

Neural correlates of dyadic interaction during infancy

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ABSTRACT

This study examines the electrophysiological correlates of dyadic interaction in 14-month-old infants. Infants were presented with three conditions of live stimuli. A baseline condition involved the observation of moving geometric shapes. In a second condition the infant observed an adult performing movements that were not in reference to the infant and were not within the infant's proficient motor repertoire, such as dancing or hopping. A third condition involved face to face dyadic interactions in the context of an imitative game, where the infant and adult engaged in copying each other's hand and facial actions. Motor activity by the infant was controlled between conditions by synchronizing EEG with video frames of action. Infant EEG data was then edited offline to match in motor intensity across conditions. We expected mu rhythm (6–9 Hz) suppression during dyadic interactions relative to the amount of mu present in the baseline condition. This prediction was confirmed. We also observed suppressed mu in the interaction condition relative to the observation condition. The mu rhythm results suggest that infants at 14 months may well utilize a functioning mirroring system during dyadic interactions.

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1. Introduction

Face to face interactions with other people are critical for the development of human social-cognitive skills (Striano and Reid, 2006). The proclivity of infants to detect communicative cues throughout early development is well documented (Reid and Striano, 2007). By the second post-natal month, infants begin to focus on the eyes and mouth of other people in dyadic situations (Johnson and Morton, 1991) and become distressed when others pose a “still-face” and stop interacting reciprocally with them (Striano

et al., 2005). The infant first produces smiling and gazing behavior. The infant then attempts to re-engage the social partner. Should these attempts fail, then the infant will display distress. This finding suggests that reciprocal interaction is the form of behavior that is anticipated by an infant in a dyadic situation.

Understanding the neural correlates of dyadic interaction is not only important for the reason that this is the most prominent way that infants interact with adults in the early months, but also because dyadic interactions remain the primary means of communication, learning, and interpersonal relations throughout the lifespan (Ickes, 2003). Furthermore, the interpretation of dyadic behavioral cues that are available through the ways that other people move, talk, and relate to each other are likely to be a predominant means by which we infer others' internal mental states such as goals and desires (Iacoboni et al., 2005; Iacoboni, 2008). Interactions specifically involving imitation appear to be preferentially attended towards in early development when contrasted with other forms of

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action (Striano et al., 2005). This is shown in the proclivity of infants to preferentially attend to peek-a-boo dyadic situations when contrasted with other forms of social communication (Crawley and Sherrod, 1984).

Currently, little is known about neural correlates in early human ontogeny for most forms of social interactions, including dyadic interactions (but see Striano et al., 2006; Parise et al., 2008). Recent work by Southgate and colleagues (Southgate et al., 2009, 2010) has shown that infant prediction of object related reaching can be detected via sensori-motor alpha (otherwise known as mu) by 9 months of age. Further, for each infant an individually identified mu rhythm (between 6 and 13 Hz) was found to be desynchronized to action execution as well as action observation.

Marshall et al. (in press) examined action execution and action observation in 14-month-old infants using a button press paradigm, where infants pressed a button and where they saw an adult press a button. The button press action was compared to a baseline measure of viewing patterns. Effects were only found in central regions, with significant desynchronization in the mu rhythm for the execution and observation of action when contrasted with baseline. This study showed that during infancy, mu desynchronization occurred for actions other than reaching and grasping.

Recent work by van Elk et al. (2008) indicates that the mu rhythm is modulated as a function of the ability to produce the observed action. They found that infants at 14–16 months who had the capacity to crawl produced more mu suppression in fronto-central areas when observing videos of crawling actions when contrasted with those infants of the same age who had less crawling experience. This work clearly shows that mu suppression induced by observing action is dependent on the experience of having the ability to perform the observed action. For a robust review of mu rhythm research with infant populations, see Marshall and Meltzoff (in press).

Research has yet to ascertain the mechanisms via which infant social perception modulates brain activity within a dyadic context when contrasted with other forms of social and nonsocial information. This is a critical issue, as our ability to imitate others' actions holds the key for understanding what it is for others to be like us and vice versa (Meltzoff and Decety, 2003; see also Lepage and Théoret, 2007). Previously, the human mirror system has been related to the mu rhythm because desynchronization of the mu rhythm can be found in subjects that either actively perform a movement or observe another person executing an act (Hari et al., 1998). Recently, Hari and Kujala (2009) stated that the term "neural mirroring system" should be used to refer to neural systems that involve both action observation and action execution. They argued that current work should focus on developmental origins of this system, in addition to the nature of interactions between various components of this system.

