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Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study

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Abstract

There is increasing interest in neurobiological methods for investigating the shared representation of action perception and production in early development. We explored the extent and regional specificity of EEG desynchronization in the infant alpha frequency range (6–9 Hz) during action observation and execution in 14-month-old infants. Desynchronization during execution was restricted to central electrode sites, while action observation was associated with a broader desynchronization across frontal, central, and parietal regions. The finding of regional specificity in the overlap between EEG responses to action execution and observation suggests that the rhythm seen in the 6–9 Hz range over central sites in infancy shares certain properties with the adult mu rhythm. The magnitude of EEG desynchronization to action perception and production appears to be smaller for infants than for adults and older children, suggesting developmental change in this measure.

Introduction

In developmental science, increasing attention is being paid to the ways in which experience with the production of motor acts may impact the perception and interpretation of similar acts performed by others (Longo & Bertenthal, 2006; Meltzoff, 2007; Meltzoff, Kuhl, Movellan & Sejnowski, 2009; Sommerville, Woodward & Needham, 2005; von Hofsten, 2007). One impetus for this attention derives from work proposing that an observed action activates the same motor processes or motor schemas in the human observer's brain that would be activated if the action was performed or planned by the observer (e.g. Hari & Kujala, 2009; Jeannerod, 2001; Prinz, 1997). Speculations about the developmental origins of this shared neural activity have tended to occur in the absence of empirical evidence from infancy (Del Giudice, Manera & Keyzers, 2009; Lepage & Thoret, 2007). However, recent studies have suggested that a neural 'mirroring' system is present in some form in infants and may provide predictive or anticipatory information about others' actions (Southgate, Johnson, El Karoui & Csibra, 2010; Southgate, Johnson, Osborne & Csibra, 2009).

One useful technique for exploring the neural correlates of action perception and production is electroencephalography (EEG) which has high temporal precision and has a history of successful use in the study of infant social and cognitive development (Marshall & Fox,

2008). A candidate EEG measure is the desynchronization of the mu rhythm, which is typically recorded from central electrode sites overlying sensorimotor cortex. In adults, the mu rhythm occurs in the alpha frequency range (8–13 Hz) but is considered to have distinct properties from other alpha-range rhythms such as the classical posterior alpha rhythm (Pineda, 2005). The mu rhythm in human adults is desynchronized during both action execution (Gastaut, Dongier & Courtois, 1954; Kuhlman, 1978; Pfurtscheller, 2003; Pfurtscheller & Neuper, 1997) and action observation (Arroyo, Lesser, Gordon, Uematsu, Jackson & Webber, 1993; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson & McNair, 2004; Perry & Bentin, 2009; Pineda, Allison & Vankov, 2000).

While the sensitivity of the mu rhythm to action observation and execution has been reported in older children (Lepage & Thoret, 2006), there is current interest in uncovering a possible infant analog of the adult mu rhythm. In a longitudinal study, Marshall, Bar-Haim and Fox (2002) noted the emergence of an alpha-range rhythm at central electrode sites during periods of attention in infants, with the relative power of this rhythm being particularly strong in the second year of life in the frequency range of 6–9 Hz. This central rhythm in infants was found to be minimally reactive to changes in illumination or eye opening/closing (Stroganova, Orekhova & Posikera, 1999), suggesting, as in adults, a functional dissociation from posterior alpha rhythms.

However, in order to make links between the infant central rhythm and the literature on the adult mu rhythm, two further requirements need to be met. First, the reactivity of the infant rhythm needs to be established for action execution and also action observation conditions. Second, given that infant EEG rhythms may not map neatly onto adult rhythms in terms of their scalp distributions and functional properties (Stroganova & Orekhova, 2007), it is important to include a consideration of the scalp topography of infant EEG responses. If the infant rhythm at central sites is similar to the adult mu rhythm, it would be expected to show a circumscribed desynchronization during voluntary actions that is specific to sensorimotor (i.e. central) regions, which is the pattern seen in adults (Pfurtscheller & Lopes da Silva, 1999). The infant rhythm should also be desynchronized over the same region during action observation, although in line with studies of adults, desynchronization of alpha-range power during action observation might be expected to be more widespread across the scalp than during action execution (Babiloni, Babiloni, Carducci, Cincotti, Coccozza, Del Percio, Moretti & Rossini, 2002).

