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Neural correlates of action understanding in infants: influence of motor experience

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Abstract

Mirror neurons are recognized as a crucial aspect of motor and social learning yet we know little about their origins and development. Two competing hypotheses are highlighted in the literature. One suggests that mirror neurons may be innate and are an adaptation for action understanding. The alternative, proposes that mirror neurons develop through sensorimotor experience. To date, there has been little direct evidence from infant studies to support either argument. In the present study, we explored the temporal dynamics and spatial distribution of electroencephalography (EEG) brain responses in young infants during the observation of three distinct types of actions: (a) actions that are within the motor repertoire of infants, (b) actions that are not within the motor repertoire of infants, and (c) object motion. We show that young infants had significant motor resonance to all types of actions in the sensorimotor regions. Only observation of human goal-directed actions led to significant responses in the parietal regions. Importantly, there was no significant mu desychronization observed in the temporal regions under any observation condition. In addition, the onset of mu desychronization occurred earliest in response to object motion, followed by reaching, and finally walking. Our results suggest that the infants may have a basic, experience-independent sensorimotor mechanism optimized to detect all coherent motion that is modulated by experience.

Introduction

The recognition of action is a fundamental prerequisite for the development of imitation, motor learning, and social development (Rizzolatti and Arbib 1998). In humans, mirror neurons, which respond to both the observation and execution of an action, have been found in the ventral premotor cortex, inferior parietal lobe (Rizzolatti and Craighero 2004), and the superior temporal sulcus (STS) (Iacoboni et al. 2005) suggesting a common coding between perception and action. These regions form a complex network in which the visual representation of motion activates an appropriate motor representation. Numerous electrophysiological and brain imaging studies now support the existence of a mirror neuron system in adults (Gallese et al. 1996; Nitashani and Hari 2000; Rizzolatti and Craighero 2004; Iacoboni et al. 2005; Keysers et al. 2006; Virji-Babul et al. 2010), children (Lepage and Théoret 2006) and infants (Shimada and Hiraki 2006;

Nystrom 2008; Southgate et al. 2009; Marshall et al. 2011). There are, however, a number of questions not accounted for by the current mirror neuron system interpretation. For example, how does the mirror neuron system develop and how is this development related to the infant's own abilities and experiences? Are mirror neurons the result of sensorimotor learning processes or genetic prewiring?

Heyes and colleagues (Heyes et al. 2005; Heyes 2010) have proposed an associative sequence learning (ASL) model that states that mirror neurons develop as a result of the correlated experience of observing and executing the same action. Support for this model comes primarily from adult studies showing that activity in the mirror neuron system is modulated by previous motor experience. For example, pianists showed stronger activations within a fronto–parietal–temporal network while observing piano playing compared to controls (Haslinger et al. 2005). In addition, dancers showed stronger responses in the premotor, parietal cortices, and STS when

they observed dance movements that they had previous experience with (Calvo-Merino et al. 2005).

An alternative hypothesis is that mirror neurons may be an adaptation for action understanding. From an evolutionary point of view, it seems reasonable that there may be some innate mechanisms in place that would be facilitated through sensorimotor learning (Del Giudice et al. 2009). However, to date, there has not been any evidence showing the existence of a mirror neuron system at birth. Another approach is to investigate the influence of previous motor experience on the perception of actions that are not within the repertoire of young infants. Van elk et al. (2008) investigated whether infants' own motor experience (crawling and walking) is related to the activation of their motor system during the perception of these actions carried out by other infants. They did not find significant differences between the two actions in the sensorimotor areas suggesting perhaps, that infants have a predisposition to perceiving all human actions.