The present study investigates the effects of dyadic interaction on ongoing functional brain activity. As previous studies have shown dampened neural responses to stimuli presented on a monitor when compared to live action (Shimada and Hiraki, 2006), we interacted with infants in a real-life context. We used mu rhythm sup-

pression as a marker of neural mirroring as this frequency has been implicated as indexing the mirroring system in action observation studies with children and adults (e.g., Obermann et al., 2005; Lepage and Théoret, 2006). Further, the application of TMS pulses to regions of putative mirroring areas have been shown to produce imitation deficits in participants (see, e.g., Heiser et al., 2003; Iacoboni, 2005, 2006). We therefore reasoned that mu rhythm suppression in infants will be evident during dyadic interactions that contain a strong element of imitation when contrasted with other forms of observed movement.

Specifically, we conjectured that mu suppression would be greatest in a condition when an experimenter is engaged in a face-to-face interaction with the infant when compared with a baseline of the same degree of infant motor activity obtained during infant observation of a control condition featuring nonbiological movement. We also anticipated greater mu suppression for dyadic interactions involving imitation when contrasted with a condition where infants observe actions by an experimenter that are not related to their own movements and would be impossible for the infant to replicate due to their limited motor repertoire. Such an effect would indicate not only that mirroring systems are generally involved in dyadic interactions, but also that the effects of motoric activity seen in van Elk et al. (2008) are also present in real-life situations.

2. Method

2.1. Participants

All research was conducted under institutional protocols, with parental informed consent for each subject. 10 infants (6 males and 4 females) were tested, with an average age of 14 months \pm 12 days. All infants were born full term (37–41 weeks) and were in the normal range for birth weight. Another 22 were tested but excluded from final analysis due to insufficient data for analysis. For the frequency analysis, a minimum of 40 s of data was required for each condition in line with work investigating low frequencies within EEG where it has been reported that data below this level adversely increases the signal to noise ratio (e.g., Nyström, 2008; Stroganova et al., 1999). It is for this reason together with the inclusion of three conditions, rather than two conditions as is typical in most infant EEG research, that attrition rates were marginally higher in this study than for other comparable studies (e.g., Bell, 2002; Reid et al., 2007).

2.2. Procedure

Each infant's electrical brain activity was measured in three contexts which were counterbalanced in order across the sample of infants: a baseline, a non-interactive condition and a dyadic interaction condition.

In the *baseline condition* the infant observed movement that was nonbiological in nature. This was produced by movements of geometric shapes that were placed on the end of a stick and moved by an experimenter who was occluded from the infant's view and was never seen by the infant. The movement of the object was directed hori-

