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Predictive motor activation during action observation in human infants

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Certain regions of the human brain are activated both during action execution and action observation. This so-called 'mirror neuron system' has been proposed to enable an observer to understand an action through a process of internal motor simulation. Although there has been much speculation about the existence of such a system from early in life, to date there is little direct evidence that young infants recruit brain areas involved in action production during action observation. To address this question, we identified the individual frequency range in which sensorimotor alpha-band activity was attenuated in nine-month-old infants' electroencephalographs (EEGs) during elicited reaching for objects, and measured whether activity in this frequency range was also modulated by observing others' actions. We found that observing a grasping action resulted in motor activation in the infant brain, but that this activity began prior to observation of the action, once it could be anticipated. These results demonstrate not only that infants, like adults, display overlapping neural activity during execution and observation of actions, but that this activation, rather than being directly induced by the visual input, is driven by infants' understanding of a forthcoming action. These results provide support for theories implicating the motor system in action prediction.

Keywords: social cognition; action perception; motor system

1. INTRODUCTION

One of the most intriguing recent discoveries in neuroscience is that the perception of others' actions induces sub-threshold motor activity in the observer, a phenomenon recorded in both monkeys and humans, and often attributed to a 'mirror neuron system' (MNS) (Rizzolatti & Craighero 2004). However, to date, there has been little evidence for any functional role for this activity (Hickok 2009), despite much speculation regarding its involvement in action understanding (Gallese *et al.* 2004) and action anticipation (Csibra 2007).

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A promising way towards elucidating the function of motor system activation during action observation is to investigate the ontogeny of this phenomenon (Kilner & Blakemore 2007). As one's own motor ability is a determinant of whether the motor system is recruited during action observation (Calvo-Merino *et al.* 2005), the limited (but developing) motor repertoire of infants has the potential to shed light on which capacities are modulated by motor system recruitment (van Elk *et al.* 2008).

To date, little direct evidence exists that young infants recruit their motor system when they observe someone else perform actions. Although a study measuring haemodynamic responses reported motor cortex activation during observation of actions (Shimada & Hiraki 2006), haemodynamic responses do not permit the kind of temporal analysis that may enable us to distinguish predictive versus reactive motor activation. A more promising route towards elucidating the functional role of motor activation is to make use of the potential of measuring motor activity using recordings of sensorimotor alpha activity in the electroencephalogram (EEG), thus providing insight into the temporal dynamics of motor reactivity to observed stimuli. However, the only study aimed at exploring modulations in sensorimotor alpha attenuation during action observation in infants failed to find clear evidence in six-month-olds (Nyström 2008).

In the current study, we used EEG to measure changes in sensorimotor alpha band activity during the course of observing predictably occurring actions in nine-month-old infants. Studies with adults have demonstrated that sensorimotor activity is modulated both by the execution and observation of goal-directed actions (Hari *et al.* 1998), and is likely to originate in the primary somatosensory cortex (Hari & Salmelin 1997). Although it is unknown to what extent this signal is related to activity in so-called MNS areas, a number of authors have speculated that such modulations may reflect activity in MNS regions (Hari *et al.* 1998). Furthermore, both sensorimotor activity and MNS activity are similarly modulated by a number of phenomena (Kilner *et al.* 2009). Measuring changes in sensorimotor alpha activity during action observation therefore provides a promising route towards exploring the ontogeny of 'action mirroring'.

2. MATERIAL AND METHODS

(a) *Participants*

A total of 15 nine-month-old infants participated in this experiment (mean age = 270 days, range = 254–285 days, nine females). An additional ten infants were tested but excluded (see electronic supplementary material).

(b) *Procedure*

The procedure for EEG data acquisition and data reduction is described in the electronic supplementary material. The experiment comprised two phases: a reaching phase (where infants reached for objects themselves) and an observation phase (where infants watched an experimenter reach for objects). The reaching phase followed the observation phase, and the data obtained from the reaching phase directed our analysis of the observation phase.

(i) *Reaching phase*

Infants were seated in front of a puppet stage with the curtains closed. When infants were still and attentive, an experimenter passed a mechanical claw, holding a small graspable toy, through the closed curtains towards the infant (figure 1). The experimenter waited for the infant to reach and grasp for the toy, before removing the claw. A second

Figure 1. Experimental setup for eliciting reaching. A mechanical claw, holding a small graspable toy, is passed through the stage curtains towards the infant.

experimenter, seated on the floor to the right of the infant, retrieved the toy after allowing the infant to briefly play with it. This procedure was repeated until the infant was bored, or until they had reached for approximately 20 different toys. Pilot data suggested that very few reaching trials were required in order to observe sensorimotor alpha suppression (see figure S1 in the electronic supplementary material for examples of single trial effects). Infants contributed a mean of 10 (s.d. = 3.5) artefact-free trials to the analysis.