One index of mirror neuron activity that has been extensively studied in humans is mu (8–13 Hz) suppression. At rest, neurons in the sensorimotor area fire synchronously resulting in large amplitude EEG oscillations in mu frequency band. When subjects perform an action, imagine, or observe movements, these neurons fire asynchronously decreasing the power of the mu band (Pfurtscheller and Neuper 1997; Muthukumaraswamy et al. 2006). It has been hypothesized that the mu rhythms reflect downstream modulation of primary sensorimotor areas by mirror neuron activity, representing a critical information processing function, translating perception into action (Pineda 2005). To date, studies on infants have studied motor resonance to human actions (i.e., reaching/grasping or walking/crawling) but have not included a condition of object motion to determine whether infants show a general motor resonance to all motion or whether motor resonance is specific to human actions. In the present study, the questions we asked were: (a) do infants show motor resonance only during observation of human actions or to both human and object motion and (b) to what extent does previous motor experience influence the network of brain regions activated during action observation? We used high-density EEG to investigate the pattern of mu rhythm modulation and study the latencies of activation of the sensorimotor regions in infants during observation of three types of actions: actions that are developmentally within the motor repertoire of infants (i.e., reaching), actions that are developmentally not within the motor repertoire of infants (i.e., walking), and object motion (i.e., toy car, ball) to distinguish the responses between human and object motion. We examined the spectral power changes in the sensorimotor, parietal, and temporal regions as well the time–frequency responses to observation of the three actions in the sensorimotor region.

Methods

Participants

A total of 14 infants between the ages of 4 and 11 months (mean age: 7.08 months, eight males, six females) participated in this experiment. Four infants were excluded from analysis due to movement or insufficient artifact free trials per condition. Parents provided information about the reaching and ambulatory experience of their infant. All infants were able to perform a reaching motion but none had started to walk at the time of the experiment according to parent reports. Parents provided written consent according to the guidelines specified by the Human Ethics Review Board at the University of British Columbia.

Stimuli

Videos of 1.5-sec duration depicting three different actions: human walking, hand reaching for objects, and object motion (toy car, rolling ball) were prepared. Adult actors were used for the reaching and walking videos. Videos were recorded against a neutral background. Unlike previous studies, we did not show the face of the actors in any of the displays. A total of 60 videos (20 walking, 20 reaching, and 20 object motion) were included.

Experimental setup and procedure

Infants were seated on their parent's lap in front of a 90-cm projector screen at a viewing distance of approximately 190 cm. A camera was placed below the projection screen to monitor the infants' eye and limb movements. Only trials with no limb movement and during which the infant observed the video displayed were included in the analysis.

EEG recording and analysis

EEG was recorded using an infant-sized 64-channel HydroCel Geodesic Sensor Nets (EGI, Eugene, OR). EEG was recorded with a Net Amps 300 amplifier at a sampling rate of 250 Hz. Scalp electrode impedances were usually less than 50 kΩ. The signal was collected referenced to the vertex (Cz). The signal was then filtered from 4 to 40 Hz, and a notch filter of 60 Hz was included.

Since our primary interest was in understanding the location and sources of brain activity, we used source modeling rather than analysis of specific sensors/electrodes. Activity in every brain region is associated with a widespread topology and thus a source montage was used to transform the EEG activity obtained from all the 151 channels into estimated contributions of a set of 15 separate brain regions using Brain Electrical Source Analysis (BESA) (MEGIS Software GmbH). Fast Fourier transforms were performed on single trials (1024 points Hanning window) and averaged for each condition. The EEG data for the central, parietal, and temporal regions

were group averaged across all infants. Power values from the left and right sensorimotor, parietal, and temporal regions for the mu rhythm (6–9 Hz) were used for statistical analyses.

In order to account for individual variability in overall power, a ratio of the power during observation relative to the baseline condition for bilateral central regions was computed for each subject. A log transform was then calculated for each ratio. A value of zero indicates no signal power change and a negative value indicates attenuation of the signal. We focused on analysis of the mu rhythm (6–9 Hz) activity for infants. Mean mu desynchronization was calculated for each condition in the central, parietal, and temporal brain regions. One sample t-tests were used to determine if the values were significantly different from zero.