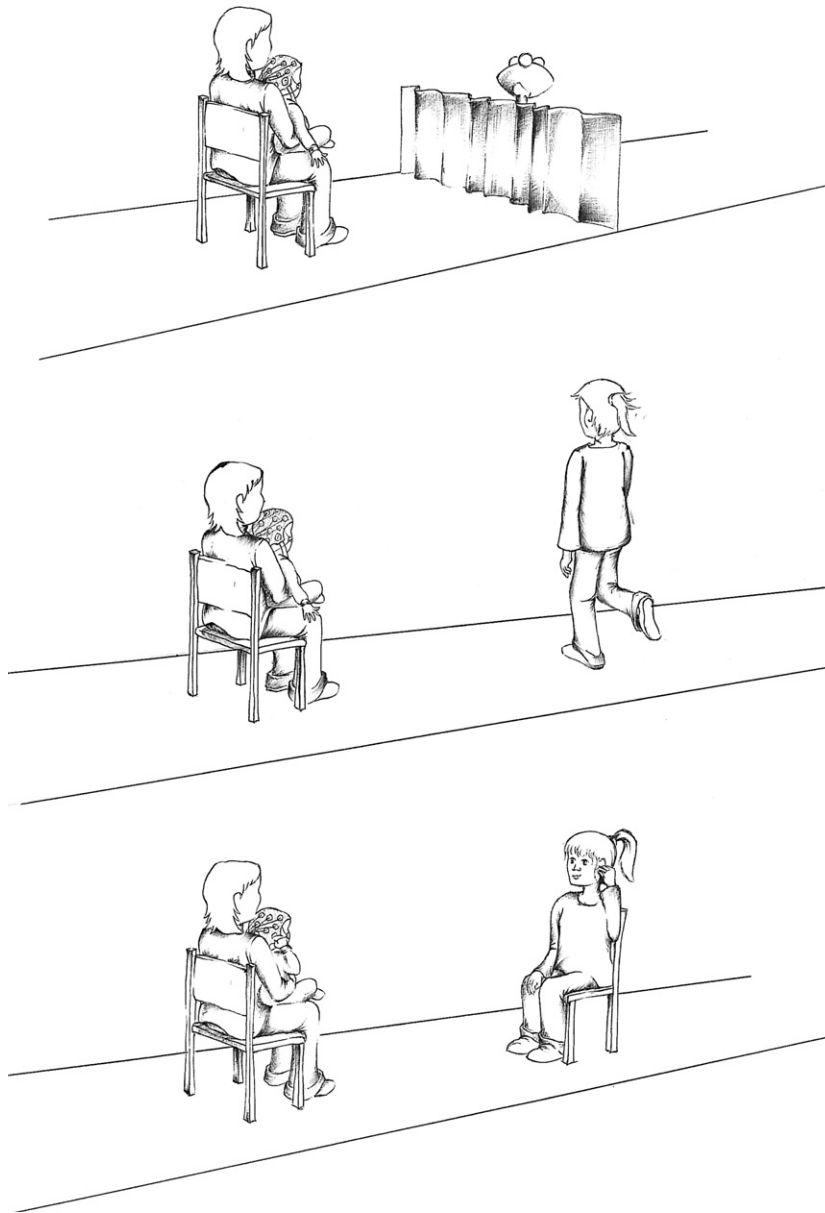


Fig. 1. The three conditions displayed to the infant. Top image depicts the baseline condition, with movement of a geometric object towards and away from the direction of the infant. Middle image shows the non-interactive condition, with the infant observing motion that could not be produced by their motor system. Bottom panel displays the dyadic interaction condition, with both experimenter and infant engaged in touching the ear.

zonally towards and away from the infant, with limited left-right movement in order to reduce eye movements in the infant. For the *non-interactive condition*, infants observed complex human movements produced by an experimenter, including hopping, a strutting walk, skipping, clapping in complex rhythms and dancing. These actions were executed without direct reference or gaze towards the infant. These actions were selected as none of them fit within the proficient repertoire of a 14-month-old infant (see, for example, Yaguramaki and Kimura, 2002), with infants either at the start of acquisition (for the case of walking) or well outside the possibility of performance. In order to reduce lateral eye movements, the

experimenter performed movements further away from the infant than the presented geometric objects, although the experimenter was nonetheless larger in visual angle than the objects in the control condition. In the *dyadic interaction condition*, the experimenter sat approximately 1 meter away from the infant and an imitation game was played. This began by the experimenter imitating a salient element of the infant's physical position, such as a hand scratching the cheek. In all cases this rapidly led to a turn taking sequence of actions where the infant would perform a movement, such as putting a hand on a cheek, and as rapidly as possible thereafter the experimenter would adopt the same pose. For example, the infant would drum

their fingers on their knee with the experimenter immediately drumming their own fingers on their own knee in the same way, with the infant watching the fingers of the experimenter. Based on infants' behavioral response, it would appear that they treated this interaction as a "game", with different positions deliberately adopted once a position that was defined by the infant was matched by the experimenter's final resting position. Due to the sitting nature of the interaction, movements were produced primarily with the fingers, hands and arms. All periods included in the final dataset for the condition comprised activity during the context of engaged and reciprocal interaction. For an illustration depicting the different conditions, see Fig. 1.

For all conditions, our criteria for inclusion required that within each condition the amount of motor activity by the infant was the same across conditions for the epochs accepted for further analysis. This was possible via a reduction in EEG data across conditions for each infant. We coded the conditions, and classified the amount of infant movement on a second by second basis. Our coding from the video was restricted in accuracy by refresh rates to 25 Hz. This procedure effectively controlled for the amount of motor activity across conditions (for details, see EEG Recording and Analysis). Further, the analyzed epochs were separated from substantive movement by at least 2 s, in order to ensure that no delayed effects of movement preparation or execution were included in the final data set (see, e.g., Pfurtscheller et al., 2000).