(ii) *Observation phase*
When infants were still and attentive, curtains opened (~700 ms) to reveal a small graspable object on the stage floor. After ~1000 ms, a hand reached through a curtain on the right of the stage (~500 ms), grasped the object and removed it from the scene (~500 ms). The curtains then closed. Trials were repeated for as long as infants were willing to watch, or until 60 trials had been viewed. A minimum of 10 artefact-free observation trials were required for infants to be included in the analysis. Infants contributed a mean of 15 (s.d. = 3.9) valid trials to the analysis.

(c) *Coding and analysis*
For both phases, the point at which the infant (reaching phase) or the experimenter (observation phase) began movement towards the object was marked on the EEG from the synchronously recorded video (see electronic supplementary material). Segments beginning 1100 ms before and ending 1600 ms after the onset of this movement were then selected for time–frequency analysis by wavelet transformation (see electronic supplementary material). For observation, segments in which infants made limb movements themselves, or did not observe the entire event, were excluded from analysis. From the retained segments, amplitude at selected frequencies was averaged over a 400-ms pre-movement baseline and compared with activity averaged over a 1600-ms time window beginning at the onset of movement (figure 2).

3. RESULTS
(a) *Reaching phase*
For each infant, the single frequency maximally attenuated, and the two adjacent frequencies, were isolated, and activity was averaged over this 3-Hz-wide band. Each infant's average amplitude was then entered into a repeated-measures ANOVA with time (baseline versus reaching) and hemisphere (left versus right) as within-subjects factors, revealing only a significant main effect of time ($F_{1,14} = 18.97$, $p = 0.001$), indicating bilateral attenuation of the sensorimotor alpha rhythm during action execution (figure 2a(i),b(i)).

(b) *Observation phase*
Each infant's individually selected 3-Hz-wide band was then used to analyse activity during observation

of actions. Activity averaged over this 3 Hz band was averaged over a 400 ms baseline period (during which the object was visible on the stage floor; figure 2a(ii)) and compared with activity over a 1600 ms period from the onset of observed movement through the hand grasping and removing the object from the scene (figure 2a(ii)). A repeated-measures ANOVA with time (baseline versus action observation) and hemisphere (left versus right) as repeated-measures factors revealed a marginally significant interaction between time and hemisphere ($F_{1,14} = 3.94$, $p = 0.067$). Separate paired-samples t-tests on data from each hemisphere revealed a significant effect of time ($t_{14} = 2.56$, $p = 0.02$) only in left hemisphere channels, confirming that there was a decrease in sensorimotor alpha activity during the observation of the hand reaching and grasping the object.

The pattern of activity over the course of observation (see figure 2a(ii),b(ii)) indicated that an initial attenuation of alpha activity actually occurred prior to the onset of observed movement, followed by a brief rebound and then a further decrease that continued for the remainder of the trial. Further statistics confirmed that both periods of attenuation differed significantly from baseline. Two further ANOVAs were performed (with time and hemisphere as within-subjects factors), comparing activity during the same 400 ms baseline period with a 400 ms period directly before the hand appeared (first decrease) and a 1000 ms period beginning at the point where the hand grasped the object and continuing through the period where the hand removed the object from the scene (second decrease). Both analyses revealed a significant interaction between time and hemisphere (first decrease, $F_{1,14} = 0.46$, $p = 0.05$; second decrease, $F_{1,14} = 6.47$, $p = 0.02$) and follow-up paired-samples t-tests confirmed that, for both time periods, there was a significant decrease in activity relative to baseline in left hemisphere channels (first decrease, $t_{14} = 2.76$, $p = 0.02$; second decrease, $t_{14} = 2.39$, $p = 0.03$), but this attenuation did not reach significance in right hemisphere channels (first decrease, $t_{14} = 1.94$, $p = 0.07$; second decrease, $t_{14} = 1.37$, $p = 0.19$). This attenuation prior to the onset of observed movement suggests that infants were quickly able to learn that a hand would appear after the curtains were opened.