Time–frequency responses were analyzed using Field-Trip (open source software, developed at the FC Donders Centre for Cognitive Neuroimaging; http://www.ru.nl/fcdonders/fieldtrip/). The data were imported into Matlab for preprocessing and group averaging. Power values were computed on all frequency and time bins of the group average. These event-related power changes were plotted for the regions of interest (i.e., frontal, central, and parietal).

Results

Mu desynchronization (6–9 Hz)

Figure 1 shows the log ratios for each of the three conditions for the sensorimotor, parietal, and temporal regions. Mean mu desynchronization was significantly different from zero for the sensorimotor regions for all three conditions (reaching: $t(9) = -2.3$, $P = .02$; walking: $t(9) = -1.7$, $P = .05$; object: $t(9) = -2.2$; $P = .03$), but only significantly different from zero for the reaching and walking conditions in the parietal regions (reaching: $t(9) = -2.4$, $P = .01$; walking: $t(9) = -2.1$, $P = .03$; object: $t(9) = -1.7$, $P > .05$). In addition, mean mu desynchronization was not significantly different from zero for any of the three conditions for the
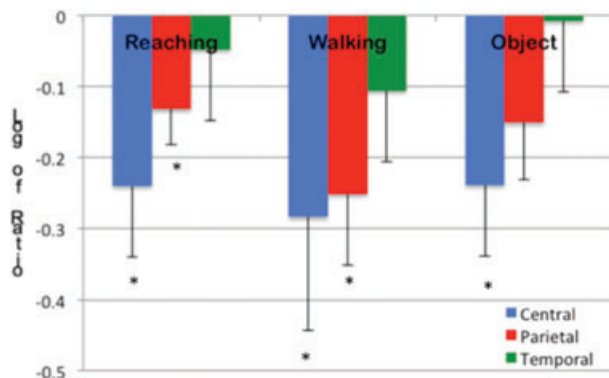
temporal regions (reaching: $t(9) = -.5$, $P = .1$; walking: $t(9) = -1.1$, $P = .01$; object: $t(9) = -.07$, $P = .1$).

Time–frequency distributions

Grand averaged time–frequency plots for the sensorimotor regions are presented in Figure 2. Source power decreases/event-related desynchronization (ERD) and power increase/event-related synchronizations (ERS) are shown in for each of the three conditions. Enhanced ERD was observed in the mu band during all three conditions. For the object motion, ERD was also observed in the beta band (15–35 Hz). Interestingly, ERS was observed in the beta band in the walking condition. There was no significant ERS noted in the reaching condition.

Latencies of mu activation

The differences in onset latencies for the mu band in the sensorimotor regions for all three conditions are shown in Figure 3. Note that the onset of mu desynchronization during observation of object motion started at 50 msec, reaching at 113 msec, and walking at 175 msec following the start of the video display.

Discussion

In the present study, we investigated the brain regions involved in the perception of object and human motion and the influence of previous motor experience. One of the main unresolved issues in the study of the mirror neuron system is whether this system is innate or acquired through sensorimotor experience (see Hayes 2010 for review). Specifically, developmental studies have not yet been able to clearly explain the role of sensorimotor experience and the extent to which this experience facilitates the development of the mirror neuron system.

In the present study, we first showed that infants show strong desynchronization to human motion in the mu frequency band in the sensorimotor regions, irrespective of their own motor experience. Infants, who had not yet started to walk, responded equally to motion depicting walking and reaching. In addition, infants showed similar mu desynchronization in the sensorimotor regions to observation of coherent object motion in the form of movement of toy cars or balls. These results extend previous work in infants (e.g., Nystrom 2008; Marshall et al. 2011) to show the presence of a fundamental motor resonance mechanism in infants that responds to all coherent motion.