Infants sat on their mother's lap in a dimly lit sound-attenuated and electrically shielded cabin. The door remained open, with the lower 1/3 occluded by a sheet in order to position the object manipulating experimenter for the baseline condition. For the other conditions, the experimenter performed actions in the space outside the cabin in view of the infant.

EEG was recorded continuously for 3 min for each condition. The behavior of the infant was video-recorded throughout the session for offline coding of looking behavior to the experimenter and to control for the amount of motor activity in each condition.

2.3. EEG recording and analysis

EEG was recorded continuously with Ag–AgCl electrodes from 23 scalp locations of the 10–20 system, with the removal of FP1 and FP2 and the inclusion of FC3, FC4, CP5, CP5, TP9 (left mastoid) and TP10 (right mastoid), all of which were referenced to the vertex (Cz). Data was amplified via a Twente Medical Systems 32-channel REFA amplifier and analyzed via in-house software. Horizontal and vertical electrooculogram were recorded bipolarly. Sampling rate was set at 250 Hz. EEG data was re-referenced offline to the linked mastoids and highpass filtered with a cutoff frequency of 1 Hz at –6 dB (1.22 Hz at –3 dB; 441-point FIR filter).

For the elimination of electrical artifacts caused by eye and body movements, EEG data was rejected off-line whenever the standard deviation within a 200-ms gliding window exceeded 80 μ V at any electrode. EEG data were also visually edited offline for excessive motor arti-

facts and to control for the amount of motor activity in each condition. This was done by synchronizing the EEG with trial information that was assigned to a video camera. The resulting synchronized film was then assessed with the EEG data offline and analyzed on a frame-by-frame basis at 25 frames/s for motor activity by the infant. A corresponding amount of motor activity was edited from the data in each condition, such that motor activity was equivalent between conditions within the final analyzed dataset. Movements were classified into four groups for each frame for each limb, head, trunk and torso: none, low, medium or high. The overall score for each second was then determined and this classification was then matched across conditions. Generally motor activity of head, trunk, and limbs was kept to a minimum across conditions; however when motor activity occurred within a body location, such as a limb or group of limbs, this was matched by the same degree of motor activity present within that body location in the other conditions for each infant. The matching was done by coding the degree of limb or body movement into one of the four categories and then selectively reducing the final epochs of EEG that were included for each condition such that the same number of movement events were present in each condition. It was during the motor coding that it was also ascertained that infant looking was towards the experimenter in the non-interactive or interactive conditions, or towards the object in the control condition.

For each electrode, the power spectral density (PSD) was calculated using Welch's method of modified periodogram averaging. Fast Fourier transforms (FFTs) were computed from artifact-free data segments with a length of 256 samples (=1024 ms). The segments were tapered with a Hann Window and zero-padded to a total length of 512 samples before FFT calculation, i.e. the virtual frequency resolution was \sim 0.49 Hz. Data segments were allowed to overlap by 75%. As a robust estimate of EEG power density, the median value across all single-segment PSD spectra was used.

For each participant, a dominant mu rhythm was identified between 6 and 9 Hz, by identifying the first harmonic of the peak mu rhythm, in the 12–18 Hz range (for further details on harmonic issues, see, for example, Lehmann et al., 2001). Further analysis was based on this frequency for each participant. Identified electrodes near to the area of activity and hypothesised area of interest were defined as frontal left (F3), frontal right (F4), central left (C3) and central right (C4) electrodes as these areas have been previously related to mu activity (Pfurtscheller et al., 1997), although lateralization is reported in some studies, but not in others with infants (lateralized effects: Nyström et al., *in press*; Southgate et al., 2009; non-lateralized effects: Marshall et al., *in press*). In order to assess differences between conditions, we subtracted mu activity in the baseline condition for each participant from mu activity in the non-interactive and interactive conditions.