Initial exploratory studies of infant neural ‘mirroring’ activity reported EEG responses to action observation, but did not include the crucial action execution condition (Nyström, 2008; van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008). More recently, two studies of 9-month-olds by Southgate and colleagues included both action observation and execution conditions. Southgate *et al.* (2009) noted a desynchronization of the ‘sensorimotor alpha’ rhythm during infants’ own reaching movements and a small but significant desynchronization while infants observed reaching and grasping (see also Southgate *et al.*, 2010). The examination of both action observation and execution conditions in these studies represents a considerable advance. However, the question of the regional properties of EEG desynchronization to action observation and execution – and the overlap between the two – remains unaddressed, because the reported statistical results were limited to one cluster of electrodes over the central and parietal region.

In the current study, we analyzed EEG from 14-month-old infants during the observation and execution of a goal-directed act (a button press). We selected this age and task based on both theoretical and empirical considerations arising from the extant literature and pilot work. First, the longitudinal data of Marshall *et al.* (2002) showed that the relative power of the central rhythm in infancy was particularly strong at 14 months of age compared with

both earlier (9 months) and later (24 months) age points. Second, previous work in our laboratory (Meltzoff, 1988), coupled with new pilot studies, showed that infants at this age were particularly attentive when viewing a button press action and that their own topographically similar act could be reliably elicited over a large number of trials by using an interactive test paradigm. The combination of these factors suggested that studying 14-month-olds would allow a confluence of infants' directed attention, their readiness to reproduce a specific goal-directed act, and psychophysiological measurement that could provide an ideal context for elucidating neural correlates of action perception–production overlaps.

We aimed to extend and advance prior work in three ways. First, in order to make firmer links to the literature on the mu rhythm in older children and adults, we wished to include a consideration of the scalp topography of alpha-range infant EEG responses by presenting analyses from a range of electrodes across the scalp. Second, the magnitudes of EEG desynchronization to action observation and execution reported for 9-month-olds by Southgate *et al.* (2009) appear to be small compared to the much stronger effects found for older children (Lepage & Thoret, 2006) and adults (Muthukumaraswamy *et al.*, 2004). We were partly interested in whether older infants (14-month-olds) would show stronger desynchronization responses, a finding which could provide useful information on development. Finally, we wished to use a new goal-directed task to examine the generalizability of the infant mu rhythm response to intentional actions other than grasping.

Methods

Participants

Families with 14-month-old infants were recruited from a diverse urban environment using commercially available mailing lists. Infants were not recruited if they were born preterm, if both their parents were left-handed, if an infant had experienced chronic developmental problems, or if the infant was on long-term medication. Fifty-eight infants participated in the study ($M = 62$ weeks, $SD = 1.3$; 26 male, 29 female). The final sample for the EEG analysis comprised 38 infants. The remaining 20 infants either became excessively fussy during attempts to place the EEG cap ($n = 7$), or their EEG signal did not provide enough artifact-free epochs for meaningful analysis to be carried out (less than three trials per condition; $n = 13$). This data loss rate is fairly typical of EEG work with infants (see DeBoer, Scott & Nelson, 2007; Southgate *et al.*, 2009).

Stimuli and trial structure

The protocol involved the use of five custom-made button boxes. Each box was decorated in a unique color scheme and had a recessed button which produced a unique 2-second electronic melody when pressed. During the protocol, the infant (who wore an EEG cap – see below) sat at a table on his or her caregiver's lap, opposite an experimenter. Prior to beginning the sequence of trials, the experimenter showed the infant one of the button boxes and then demonstrated the button press to the infant.

Each trial consisted of four parts: An action execution epoch, an action observation epoch, and two baseline epochs. At the start of each trial, the experimenter brought out one of the button boxes from behind a screen and placed it on the table with the button facing the infant. In the action observation epoch, the infant observed the experimenter reaching towards the button box with her right hand and producing a button press. In the action execution epoch, the infant was presented with the button box so that he or she could imitate the button press. When presented with the button box, infants almost always pressed the

button (> 95% of trials), as is consistent with the literature on infant imitation at this age (Meltzoff, 1988).

For each infant, the first trial always began with an action observation epoch in which the infant saw the experimenter push the button. For subsequent trials, we alternated whether the action observation or action execution epoch came first within the trial. Within each trial, the execution and observation epochs were each preceded by a visual baseline period consisting of the experimenter presenting a flashcard with an abstract pattern for approximately 3 s. After each observation or execution epoch, the button box was placed back behind the screen and then brought out again. The experiment continued for as long as the infant continued to tolerate the EEG cap and remained interested. For the infants included in the EEG analyses, the mean number of trials accomplished was 16 ($SD = 8$).