Interestingly, although our results indicate the presence of a basic perceptual-motor mechanism early in infancy, we also observed two striking differences—first in terms of the pattern of activity in traditional mirror neuron regions, and second in relation to the latencies of activation. These two task specific patterns point to the emergence of an
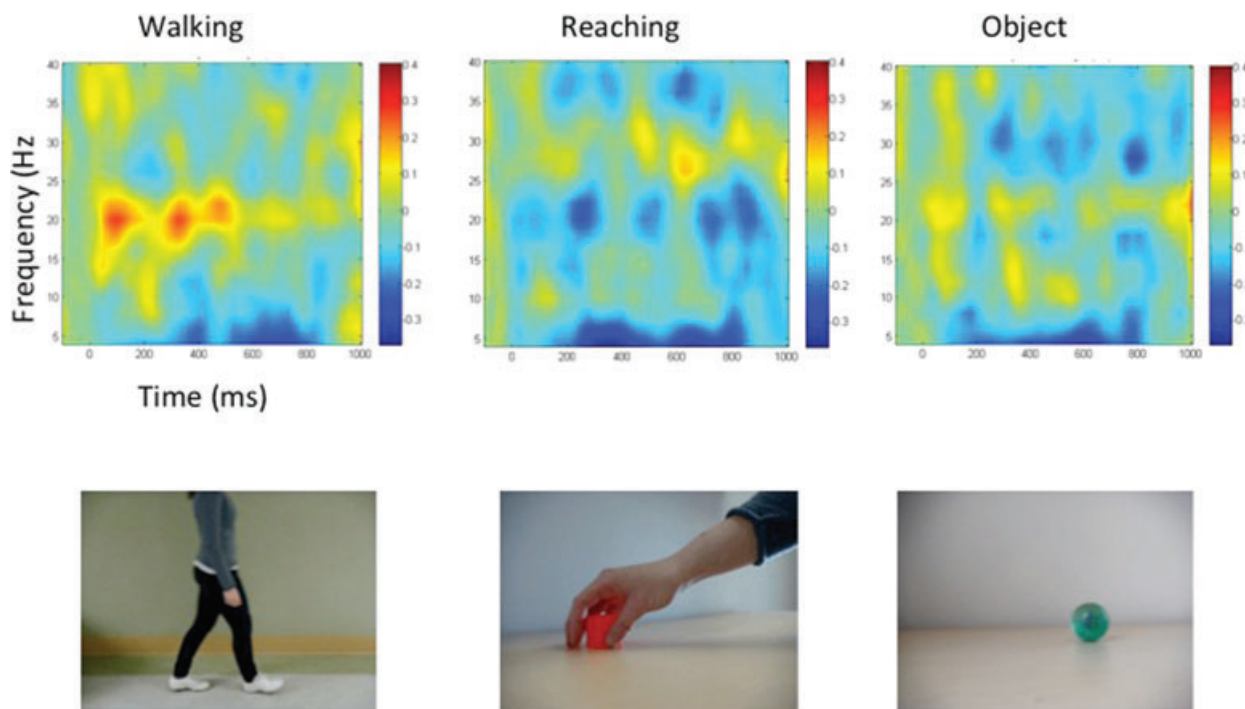

Figure 1. Mu power as a function of condition.

Figure 2. Grand average time–frequency plots during action observation under each of the three conditions: (a) object motion, (b) reaching, (c) walking. The time–frequency plots reflect changes in power over the sensorimotor region time locked to the presentation of the video (*t* = 0 sec). Strong modulation was observed in the mu band for all conditions.
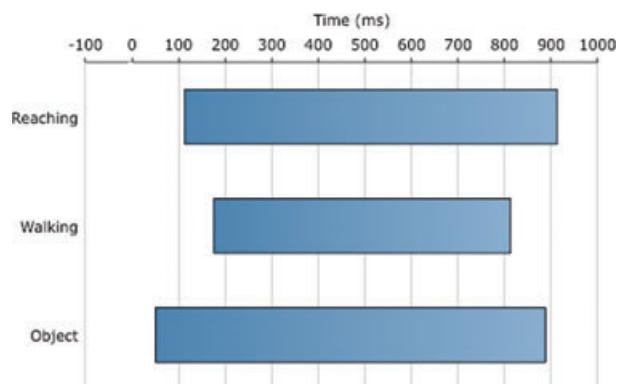

Figure 3. Latencies of mu desynchronization for each of the three observation conditions.

experience-dependent modulation of the basic mechanism early in infancy.

