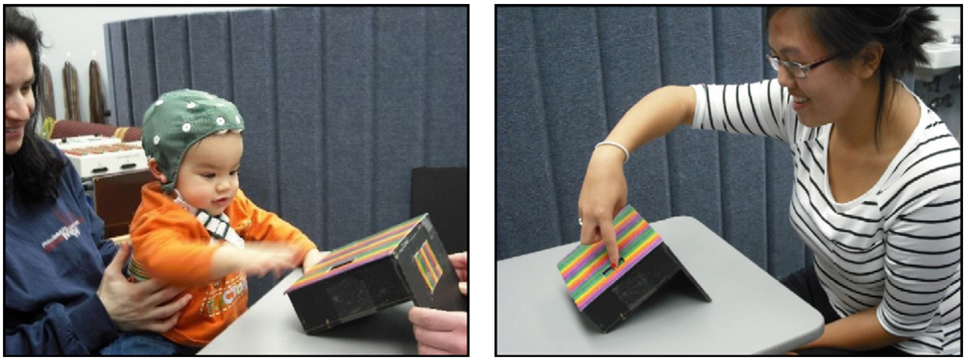

Fig. 1. Photos demonstrating the execution (left) and observation (right) conditions in Marshall et al. (2010). EEG analyses were conducted on the epoch ranging from ±500 ms of the button push by the infant or adult. During observation infants did not have an object; they simply watched.

C3/Cz/C4) during epochs in which infants executed the button press act. There was also a significant desynchronization at central sites when infants observed an adult perform the same act. We extended our analyses to a range of other scalp regions and found that although the reduction in 6–9 Hz band power during action observation extended beyond central sites (to frontal and parietal regions), the significant desynchronization during action execution was specific to central sites. This finding that the central region was the only region in which there was a common desynchronization of 6–9 Hz band power during both action execution and observation is congruent with work on the adult mu rhythm, in which similar regional specificity has been reported (Muthukumaraswamy and Johnson, 2004). Our findings using a goal-directed task (button-press action) further suggest that mu rhythm desynchronization in infants, as in adults, occurs to intentional actions that extend beyond the biologically relevant act of grasping.

6. Five open theoretical questions about the infant mu rhythm response

We have summarized findings suggesting that the 6–9 Hz EEG rhythm at central sites reflects the infant mu rhythm, and is a candidate measure for studying the neural processes involved in infants' action processing. Here we suggest five open questions that are relevant to constructing a more comprehensive theoretical base about the measurement and meaning of mu rhythm desynchronization in infancy, and its potential connection to infant imitation and other aspects of infant social cognition.

6.1. Are there developmental changes in the mu rhythm response?

In compiling the infant EEG studies to date, one can discern signs of a developmental change in the magnitude of mu desynchronization. Consider first the data from action execution. In the study of older children (mean age of 8 years), Lepage and Théoret (2006) reported that the mean extent of desynchronization of mu power at central sites during execution of a hand grasp relative to a baseline epoch was around 60%, which is similar to that reported for adults (Muthukumaraswamy et al., 2004). Marshall et al.'s (2010) work with 14-month-old infants, found a much smaller decrease in power (around 12%) during action execution, relative to a baseline in which the infants looked at an abstract visual pattern. In the Southgate et al. (2009) study with 9-month-old infants, the extent of desynchronization during reaching compared with a baseline epoch just prior to reaching also appears to be small relative to the work with older children and adults (around 10%).

Intriguingly, there are similar differences for the observation of others' actions. Lepage and Théoret's (2006) work with older children showed a desynchronization of around 25% during action observation relative to baseline, which is again consistent with adult work (Muthukumaraswamy et al., 2004). Marshall et al. (2010) found a smaller decrease (around 14%) in band power at central sites when 14-month-olds observed the adult's action. In the Southgate et al. (2009) study of 9-month-olds, the extent of desynchronization during action observation appears to be even smaller (around 5%).