Timing synchronization of behavioral and EEG records

The experimental procedure was videotaped, with a vertical interval time code (VITC) signal being placed on the video signal during recording. Calibration procedures had ensured that the VITC time code on the video signal was synchronized with EEG collection, such that the video signal was aligned with the EEG data to the precision of one NTSC video frame (33 ms). This allowed the accurate isolation of the baseline epochs and the epochs in which either the experimenter or the infant was reaching for the button box, as well as the precise time point at which the experimenter or infant pressed the button. In the sample of infants used in the EEG analyses, the mean durations of the epochs of interest were as follows: 3.39 s ($SD = 1.11$) for the observation baseline, 3.46 s ($SD = 1.15$) for the execution baseline, 5.00 s ($SD = 1.7$) for the action execution condition and 2.59 s ($SD = .33$) for the action observation condition.

While our EEG artifacting procedure resulted in the exclusion of baseline and observation epochs containing gross motor movement (see below), these epochs were also coded from video for more subtle infant movements, with a focus on identifying epochs in which infants carried out arm and hand movements that resembled a reaching, pointing, or button-pressing action. Epochs which contained such movements were flagged and were not included in the subsequent EEG analyses.

EEG collection and processing

Using a lycra stretch cap (Electro-Cap International, Inc.), EEG was collected from a range of sites across the scalp: Fp1, Fp2, F3, F4, Fz, F7, F8, C3, C4, T7, T8, P3, P4, Pz, P7, P8, O1, O2 as well as the left and right mastoids. The EEG signal was amplified by optically isolated, high input impedance (>1 G Ω) custom bioamplifiers (SA Instrumentation) and was digitized onto the hard drive of a Pentium IV PC using a 16-bit A/D converter (± 5 V input range). Scalp electrode impedances were usually under 25 kilohms. Bioamplifier gain was 4000 and the hardware filter (12 db/octave rolloff) settings were .1 Hz (high-pass) and 100 Hz (low-pass). The signal was collected referenced to the vertex (Cz) with an AFz ground, and all EEG data were re-referenced offline to an average mastoids reference prior to further analysis. In order to clear the EEG data of ocular and muscle artifact, a procedure involving independent component analysis (ICA) was used which was an automation of the method described by Jung, Makeig, Humphries, Lee, McKeown, Iragui and Sejnowski (2000). Following this procedure, any epochs in which the EEG signal for any channel exceeded ± 250 μ V were excluded from further analysis.

Event-related changes in band power between the baselines and the observation or execution epochs were computed using established methods for computing event-related desynchronization (ERD; Pfurtscheller, 2003). In line with work on alpha-range EEG

frequency bands in infants of this age (Marshall *et al.*, 2002), the primary frequency band of interest was taken to be 6–9 Hz. For the computation of ERD scores, the following sequence was used: (a) Bandpass filtering of the EEG signals between 6 and 9 Hz; (b) Squaring of the filtered signals to convert to a power metric; (c) Computation of event-related averages for each condition within each participant; (d) Computation of the mean power of the event-related signal in 125 ms epochs.

Desynchronization values were computed for each 125 ms epoch as $([A - R]/R) * 100$, where A is band power during action observation or execution, and R is band power during the corresponding baseline reference condition (Pfurtscheller & Lopes da Silva, 1999). Negative ERD scores reflect desynchronization (i.e. a decrease in band power relative to the baseline), while positive values reflect synchronization (i.e. an increase in band power relative to the baseline). The computation of ERD scores was time-locked to the achievement of the goal-directed act (i.e. the point at which the infant or adult pressed the button), with the dependent variable in the analyses being mean ERD over a fixed 1000 ms time interval extending 500 ms before and after the button press.

Results

Action execution

Mean ERD scores using an average of seven artifact-free execution trials per participant (range: 3–15 trials) were computed for central (sites C3/Cz/C4), frontal (F3/Fz/F4/F7/F8), parietal (P3/Pz/P4/P7/P8), and occipital (O1/O2) regions. Nine of the 38 participants had extreme ERD values (more than 1.5 times the interquartile range from the median) at one or more regions and were excluded from subsequent analyses.

