Published in final edited form as:

Br J Dev Psychol. 2016 March ; 34(1): 24–37. doi:10.1111/bjdp.12115.

Desynchronization in EEG during perception of means-end actions and relations with infants' grasping skill

Kathryn H. Yoo, Erin N. Cannon, Samuel G. Thorpe, and Nathan A. Fox

Department of Human Development and Quantitative Methodology, University of Maryland, College Park, MD, USA

Abstract

The current study examined age-related differences in EEG activity during perception of means-end actions and production of grasps, and how EEG activity may relate to infants' motor competence. We collected data from 9- and 12-month-old infants during perception of means-end actions made with a tool and during execution of their own grasps. We computed event-related desynchronization (ERD) during perception and production events, and assessed infants' reach-grasp competence by looking at their latency to complete grasps. Although we found greater ERD during perception of means-end actions in 9-month-olds compared to 12-month-olds, we found the relation between ERD during perception and emerging reach-grasp competence to be specific for 12-month-olds and not for 9-month-olds. These results provide evidence for an emerging neural system that supports the coupling of action and perception with infants' emerging motor competence in the first year of life.

Introduction

In the first year of life, there are fundamental changes in infants' abilities to link action production and perception, which facilitate motor skill learning through continuous coordination of their motor abilities with incoming perceptual information (Thelen, 1995). One neural signal used to investigate the coupling of action and perception is the mu rhythm. The mu rhythm is a brain oscillation identified in the electro/magnetoencephalogram (EEG/MEG) recorded over the sensorimotor areas that has been implicated in both the production and perception of motor actions (Marshall, Young, & Meltzoff, 2010; Neuper & Pfurtscheller, 2001; Pineda, 2005). Mu rhythm is found in the alpha frequency band (~8–13 Hz for adults) during both the production and perception of motor actions in adults, and has been associated with sensorimotor neural activity (Arnstein, Cui, Keyser, Maurits, & Gazzola, 2011; Avanzini et al., 2012; Muthukumaraswamy & Johnson, 2004; Pineda, 2005). And, by 9- to 10-months of age, the mu rhythm is found in the 6–9 Hz frequency band (Marshall, Bar-Haim, & Fox, 2002). Several recent studies suggest that mu rhythm indirectly reflects action-perception coupling in infants (Marshall & Meltzoff, 2011). As is the case with adults, infant mu rhythm desynchronizes (i.e., decreases in spectral power) during action perception (Gerson, Bekkering, & Hunnius, 2014; Marshall,

Young, & Meltzoff, 2010; Ruyschaert, Warreyn, Wiersema, Metin, & Roeyers, 2013; Warreyn et al., 2013) and action production (see Cuevas, Cannon, Yoo, & Fox, 2014 for review; Saby, Marshall, & Meltzoff, 2012; Southgate, Johnson, El Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, & Csibra, 2009). This decrease in spectral power from a baseline is also known as event-related desynchronization (ERD).

However, the extent to which mu ERD reflects activity of a sensorimotor network and how it may relate to infants' motor competence remains unclear. Adult studies have reported mu ERD during perception and production of actions to be specific to the sensorimotor areas (Avikainen, Forss, & Hari, 2002; Hari et al., 1998; Ritter, Moosmann, & Villringer, 2009). However, infant studies—including our own—report a widely distributed ERD beyond sensorimotor scalp areas during action observation and production (Cannon et al., 2015; Marshall et al., 2010; Virji-Babul et al., 2012; Warreyn et al., 2013). The current study aimed to elucidate how ERDs over various regions may specifically relate to infants' motor competence.

In adults, there exists evidence of the relations between mu rhythm activity and motor skills. In particular, expertise in a specific motor domain is associated with increased responses of motor-related areas during perception of the specific action (Calvo-Merino et al., 2005; Hadjidimitriou et al., 2011). Mu rhythm studies report greater mu ERD during perception of actions with which the participants are familiar compared to actions with which they are not (Hadjidimitriou et al., 2011; Marshall, Bouquet, Shipley, & Young, 2009). Studies have examined various motor skills from dancing to training adults to operate a tool and have found that individuals with experience in a specific motor domain exhibited greater mu ERD compared to non-dancers or novices without training (Cannon et al., 2014; Orgs et al., 2008). Based on these findings, mu rhythm appears to reflect the motor experiences or expertise of an individual.