If these changes in the magnitude of the mu response indicate a genuine developmental increase in activity of a neural system subserving action perception–production maps, it would be of considerable theoretical interest. We note, however, that at present there are differences between the studies that make a definitive interpretation difficult. For example, the Marshall et al. (2010) procedure involved a socially interactive, reciprocal imitation protocol with a live experimenter, rather than the blocked presentation of execution and observation conditions (with no give-and-take turn-taking) that was used by Southgate et al. (2009). It is possible that the socially interactive nature of our protocol induced greater EEG desynchronization during action observation.

A direct comparison of the extant studies is further complicated by differences in other methodological details, such as the specific frequency band used, the algorithms employed to compute mu amplitude, the scalp regions analyzed, and the temporal epochs examined. More generally, the variations in these details present a significant issue for constructing a comprehensive picture of the nature and properties of the infant mu rhythm response. Another relevant factor is that there appears to be a great deal of individual variability in the infant mu response, which may partly be a function of the relatively low numbers of trials that are inherent in infant EEG work relative to work with older children and adults.

Two theoretical issues also merit attention. The first concerns the possible emergence of the infant mu rhythm at ages younger than those tested so far. Some of the descriptive work on the infant mu rhythm has suggested that a prominent mu peak is present in the EEG power spectrum in the second half of the first year of life, but not before (Hagne et al., 1973; Marshall et al., 2002). However, the lack of a visual peak in the power spectrum noted in this work does not preclude the possibility that a low-amplitude mu rhythm is present in the first six months of life. In this respect, the requisite studies of EEG responses to action execution and action observation have not yet been carried out with younger infants. Careful studies in the first 6 months of life are needed which comport to the logical requirements outlined earlier (Section 3.2).

Another related issue concerns hemispheric asymmetries in the mu rhythm response to action observation and action execution. The adult literature on the mu rhythm shows inconsistencies (see e.g., Muthukumaraswamy et al., 2004; Perry and Bentin, 2009; Streltsova et al., 2010), and findings from infants are also not clear. For instance, Southgate et al. (2009) reported lateralization of the infant mu response for observation but not execution, but Marshall et al. (2010) found bilateral activation for both conditions. One possible pointer for future investigation comes from work in adults which suggests that lateralization of the mu response may change from early to late stages of action processing (Crone et al., 1998), a possibility which could be further examined in infancy.

6.2. What are the main caveats and technical constraints for clarifying the nature of the neural overlap between action observation and execution in infancy?

As documented above, recent studies from our own laboratories and others have identified a common desynchronization of the infant mu rhythm to action observation and execution. However, findings of regional overlaps between patterns of neural activation via EEG are not, by themselves, sufficient to infer activation of the same underlying neural systems. Here we raise three interrelated issues which span both adult and infant studies using EEG measures.

The first concerns the functional specificity of changes in alpha-range power over central sites. Given that EEG desynchronization in the alpha frequency range can be induced across multiple scalp regions by the engagement of general attentional or effortful processes (Klimesch, 1999), it is important to establish that changes at central sites reflect changes in the mu rhythm rather than being part of a generalized suppression of alpha-range power across the scalp. This issue is not restricted to infancy studies and indeed runs through some recent work on the mu rhythm in adults (e.g., Perry et al., 2010). One related possibility is that volume conduction from other regions contributes to apparent changes in mu power at central sites, which can also make it difficult to establish the functional specificity of such changes. Such considerations make it particularly important for studies to present analyses from a range of scalp regions. The use of Laplacian reference configurations which account for the activity of surrounding electrodes may also be of assistance here, and although these have been used in a few studies of the adult mu rhythm (e.g., Muthukumaraswamy and Johnson, 2004), they have not been utilized in developmental research.

The second issue relates to other difficulties in interpreting changes in mu power at central electrode sites. Work in adults has suggested that changes in oscillatory EEG activity reflect the recruitment of complex combinations of global and local processing networks, which can even be intermixed within the alpha frequency band over the same scalp region (Andrew and Pfurtscheller, 1997). Moreover, in adults, the mu frequency range can be subdivided into upper and lower bands, which have different functional properties (Pfurtscheller, 2003). To this point, developmental studies have not examined these potential complexities.