3. Results

Frequency results were analyzed via a $2 \times 2 \times 3$ repeated measures ANOVA for dependent samples with laterality (left hemisphere, right hemisphere) by location (frontal,

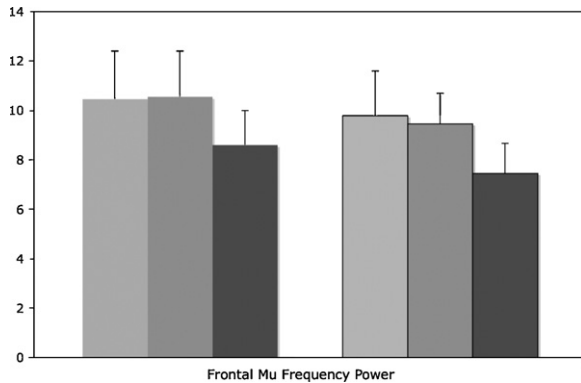


Fig. 2. Mu power and standard error in (left three columns) left frontal channels and (right three columns) right frontal channels for the baseline condition, the non-interactive and interactive conditions. Key: light tone = baseline condition; grey tone = non-interactive condition; dark tone = interactive condition; bars not outlined = left hemisphere; outlined bars = right hemisphere. The effect of condition is clear, with significant suppression in the interactive condition in frontal locations when compared with the baseline condition and bilaterally in frontal locations when compared with the non-interactive condition.

central) by condition (baseline, non-interactive, interactive).

The ANOVA indicated a main effect of condition $F(1,9) = 4.543, p = 0.025$. There was also a significant effect of location $F(1,9) = 12.048, p = 0.007$, indicating that overall the mu power was lower at central locations than at frontal locations (central: $M = 8.458, SD = 4.757$; frontal: $M = 9.001, SD = 4.63$). A main effect of laterality was also found $F(1,9) = 6.194, p = 0.034$, displaying lower mu power in the right hemisphere ($M = 7.462, SD = 4.101$) than in the left hemisphere ($M = 9.124, SD = 5.349$). There was no interaction between location and laterality $F(1,9) = 1.881, p = 0.203$ or interaction between location and condition $F(2,18) = 1.061, p = 0.367$, laterality and condition $F(2,18) = 0.585, p = 0.567$ or interaction between the factors location, laterality and condition $F(2,18) = 1.078, p = 0.361$ (see Figs. 2 and 3).

In order to resolve the significant effects, we conducted exact left tailed follow up permutation t -tests as we had clear predictions related to the effects of condition. Significance of the tests was assessed by applying the Bonferroni–Holm sequential procedure that controlled the family-wise error-rate at the 5% level. We found that the t values clearly show that mu power is significantly suppressed in the interactive condition with respect to the baseline and non-interactive conditions (interactive–baseline: $t(9) = -3.340, p = 0.005$; interactive–non-interactive: $t(9) = -2.478, p = 0.02$). There was, however, no significant difference between the non-interactive condition and baseline ($t = -0.528, p = 0.329$).

4. Discussion

This study was designed to investigate the electrophysiological correlates of dyadic interactions in infants. Infants participated in three conditions. One condition was a baseline measure, where infants observed moving geometric shapes. In a non-interactive condition the infant

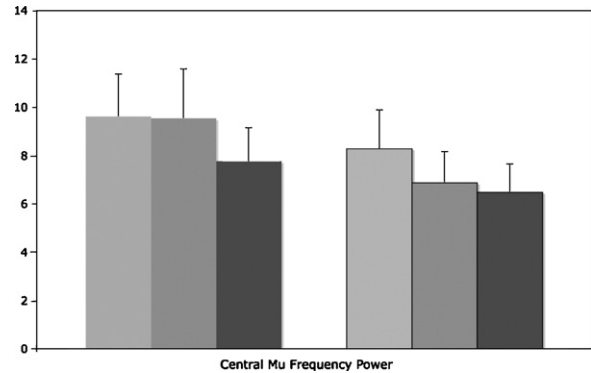


Fig. 3. Mu power and standard error in (left three columns) left central channels and (right three columns) right central channels for the baseline condition, the non-interactive and interactive conditions. Key: light tone = baseline condition; grey tone = non-interactive condition; dark tone = interactive condition; bars not outlined = left hemisphere; outlined bars = right hemisphere. The effect of condition is clear, with significant suppression in the interactive condition in central locations when compared with the baseline condition.