There are several infant studies that examine the relations between mu rhythm and motor experience (Gerson, Bekkering, & Hunnius, 2014; Marshall, Saby, & Meltzoff, 2013; Paulus et al., 2012; van Elk et al., 2008). Paulus and colleagues (2012) trained 8-month-old infants to shake a novel rattle that made a specific sound when it was shaken. They found that the magnitude of mu rhythm desynchronization during the presentation of the sound related to the duration of training (i.e., number of training days). Gerson and colleagues (2014) found greater mu desynchronization to sounds associated with actions with which 10-month-old infants had active training compared to sounds that were familiar via observational training (i.e., watching the action performed by another). These studies, however, measure experience quantitatively (Paulus et al., 2012) or group infants based on whether they demonstrated the action after training (Gerson, Bekkering, & Hunnius, 2014). There is limited evidence to show how qualitative measure of infants' motor abilities at different stages in development (i.e., age) relate to mu rhythm activity.

In the following study, we examined age-related differences in: 1) EEG desynchronization during perception of means-end actions made with a tool and execution of grasp, and 2) the relations between infants' reach-grasp skill and EEG desynchronization during perception of means-end actions. The first aim examined whether there are age-related differences in the

magnitude of EEG desynchronization in 9- and 12-month-olds during perception of means-end actions and during execution of grasps. Infant behavioral work demonstrates that between 8 and 12 months of age, infants begin to produce more complex actions such as means-end actions (Barrett, Davis, Needham, 2007; Provasi, Dubon, & Bloch, 2001). The second aim followed the work by Cannon and colleagues (2015), which examined the association between 9-month-olds' reach-grasp efficiency and EEG desynchronization during perception of grasping actions. In their study, infants who were more competent at reaching and grasping exhibited greater desynchronization over the sensorimotor areas during perception of grasps compared to infants who were less competent at reaching and grasping, providing support for an emerging system that couples one's own actions with the perception of actions executed by others (Cannon et al., 2015).

Based on the evidence that by 12 months, infants interpret means-end actions as meaningful, i.e., goal-directed (Biro, Verschoor, & Coenen, 2011), we predicted that 12-month-olds would exhibit greater EEG desynchronization, particularly over the sensorimotor areas, compared to 9-month-olds during perception of means-end actions. In addition, based on studies showing greater ERD with greater motor experience, we predicted that ERD during execution of grasps, particularly over the sensorimotor areas would be greater for 12-month-olds compared to 9-month-olds. We were also interested in looking at whether the relation between infants' reach-grasp skill and ERD extended to the perception of means-end action made with a tool, and we predicted that this relation would be specific to centro-parietal ERD. However, the few studies that exist have examined ERD during production as a predictor of behavior (Babiloni et al., 2008) and during perception as an outcome of behavior (Cannon et al., 2014; 2015). Based on these findings, we implemented an exploratory analysis examining ERD as a predictor of behavior, and behavior as a predictor of ERD.

Method

Participants

Two groups of full-term infants (minimum 37 week gestation) were recruited for the study. The final sample included 26 nine-month-olds (13 females, $M_{age} = 9.16$, $SD = 0.34$) and 34 twelve-month-olds (19 females, $M_{age} = 12.08$, $SD = 0.34$). An additional 8 infants in the 9-month-old group were tested but excluded from the analyses due to fussiness ($n = 6$), never grasping toy during the experiment ($n = 1$), and having less than 4 trials post-artifactual ($n = 1$). An additional 13 infants for the 12-month-old group were tested but excluded from the analyses due to fussiness ($n = 7$) and technical difficulties ($n = 6$).

Procedure and stimuli

The infants sat on their caregiver's lap approximately 40 cm from the front of a black puppet stage (99 cm (W) $\times$ 61 cm (L) $\times$ 84 cm (H)) placed on a tabletop covered with black cloth. Black panel curtains covered the areas immediately surrounding the stage to hide the experimenter and the equipment from infants' view. A video camera was placed behind the presenter focused on the infant and the presenter to capture events of interest during testing.

Caregivers were instructed to remain as observers and not display behaviors (e.g., pointing at the experimenter) that may shift their infant's attention.

A trial consisted of an observation and an execution condition (see Figure 1). A taupe curtain was raised and lowered at the start and end of each observation and execution. To begin the observation condition (presented live), the curtain was raised, revealing a female presenter sitting across from the infant. The presenter then made eye contact with the infant to capture his or her attention then shifted her gaze towards a toy that was placed at the center of the stage, but not within the infants' grasp. Then, the presenter reached for the toy with a hand-operated claw-like tool, picked up the toy with the tool, brought the toy to herself, and gave the toy a brief shake. Then, the curtain was lowered to mark the end of this event, which lasted approximately four seconds.

During the execution condition, a toy was placed on the tabletop, and the presenter hiding from the infants' view, pushed the tabletop towards the infant within reaching distance as the curtain was raised. Infants were given approximately sixty seconds to reach for the toy, and if not, the event ended and the procedure continued on to the next event. After the infants obtained the toy, the tabletop was retracted, the curtain lowered to mark the end of this event, and the experimenter retrieved the toy from the infant.