The third issue comes from suggestions in the adult cognitive neuroscience literature that newer, more complex test paradigms (e.g., crossmodal adaptation or repetition suppression protocols) may provide more stringent tests of shared activation than the procedures used to date (e.g., Dinstein, 2008). The logic behind this suggestion is that activation of brain areas with putative mirroring properties should show adaptation across repeated presentations of the same action, regardless of whether that action is executed or observed. Adult neuroimaging work using fMRI has begun to use such approaches (Chong et al., 2008; Dinstein et al., 2007; Kilner et al., 2009), although there is some debate about the merits of this method as a test of mirroring activity. No relevant EEG work on crossmodal adaptation of the mu rhythm response has been carried out, either in adults or developmentally.

To this point, developmental examinations of the mu rhythm have not engaged with the three foregoing issues; future work should rectify this, a process which could begin by better integrating developmental findings with the cognitive neuroscience literature on the mu rhythm in adults. What may also assist is a deeper engagement by developmental scientists studying mu with the neurophysiological literature on the properties of sensorimotor EEG rhythms from the perspective of motor control (e.g., MacKay, 2004).

There are also technical advances that are likely to further our understanding of the infant mu rhythm response. New MEG technologies adapted for use with infants (Imada et al., 2006; Kuhl, 2010) promise to provide much more specific information about the functional properties and the neural generators of the infant mu rhythm, as has been the case for the adult mu rhythm (Hari and Salmelin, 1997). Near-infrared spectroscopy is also emerging as a candidate technique in infancy (Gervain et al., 2010), but has not been much used to study action processing beyond an initial, exploratory study by Shimada and Hiraki (2006).

Finally, we note a caveat and challenge faced by developmental researchers who are investigating the mu rhythm. The propensity for infants to move during experimental protocols raises particular issues for all neuroscience techniques, including EEG studies of the mu rhythm. Although studies with infants have generally excluded trials in which participants performed overt movements, it will be helpful for future work to seek improved methods to rule out subtle movements (such as the use of tilt sensors, as in Stapel et al., 2010) or even latent muscle contraction. In some studies of adults, but not all, the latter issue has been addressed by measuring electromyographic (EMG) activity during action observation (Muthukumaraswamy et al., 2004), but to date this has not been done with infants.

6.3. Can we build bridges between the infant neuroscience work and behavioral evidence showing the flexibility of human imitation?

A key question concerns whether the mu rhythm response to action observation varies according to the specific bodily transformations used by the infant: Would the mu rhythm be equally responsive to conditions in which different movements are used to achieve the same goal? This question relates to issues in the ongoing debate in the adult cognitive neuroscience literature concerning a putative adult human MNS. Two particular issues in this debate concern the sensitivity of such a system to the goal of an act versus the specific movements used to achieve that goal (for disparate views see Csibra, 2007; Hamilton et al., 2007; Rizzolatti and Sinigaglia, 2010), and more generally the role of top-down influences and modulation by social, cognitive, and contextual factors, rather than direct "motor resonance."

This issue is particularly relevant to developmental scientists, given the extensive literature on infant imitative learning and the ultimate aim of connecting behavioral, cognitive, and neuroscience perspectives on development.

Behavioral studies show that a variety of specific factors influence whether young children imitate the precise body transformation they observe (the "means" used or "how something is done") versus the goal of the act. Behavioral studies also indicate that human children are flexible imitators and not slavish or rote copiers; rather than an automatic echoing of what is in the visual field, there appears to be a good deal of top-down regulation of who, when, and what infants imitate.

Four examples will suffice. First, imitation of the specific bodily transformations occurs in young infants (Meltzoff and Moore, 1997), but in slightly older children it is more likely when the goal of an act is unclear or difficult for the child to discern (e.g., Bekkering et al., 2000; Gattis et al., 2002; Gleissner et al., 2000; Williamson and Markman, 2006) or when children see actions performed by a socially engaging adult who seems to be showing them *how* to perform a novel act (e.g., Gergely et al., 2002; Meltzoff, 1988).