An initial repeated-measures ANOVA showed a significant main effect of region, $F(3, 84) = 3.20, p < .05$, after Greenhouse-Geisser Correction (see Figure 1). Follow-up contrasts showed more desynchronization over the central region ($M = -12.40, SD = 25.3$) than over the frontal ($M = 3.9, SD = 41.7, p < .01$), parietal ($M = .03, SD = 45.1, p = .07$) and occipital ($M = 8.8, SD = 52.1, p < .05$) regions. Further planned *t*-tests indicated that the ERD score for the central region was significantly different from zero, $t(28) = -2.64, p < .05$, whereas mean ERD scores for the other three regions did not differ from zero. Supplementary analyses showed no significant hemispheric asymmetry in ERD at central sites and no effect of the hand infants predominantly used (left, right, both) to press the button.

Action observation

Mean ERD scores using an average of 12 artifact-free observation trials per participant (range 3–27) were computed for central (C3/Cz/C4), frontal (sites F3/Fz/F4/F7/F8), parietal (P3/Pz/P4/P7/P8), and occipital (O1/O2) regions. Eleven of the 38 participants had extreme ERD values (more than 1.5 times the interquartile range from the median) for one or more regions and were excluded from subsequent analyses.

An initial repeated-measures ANOVA showed no significant main effect of region, $F(3, 75) = 1.24, p = .30$ (see Figure 2). Planned *t*-tests indicated that mean ERD scores were significantly different from zero for frontal ($M = -20.1, SD = 33.9, t(25) = -3.03, p < .01$), central ($M = -13.7, SD = 26.1, t(25) = -2.67, p < .05$) and parietal ($M = -11.2, SD = 25.9, t(25) = -2.21, p < .05$) regions, but not for the occipital region ($M = -9.8, SD = 36.7, p = .18$). Supplementary analyses showed no significant hemispheric asymmetries in ERD over any region.

Discussion

We tested for EEG desynchronization when infants observed an experimenter carry out a goal-directed act (a button press) and when they executed the same action. We were particularly interested in the reactivity of the infant EEG rhythm occurring at 6–9 Hz over central electrode sites (Marshall *et al.*, 2002) to the action observation and execution conditions relative to baseline epochs in which infants viewed an abstract visual pattern. The digitized EEG signal was synchronized with the behavioral record enabling precise time-locking of our EEG analyses to the button press in both the action execution and observation conditions. This allowed us to carry out an infant adaptation of studies in older children (Lepage & Thoret, 2006) and adults (Bernier, Dawson, Webb & Murias, 2007; Muthukumaraswamy & Johnson, 2004) in which EEG analyses were locked to the temporal culmination of an object-directed act.

As noted earlier, there are two requirements that investigations of the mu rhythm as an index of infant ‘mirroring’ activity should strive to meet: (a) EEG reactivity to both action execution and action observation needs to be documented, and (b) the regional overlap of desynchronization to action execution and action observation should be examined. The current study simultaneously addressed both of these considerations.

Consistent with the findings of Southgate *et al.* (2009), we observed significant event-related desynchronization at central sites during epochs in which infants executed a goal-directed act, and found a similar desynchronization at central sites during observation of the same act. Unlike prior studies of infancy, we also extended our analyses to a wide range of other scalp regions and found that although the reduction in band power during action observation went beyond central sites to frontal and parietal regions, the desynchronization during action execution was specific to central sites. The specificity of desynchronization to central sites during action execution is consistent with studies of adults (Pfurtscheller & Lopes da Silva, 1999) and may reflect the focused nature of the hand and finger movements involved in our button press task. The finding of a more diffuse desynchronization during action observation is also consistent with EEG studies of adults, which have generally found a relatively widespread reduction of alpha-range power during action observation (e.g. Babiloni *et al.*, 2002; Calmels, Holmes, Jarry, Hars, Lopez, Paillard & Stam, 2006; Marshall, Bouquet, Shipley & Young, 2009; Orgs, Dombrowski, Heil & Jansen-Osmann, 2008). We found that the central region was the only scalp region that showed a common desynchronization to both action execution and observation, which is again congruent with work on the adult mu rhythm (Muthukumaraswamy & Johnson, 2004).