observed an adult performing movements that were not in reference to the infant as no overt communicative cue was provided, such as direct eye contact. Movements in the non-interactive condition were not within the infant's motor repertoire. A third condition involved face to face dyadic interaction within the context of an imitative game. We expected a suppressed mu rhythm for the dyadic condition relative to the amount of mu present in the other conditions. This prediction was confirmed. This result is comparable with investigations on the properties of the mu rhythm in adults and children (Nishitani and Hari, 2000, 2002; Lepage and Théoret, 2006; Obermann et al., 2005; Muthukumaraswamy et al., 2004). The mu rhythm results provide evidence that infants at 14 months most likely utilize a functioning mirroring system during dyadic interactions with others.

It was hypothesized in this study that the dyadic interaction condition would include stimuli that would best induce desynchronization of the mu rhythm. Simultaneous action perception and corresponding motor production have been shown to provide optimal stimuli for such activity, particularly when involving distal finger movements (Iacoboni et al., 1999; Gillmeister et al., 2008). In contrast, the non-interactive condition featured observed actions such as strolling, dancing and hand clapping in complex rhythms. These are actions that are not within the proficient motor repertoire of the infant with complex mastery not yet attained. In congruence with work by van Elk et al. (2008), the results of the present study support the concept that mu frequencies are engaged when viewing and performing actions that are fully established within one's motor repertoire. The present study effectively brings the results of van Elk and colleagues into the realm of live interactions.

Crucially, the amount of motor activity present in the data was controlled between the conditions. Infant movement was coded from video recordings that were calibrated with the EEG recordings. The amount of physical movement observed in the selected EEG data was matched across

conditions on a second by second basis via coding of the video tapes and reduction of EEG data. This ensured that overall differences between conditions in the motor output of the infant did not account for the differences seen between conditions in terms of mu suppression. Further, despite the need to control motor activity, the inclusion of a minimum of 40 s of data for each condition compares well with studies that use similar live paradigms or analysis techniques (e.g., van Elk et al., 2008; Reid et al., 2007).

The current study provides evidence for substantive differences in the neural processing of observed actions produced by others and actions performed in the context of dyadic interactions involving imitation. What this study does not achieve, however, is the disambiguation of individual components within the dyadic interaction. It may well be that direct components of dyadic imitation that are key include the synchrony of the observed to executed action. Another possibility may be that the nature of eye contact may induce suppressed mu rhythms. It is possible that all forms of activity involved in dyadic interaction are required for the detection of differences in mu rhythm as was seen in the present study. These subtleties will need to be dissociated via further research utilizing targeted manipulations.

Facial imitation tasks (Carr et al., 2003; Dapretto et al., 2006) and even some 'social' action observation tasks (Iacoboni et al., 2005) have been generally associated with right lateralized activations in inferior frontal cortex. Recent work by Nyström et al. (in press) indicates right hemisphere effects in mu rhythm desynchronization when 8-month-old infants view grasping actions when contrasted with other forms of hand action. It is possible that mu rhythm is lateralized when involved in the observation of hand, rather than body, movements.

We did not find differences between the non-interactive condition and baseline condition. Were the present results precisely comparable with Obermann et al. (2005), a study which used minimal, non-interactive stimuli with children, then we would expect differences between the non-interactive condition and the baseline condition. The present study is different in two critical ways. First, the stimuli were all live and not presented via a monitor, with prior work indicating reduced effects for monitor delivered stimuli (Shimada and Hiraki, 2006). Second, the baseline measure that we used was presented live and was entirely nonbiological in nature, although an element of the movement was inevitably biological, in the sense of having a minimum-jerk movement profile.

Asymmetries in mu rhythm have been noted in work investigating memory systems during infancy. Bell (2001) found that there was an increase in mu for components of a task that were higher in cognitive demand than other elements. Orekhova et al. (2007) found in 8–11 months old infants that when sustained attention was required in a peek-a-boo game, the mu rhythm was enhanced in power. This suggests that mu has a number of cognitive properties associated with its activity, many of which remain to be explored.

In summary, this study provides the first EEG correlates of live dyadic interactions during early development. This is the first evidence of neural mirroring, as indexed by the mu

rhythm, during early dyadic interactions. Thus, these data support the hypothesis that neural mirroring is important in social interactions and that this is the case during infancy.

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