Second, infants are not only sensitive to both the means used and the goal obtained, but they also can abstract and re-enact human goals when they are *inferred* and not directly seen or achieved. For example, in one study an adult struggled to pull apart a dumbbell-shaped object but was unable to do so because his hands slipped off the sides as if the object was stuck (Meltzoff, 1995). The object remained unchanged. Infants saw a pattern of three attempts to pull apart the object. When they were given the object themselves infants adopted different means from that used by the adult; they wrapped their fingers securely around the ends and pulled it apart (something they had not seen). They did not imitate what the adult actually did, but what he "was intending to do" – the goal of the act, not the literal behavior itself.

Third, children can imitate from memory after performing intervening motor acts between observation and execution. This temporal flexibility raises questions about theoretical appeals to direct "resonance" mechanisms. In one study, investigators showed young children how to open a drawer using an innovative technique (Williamson et al., 2008). Children at first tried their own usual means, but when they failed (as assured by the experimental setup), they used their memory of the adult's act. Thus they at first rejected the adult's act. After performing an intervening act and failing, they imitated from memory. This is related to the powerful phenomenon of deferred imitation in infancy. In the "observation-only" test paradigm for deferred imitation, infants are confined to observing a goal-directed act at Time 1 but are not given the object to touch or handle. After a delay, they return to the laboratory and are presented with the object to pick up for the first time. The results show that infants can imitate after a week's delay, performing the act from long-term memory, despite that fact that the adult is now sitting passively and there is no action in the visual field with which to "resonate" (Meltzoff, 1988).

Fourth, infants can inhibit their imitative responding. One study showed that imitation of a goal-directed act was modulated as a function of the emotional response that the act elicited in a third-party observer. Infants witnessed that when an adult experimenter performed the act, an adult observer reacted with negative emotion. This emotion was not directed towards the infant and was not contingent on their actions; the infant was simply observing the adult-adult social interaction. The results showed that infants self-regulated their subsequent imitation. They were loathe to imitate the act as long as the observer was visually monitoring the infant's behavior (Repacholi et al., 2008). Infants selectively chose when it was propitious to imitate based on a conjunction of the emotional history of the observer and whether that observer could visually monitor the infant's response.

All this behavioral research on child development raises two clusters of questions for future neuroscience studies–one concerning top-down influences and the other concerning the aspects of the display ("means or goals") to which the mu rhythm responds. Future research in infants and adults alike will need to isolate whether mu desynchronization during action observation reflects the precise bodily transform used, or whether it reflects an alternative set of movements that could accomplish the same goal. One relevant proposal comes from Southgate et al. (2010), who suggested that the infant mu rhythm response during infants' observation of ongoing actions reflects "motor system activation" which has a predictive quality. This interpretation grows from Csibra's (2007) ideas about neural systems which predict the consequences of other's actions without necessarily mirroring the movements of the actor (see also de Vignemont and Haggard, 2008; Jacob, 2008; Prinz, 2006). However, at this point the EEG research has not allowed for an effective separation of means and goals between action observation and action execution, leaving the extant mu rhythm findings open to multiple interpretations in both infants and adults (see also Chaminade et al., 2002; Gazzola et al., 2007; Jastorff et al., 2010 for discussion of similar issues in adult fMRI and PET work). It is also possible that the infant mu response may be too limited to address such subtleties.

Regarding top-down influences, future studies will need to take into account that although some form of automatic and direct resonance with a visual stimulus may occur in human infants, it is not clear that this notion is sufficient, or maximally helpful, in our attempts to understand the selective, flexible, memory-based imitation that composes the imitative prowess of the human young, and their choices about what, when, and how to imitate (see Meltzoff, 2007a,b for discussion). A deeper examination of these issues is highly relevant for theories of action representation, imitation, and how infants learn causal means-end skills from observing experts in their culture.