The current findings provide firmer support for the tentative suggestion that the infant central rhythm at 6–9 Hz is distinct from alpha-range rhythmic activity in other scalp regions (Stroganova *et al.*, 1999), and they further advance the argument that the infant rhythm shares functional properties with the adult mu rhythm. This represents progress in the study of the EEG correlates of action perception–production links in infants. It has long been known that infant EEG rhythms differ from adult rhythms in terms of their frequency ranges, but infant rhythms may also not map neatly onto adult rhythms in terms of their scalp distribution or functional properties (Stroganova & Orekhova, 2007). For instance, Orekhova, Stroganova, Posikera and Elam (2006) suggested that a more anterior central sulcus in infants versus adults could create a more frontal scalp distribution of the mu rhythm in infants. Our findings suggest that despite such potential issues, the infant EEG rhythm at 6–9 Hz over central sites may be a functional analog of the adult mu rhythm over the same scalp region. Our findings also fit well with the assumptions about the properties of the central rhythm in other studies of action perception–production links in infants (Southgate *et al.*, 2009, 2010). However, it should be noted that given the lack of spatial

specificity of EEG, documenting overlaps in desynchronization between observation and execution conditions, in this study and others, does not necessarily indicate the activation of the same neural systems. Infant work using other imaging technologies with finer spatial properties, particularly infant magnetoencephalography (MEG), may be useful in addressing this issue for goal-directed actions, as it is doing for the representation of speech in infants (Imada, Zhang, Cheour, Taulu, Ahonen & Kuhl, 2006).

The current findings immediately raise developmental questions. One concerns differences in the magnitude of band power desynchronization seen across prior EEG studies of action execution and observation. In a study of children aged between 4 and 11 years of age, Lepage and Thoret (2006) report 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). In the current study with 14-month-old infants, we observed a 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 study of Southgate and colleagues (2009) with 9-month-old infants, the extent of desynchronization during reaching execution compared with a baseline epoch just prior to reaching appears to be broadly similar to our study (around 10%). There are also developmental differences between studies in the extent of EEG desynchronization during action observation. Lepage and Thoret (2006) reported a desynchronization of around 25% during action observation relative to baseline, which is again consistent with adult work (Muthukumaraswamy & Johnson, 2004). In the current study we found a smaller decrease (around 14%) in band power at central sites while 14-month-olds observed the adult's action. In the study of 9-month-olds by Southgate *et al.* (2009), the extent of desynchronization during action observation appears to be smaller still (around 5%).

Of course, the studies differ in a number of procedural and methodological aspects which may impede direct comparisons of findings. Further work is needed in this area to disentangle the effects of age and different types of actions on mu desynchronization. However, the increase in reactivity to action execution and action observation seen across the extant studies may represent a developmental increase in the reactivity of the mu rhythm. If this change in reactivity represents a developmental increase in activity of a neural system sub-serving action perception–production maps, it would be of considerable theoretical interest.

There has been a good deal of recent debate about the nature, scope, and involvement of a so-called mirror neuron system (MNS) in action interpretation (e.g. Hickok, 2009), with recent theoretical proposals arguing against a simple resonance account (e.g. Csibra, 2007). Instead, it has been suggested that a neural mirroring system may provide anticipatory or predictive information as part of a wider system for action interpretation, with this function being present in infancy (Southgate *et al.*, 2009, 2010). The flexibility of the imitative capabilities demonstrated by infants certainly suggests that neural linkages between action perception and production go beyond simple resonance mechanisms (e.g. Meltzoff, 1995, 2007).

Further advances may come from experiments designed to adapt neuroscience techniques to a broader set of ages and questions. Are there skeletal linkages between perception and production at birth that can be measured not only behaviorally (Meltzoff & Moore, 1997) but also neurally? How might such perception–production links be engendered or altered by experience? Is development principally driven by self-generated intermodal experience, for example, watching oneself produce hand movements and goal-directed reaches? Or does contingent responding by external social agents play a role, for example, seeing a caretaker mirror one's own acts in reciprocal imitation games? It will be equally informative to

explore the impact of unimodal experience: There may be important consequences of simply observing systematic acts of others or even producing motor acts oneself in the absence of observation (including prenatal motor experience; Meltzoff & Moore, 1997). By combining neuroscientific and behavioral studies with a developmental perspective we will deepen our understanding of the representation of action, and the degree to which perception and production draw on shared psychological and neural resources.

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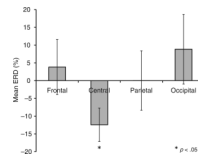


Figure 1. Action execution: Mean event-related desynchronization (ERD, in %) scores by region (frontal, central, parietal, occipital). Error bars show ± 1 standard error. Significant differences from zero are indicated.

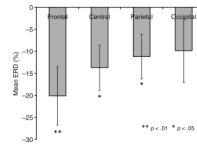


Figure 2. Action observation: Mean event-related desynchronization (ERD, in %) scores by region (frontal, central, parietal, occipital). Error bars show ± 1 standard error. Significant differences from zero are indicated.