Baseline events were recorded during a short period of rest preceding each observation and execution event. Thus, one trial consisted of baseline, observation, baseline, and execution with the order in which the observation or the execution condition was presented first was pseudo-randomized. There were ten trials in which the observation condition came first and ten trials in which execution condition was presented first (up to 20 trials), and these trials were pseudo-randomized. This set randomized sequence of observation/execution trials was used for all the infants. Ten unique toys were used, with the same toy used within one trial for observation and execution. The same toys were reused for the second set of 10 trials. On average, both 9- and 12-month-olds completed 12 trials ($SD = 5$).

Latency to initial grasp measure

Based on the Cannon et al. (2015) study, we examined infants' grasping skill efficiency during execution trials. We determined the latency with which infants grasped the toys as a marker of their grasping skill efficiency. We used grasp latency to examine grasp competence based on Cannon et al.'s (2015) findings to be driven by the grasp latency measure. The average amount of time was calculated from the touch that resulted in a grasp until the completion of the grasp (9-month-olds: $M = 1.02$ seconds, $SD = 0.43$; 12-month-olds: $M = 1.19$ seconds, $SD = 0.81$). Grasp completion was coded as the beginning of the toy pick up or infants' fingers wrapped around the toy if there was no pick up. Touches that led to a toy grasp, but not touches that did not lead to a grasp, were included in the latency to grasp measure. The inter-rater agreement within three frames was achieved on 93% of the trials for the timing of the touch that resulted in a grasp, and at least 86% of the trials for the timing of the completion of the grasp. The coders were blind to the hypotheses, and mean latencies of 9- and 12-month-olds were not statistically different from each other ($p = 0.30$).

Behavioral coding for EEG segmentation

Recorded video was synchronized to the EEG at a resolution of 320×240 pixels and at a frame rate of 30 Hz, enabling the coding accuracy to be within approximately 33 ms for behaviors of interest. Two independent coders viewed each video offline (100%) frame-by-frame and identified the following events: a) frame in which the presenter first made contact with the toy using the claw-like tool that resulted in grasp completion of the toy (observation condition), and b) frame in which the infant first made contact with the toy that resulted in grasp completion of the toy (execution condition). The inter-rater agreement within three frames was achieved on at least 91% of the trials for observation and on 93% of the trials for execution. The EEG data were segmented around these observation and execution events. In addition, trials in which infants were not attending to or reaching/grasping during the observation event were coded and excluded.

EEG acquisition and processing

EEG was recorded using a 64-channel HydroCel Geodesic Sensor Net and sampled at 500 Hz via EGI software (Net Station v4.5; Electrical Geodesics, Inc., Eugene, OR). The eye lead channels 61 through 64 (above and below the eyes) were removed from the net, thus, EEG data were collected from 60 channels referenced online to the vertex. Impedance values for all channels measured less than $100 \text{ k}\Omega$ at the start of EEG acquisition.

The pre-processing and computation of desynchronization were carried out using MATLAB (R2013b; Mathworks, USA). Continuous EEG data were baseline corrected and forward/reverse Butterworth filtered (1–50 Hz pass band, 0.1–59 stop band, 10 dB attenuation, and 3 dB maximum ripple) and re-referenced to the average of 58 electrodes, because we excluded from this reference a pair of channels (23 and 55), which lie about the sides of the face, and as such are heavily prone to net displacement artifact. A threshold of $\pm 150 \mu\text{V}$ was used for artifact editing to remove excessive movements and spurious noise. Continuous EEG data were sectioned into 125 ms epochs and epochs in which more than 5 channels (based on Cannon et al., 2014; Thorpe, Cannon, & Fox, 2015) exceeded this threshold were rejected (the sample numbers of all such discontinuities were recorded for purposes of identifying bad trials after segmentation). The resulting data were then decomposed into Independent Components using the FastICA algorithm developed by Hyvärinen and colleagues (1999; 2004). The implementation of an ICA converts the EEG data into a matrix that contains spatially fixed and temporally independent components in which the number of EEG channels matches the number of components (Lee, Girolami, & Sejnowski, 1999).

Components related to eye movement and net displacement over the front of the head were identified for rejection using a two-fold criterion. First, rejected components had to have greatest loading magnitude at one of the designated set of channels located over the most anterior part of the head positioned closest to the eyes (specifically channels 1, 5, 10, 17, 18, and 58). Second, rejected components had to have peak spectral power outside a band of interest chosen as 4–16 Hz. This second criterion ensured we only reject frontally dominant components with EEG peaked in either the 0–4 Hz delta band (such as the components related to blink/saccade/net-displacement waveforms) or $>16 \text{ Hz}$ (such as components related to high frequency broadband muscle artifact). We utilized this method of artifact

rejection based on previous infant EEG studies (Thorpe, Cannon, & Fox, 2015; Cannon et al., 2015).