In the adult literature, three key brain regions are thought to comprise the mirror neuron system: the premotor cortex, inferior parietal cortex (Rizzolatti and Craighero 2004), and the STS. The parietal cortex is thought to have a central role in representing and interpreting the goals of observed actions (Hamilton and Grafton 2006). The STS is thought to be critical in cognitive processing related to perspective taking (Schulte-Rüther et al. 2007) and is involved in discriminating self-produced actions from the actions of others (Keysers and Perrett 2004). We have shown recently that during the observation of a goal-directed reaching movement in a live model, the first brain area to be activated was the right temporal region (Virji-Babul et al. 2010), followed by activity in the sensorimotor and parietal regions suggesting that this discrimination between self and other may be mediated by early interactions between the temporal regions and the sensorimotor regions. Thus, the premotor cortex, parietal region, and the STS are considered to be a functional circuit with reciprocal connections that facilitates social understanding (Keysers and Perrett 2004).

Within the context of the adult mirror neuron system, our results indicate that the infant mirror neuron system is characterized by an emerging network circuit, encompassing only the sensorimotor and parietal regions. In our study, both goal-directed human actions were associated with activity in the sensorimotor and parietal regions. In contrast, object motion was associated with activity only in the motor regions, suggesting that infants may be capable at a very fundamental level to distinguish between human goal-directed actions and object motion—a function associated with the parietal region.

This discrimination may be reflected in the timing of mu desynchronization in which the earliest onset of activity occurred in response to object motion. We have shown previously that observation of coherent object motion results in earlier activation of occipital, parietal, and sensory-motor regions in comparison with the observation of human motion (Virji-Babul et al. 2008). The processing of human motion requires higher level processing that may require more complex interactions between different brain regions.

Overall, these data suggest that infants may be predisposed early in life to understand coherent human and object action. These data corroborate with recent results demonstrating that newborn babies have an inborn, experience-independent perceptual mechanism in place to detect biological motion (Simion et al. 2008). Our data add to this finding by demonstrating that this perceptual mechanism extends to both human and object motion. This basic mechanism may be crucial for developing imitation skills (Meltzoff and Decety 2003).

Several researchers have suggested that early in life, infants may display a broadband response to human motion and coherent motion in the form of moving objects (Shimada and Hiraki 2006). This response may be refined with experience through a process of Hebbian learning (Del Giudice et al. 2009), providing a mechanism for the integration of perceptual-motor learning with a genetic predisposition to motion resulting in the emergence of the mirror neuron system. Nagai et al. (2011) have recently proposed a computational model of the development on the mirror neuron system in which they propose that there may be a correlation between the development of visual perception and sensorimotor development. In their model, they show that in the early stages of development, all motion is perceived and processed at a very basic level; as the spatiotemporal resolution of vision develops, the robot model can begin to discriminate between its own motions and the motions of others. Through feedback and sensorimotor learning, an association is created between the motor commands of the self and the motions of others. These modeling results provide a theoretical basis of how perceptual-motor coupling may develop in the infant and provides directions for future research.

One limitation of our study is that we did not have an action execution condition to compare our results with previous studies. A direct comparison of action execution with action observation using a source level analysis of brain responses will significantly advance our understanding of the fundamental mechanisms underlying the development of the perceptual-motor system.

Acknowledgments

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