In accordance with this, additional statistical tests revealed that the attenuation of sensorimotor alpha, although not evident in the first three trials, emerged in the subsequent three trials. We compared activity averaged over the first three trials with activity averaged over the second three trials (trials 4–6) in a repeated-measures ANOVA with time (baseline versus 400 ms period prior to the hand appearing) and trial set (first three trials versus second three trials) as factors. One infant was excluded from this analysis because of movement during the first few trials. This ANOVA revealed a significant interaction between time and trial set ($F_{1,13} = 8.11$, $p = 0.01$). Follow-up paired samples t-tests comparing activity during baseline with activity during the pre-appearance window revealed that there was a marginally significant increase in alpha activity from baseline for data averaged over the first three trials ($t_{13} = 2.05$, $p = 0.06$), but a
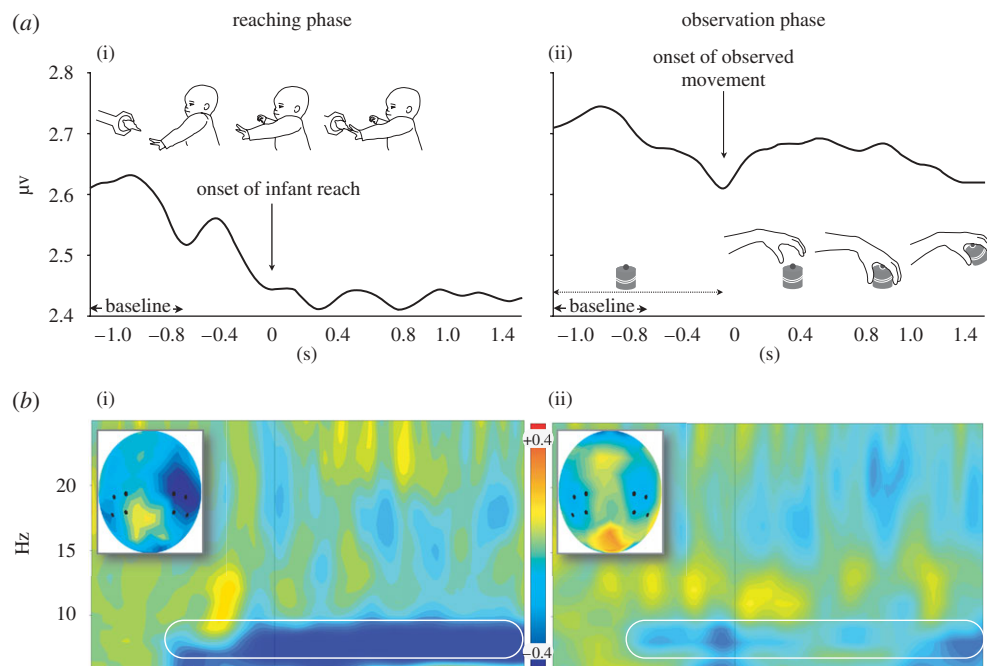
Figure 2. Sensorimotor alpha rhythm modulation. (*a*) Grand averaged amplitude modulation across all sensorimotor channels during action execution (i), and across left hemisphere channels during action observation (ii). (*b*) Baseline corrected time-frequency plots of the same activity. Topographic map inserts show averaged amplitude over a window spanning 1000 ms from onset of self (i) and other (ii) movement in time, and 6 to 9 Hz in frequency. Black dots, sensorimotor channels.

significant decrease in alpha activity from baseline for data averaged over the second three trials ($t_{13} = 2.31$, $p = 0.04$).

4. DISCUSSION

This study is the first to demonstrate that infants exhibit sub-threshold motor activity during action observation that matches directly the neural signal occurring during their own actions. Although we found that attenuation of the alpha rhythm was characteristically bilateral for action execution (Hari & Salmelin 1997), attenuation was stronger in the left hemisphere for action observation. Stronger activation over the sensorimotor cortex, contralateral to the area in space where movement is seen, has been reported (Kilner *et al.* 2009), and may account for our lateralized effect as infants always saw movement presented from the right side of the stage.

Interestingly, rather than occurring only in response to an observed action, motor activation was evident prior to the onset of the observed action once infants could anticipate its occurrence. The fact that predictive motor activation was not elicited during the first three trials suggests that this effect was not a response to the sight of the object on the stage[1] or to the opening of the curtains. Our finding is consistent with previous reports demonstrating that adults activate their motor system when they can predict that someone will perform an action (Kilner *et al.* 2004, but see Caetano *et al.* 2007 for an anticipatory effect in the beta, but not alpha band), and fits with more recent proposals that motor activation during action observation may reflect a process of anticipating how an action will unfold (Csibra 2007).

Although previous studies have not examined the temporal pattern of sensorimotor alpha attenuation (Lepage & Theoret 2006), our demonstration that it is possible to measure such activity during the observation of actions presented in a live setting presents an opportunity to elucidate the role of the motor system in action perception. Although paradigms with adults can be ambiguous with respect to which elements of action interpretation they tap (Agnew *et al.* 2008), the existence of paradigms designed to test different elements of action understanding (goal attribution, action anticipation) in infants (Woodward 1999; Southgate & Csibra in press) offers a unique opportunity to relate motor activity to performance on behavioural tasks. Although the actions presented to infants in this study were within their motor repertoire, future studies can exploit the same methodology to relate motor development to behavioural task performance.

ENDNOTE

[1] The objects were out of reach of the infant (see electronic supplementary material). Infants of this age are competent at perceiving whether or not objects are within reach, and do not attempt to reach for out-of-reach objects (Cruikshank, 1941).

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