6.4. *What are the theoretical implications of the somatosensory origins of the mu rhythm?*

In the literature from adults and infants on EEG responses to action observation, changes in mu rhythm amplitude have often been characterized as indexing "motor activation." However, as noted by Southgate et al. (2009), how the mu rhythm relates to the activity of the motor system is not well understood. It is relevant that historical accounts of the mu rhythm have long noted its relation with somatosensory activation (Chatrian et al., 1959; Kuhlman, 1978). Links between the mu rhythm and the somatosensory system have been further strengthened by recent studies from adults which have used concurrent EEG/fMRI recording or MEG localization methods to show that the EEG mu rhythm reflects activity in (and likely originates in) primary somatosensory cortex (Formaggio et al., 2008; Hari and Salmelin, 1997; Oishi et al., 2007; Ritter et al., 2009; Yuan et al., 2010).

Future work should be directed towards exploring the connections between the mu rhythm, motor system activity, and somatosensory processing. For example, there is an increasingly large body of research showing that activity in primary somatosensory cortex – from where the mu rhythm seems to originate – is heavily influenced by top-down factors (Blakemore et al., 1998), suggesting complex, bidirectional connections between the somatosensory system and a variety of other neurocognitive systems, not only the motor system *per se* (Dijkerman and de Haan, 2007; Longo et al., 2010).

Recent work on how mu desynchronization relates to action processing has taken a particular approach to framing the somatosensory origins of the mu rhythm in the context of its use as an index of motor system activation. According to this view, changes in mu rhythm amplitude index the downstream modulation of somatosensory cortex by activity in areas of motor cortex, particularly premotor areas (Pineda, 2005). In support of this assumption, there is evidence from the adult literature showing the modulation of the somatosensory system by motor system activity during action planning and execution (Voss et al., 2006, 2008).

We suggest that another role for the somatosensory system has been overlooked or downplayed, and that it may be important to understanding the utility of this rhythm (see also Pineda, 2008). One impetus for our suggestion comes from the neuroimaging work in adults by Gazzola and Keysers (2009), who found consistent activation of primary somatosensory cortex across both action execution and observation conditions. These authors argued that this activation during action observation may reflect the simulation of the proprioceptive and tactile consequences of observed actions (see also Keysers et al., 2010). Also in the adult literature, activation of somatosensory cortex has been noted during the observation of tactile stimulation of another person (Blakemore et al., 2005; Keysers et al., 2004).

Further examination of how the mu rhythm response relates to the proprioceptive and tactile (somatosensory) consequences of observed actions may prompt more nuanced thinking in both the adult and infant literatures. With regard to developmental work, it is notable that one theory of infant imitation has emphasized the role of somatosensation (particularly proprioception) in the intermodal mapping of the observed acts of others onto one's own bodily acts (Meltzoff and Moore, 1997). Although connecting these considerations to the infant mu rhythm is speculative at this point, this possibility merits further consideration and may eventually lead us to learn that the infant mu response reflects more than motor system activation alone.

6.5. *How do action experience and learning influence action perception?*

An enduring issue for theories of action representation concerns the role of an observer's prior self-experience. Work with adults using a range of methodologies from cognitive psychology has explored the ways in which experience with specific actions influences the perception of those actions when performed by others. A variety of behavioral evidence has suggested that the perceptual processes involved during the viewing of others' actions vary according to the observer's experience with those actions (e.g., Schütz-Bosbach and Prinz, 2007). From a neuroscience perspective, adult fMRI work has shown that the level of activation of premotor cortex during action observation is positively related to the observer's expertise with performing the action (Calvo-Merino et al., 2005, 2006; Cross et al., 2006). However, there are some inconsistencies in this literature when it comes to adult EEG work on the mu rhythm. For instance, although some EEG findings align with the foregoing fMRI results (Marshall et al., 2009; Orgs et al., 2008), a recent finding from adults suggests that increased expertise with actions is associated with *less* desynchronization of alpha-range rhythms, including the central mu rhythm, during observation of those actions (Babiloni et al., 2010).

Turning to developmental questions, various proposals (based on behavioral data) have emphasized the influence of infants' first-person experience with behaviors on their processing of those behaviors when they are subsequently observed (e.g., Kuhl and Meltzoff, 1982; Meltzoff and Brooks, 2008; Sommerville et al., 2005; Woodward et al., 2009). There is very little neuroscience research on this issue, but some work is emerging. As noted earlier, van Elk et al. (2008) reported that infants with more crawling experience showed greater EEG desynchronization to watching videos of crawling versus walking infants. Although Nyström et al. (2010) did not test a variety of ages, they speculated that the 8-month-olds in their study may have shown mu rhythm desynchronization to a grasping action because they had themselves mastered the production of the same kind of action. Further infant studies that combine EEG measures with individual differences in action experience are clearly needed in order to better evaluate such suggestions.

On the other side of the coin, emerging work in the developmental neurosciences will need to consider that infants can imitate novel actions (Meltzoff, 1988). Thus, a neural system linking observation and execution cannot be limited *only* to well-practiced habits for which specific associative links have been built up. One key here will be to integrate a developmental neuroscience perspective with existing cognitive models that have posited the notion of an "act space" by which the generative capacity of human imitation – for example, the imitative learning of new skills and routines – could be realized (Meltzoff and Moore, 1997).

7. Conclusions and future directions

We have reviewed research which suggests that a rhythm in the infant EEG resembles the adult mu rhythm in terms of its topography and function. We have analyzed what is currently known about the reactivity of this rhythm to action observation and execution in infants, and have outlined a number of open theoretical questions concerning the nature and function of the infant mu rhythm response. The literature in this area is still rather small, although it is a topic which promises to be one of the more rapidly growing areas in developmental social–cognitive neuroscience. If carefully conducted, future studies of infants involving EEG and related methods such as MEG have the potential to significantly advance our understanding of the fundamental links between action perception and action production and their ontogenesis.

Looking ahead, issues relevant to learning and development are crucial. In particular, a detailed examination is needed of how neural mirroring systems are engendered and transformed by two types of behavioral experience: (a) self-generated actions (watching oneself produce hand movements and other goal-directed acts) and (b) experiencing contingent social interaction (seeing a caretaker mirror one's own acts, e.g., in reciprocal imitation games, Meltzoff, 2007a). It is likely that both seeing oneself act, as well as watching others' responses, play interwoven developmental roles.

By combining neuroscientific and behavioral studies with a developmental perspective we will enhance our understanding of the representation of action. Such work will also address a central question in developmental science: What neural processes allow humans to accelerate learning about the material and social world by watching the actions of our conspecifics? Human beings learn not only through temporal contingencies which bind actions and their consequences (conditioning), we also learn by proxy, watching the acts of others in order to formulate our own action plans via imitation. This fundamental learning process depends on links between perception and production, which connect self and other prior to language, and indeed support language learning (Meltzoff et al., 2009).

Further work is clearly needed to tie the nascent findings in developmental cognitive neuroscience to the large behavioral literature on perception–action coordination and imitation in infancy. The type of research that is needed is not well characterized as a search for the "neural mechanisms explaining the behavior." This kind of phrasing suggests a unidirectional view of brain–behavior relations (for a nuanced discussion of the construct of mechanism in neuroscience, see Craver, 2007). Instead, neuroscience data could be seen as reflecting a different level of analysis with no more explanatory power than other levels such as behavioral or cognitive levels (Miller and Keller, 2000) – although even that view does not capture the full dynamic complexity of the brain–body–environment interface (Marshall, 2009).

Moreover, the bidirectional influence of brain and behavior can be seen to influence both the development of infants and the development of theories. Regarding the former, it is not only that neural development drives behavior, but that behavior itself provides experience and input that organizes and influences biological plasticity and change (e.g., Gottlieb, 2007; Greenough et al., 1987). Regarding the latter, although neuroscience often enriches our understanding of behavior, it could be argued that the behavioral evidence is often in advance of, and heavily influences, the neuroscience work (Hatfield, 2000). For instance, before related neuroscience work was available, the behavioral data on infant imitation suggested the preverbal coupling between action perception and production in the human case (Meltzoff and Moore, 1997). Indeed, infant imitation, visually guided reaching, and social turn-taking all illustrate perception–production links, and suggest specific hypotheses and constraints for the elucidation of the neural processes that support them. As this search for neural processes continues, a theoretical stance which recognizes the dynamic, bidirectional influences between brain and behavior, as well as the crucial importance of learning and development, will ultimately be more productive than less integrative approaches.

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