For the observation and execution events, a 1,000 ms window was used to segment the EEG. For both events, the segmentation window was $-1,018$ to -18^1 ms *prior* to the touch that resulted in obtainment of the toy (i.e., when the infant had physical contact with the toy until the toy was lifted from the table or if there was no toy lift, when multiple fingers were wrapped around the toy or when the mechanical tool had physical contact with the toy). Evidence indicates that mu rhythm starts to desynchronize before action completion, thus, this time period was chosen for analysis (Neuper & Pfurtscheller, 2001; Southgate et al., 2009). Baseline event was considered as a period of rest prior to the start of each observation and execution trial. Thus, 1,000 ms baseline segments were derived from segmenting $-2,018$ ms to -982 ms from the start of the observation and execution event (i.e., before the observation events began when the experimenter is sitting still or before execution trials began). Importantly, any trials for which the earlier artifact thresholding procedure resulted in a discontinuity occurring anywhere in the window of analysis for either the baseline or observation/execution event segment was excluded from analysis.

Event-related de/synchronization (ERD/ERS) across scalp locations was computed in the 6–9 Hz band *a priori* for each observation and execution trial and channel. Previous infant studies of mu rhythm activity have demonstrated that infant mu rhythm is found in this frequency band (Marshall, Bar-Haim, Fox, 2002; Saby, Marshall, & Meltzoff, 2012). The primary channels of interest for mu rhythm activity were clusters of electrodes over the central and parietal sites according to the 10/20 system (C3: 15, 16, 20, 21, 22; C4: 41, 49, 50, 51, 53; P3: 28, 26, 27, 31; P4: 40, 42, 45, 46). Central and parietal clusters were averaged together based on previous studies that localized mu rhythm to centro-parietal areas (Avikainen, Forss, & Hari, 2002; Hari et al., 1998; Thorpe, Cannon, & Fox, 2015). In addition, to explore event-related de/synchronization (ERD/ERS) of EEG power in the same frequency band as mu rhythm and for comparison during analysis, frontal and occipital electrodes were also analyzed (F3: 9, 11, 12, 13, 14; F4: 2, 3, 57, 59, 60; O3: 35; O4: 39). The ERD/ERS compared spectral power of observation and execution trials to baseline segments that preceded each of the observation and execution trials. Fourier coefficients for each segment were obtained via Fast Fourier transform (FFT). ERD/ERS at the 6–9 Hz band was computed in dB units (i.e., ten times the log (base 10) ratio of power in the observation (or execution) and power in the baseline segment). Negative values indicate desynchronization with respect to baseline whereas positive values indicate synchronization. This computation was performed for each of the channels of interest. After ERD was computed for each observation and execution trial and for each channel, ERDs for observation trials were averaged over frequency bins (6–9 Hz; 1 Hz bins) and subsequently over the electrode clusters to derive ERD values over frontal, centro-parietal, and occipital

¹These segmentation windows reflect the corrected values to deal with data/event timing offset introduced by the NA300 anti-aliasing filter (detailed in an advisory notice released by EGI in August 2014). All events marked in the continuous recording during acquisition were moved back in time by the manufacturer specified offset of 18 ms, thus, these segmentation values reflect this 18 ms offset.

sites. An identical process was implemented for the execution trials to yield an average ERD for the execution condition for frontal, centro-parietal, and occipital sites.

To examine ERD magnitudes in 9- and 12-month-olds, we used SPSS for statistical analysis. Also, to investigate how the relation between grasp latency and ERD during observation in the centro-parietal region depended on the age group, a moderated regression analysis was performed using the SPSS toolbox PROCESS (Hayes, 2012).

Results

For the first aim, we examined age-related differences in ERD (dB) during observation of means-end actions made with the claw-like tool and during production of infants' grasps. We computed an omnibus mixed repeated-measures analysis of variance (ANOVA) with Condition (observation, execution) $\times$ Region (frontal, centro-parietal, occipital) $\times$ Hemisphere (left, right) with Age group (9-month-olds, 12-month-olds) as a between-subjects factor. Mauchly's Test indicated that the assumption of sphericity had been violated for factors Region and Condition $\times$ Region (Region: $X^2(2) = 16.48, p < .001$; Condition $\times$ Region: $X^2(2) = 38.99, p < .001$). Therefore, degrees of freedom and p values were corrected using Greenhouse-Geisser estimates of sphericity, where appropriate (Region: $\epsilon = 0.79$; Condition $\times$ Region: $\epsilon = 0.66$). The analysis revealed a main effect of Condition, $F(1, 56) = 5.85, p < .02, \eta_p^2 = 0.10$, qualified by a Condition $\times$ Age group interaction, $F(1, 58) = 17.45, p < .01, \eta_p^2 = 0.24$. A follow-up analysis revealed that across the scalp, there was greater ERD in the execution condition ($M = -1.40, SE = 0.16$) compared to the observation condition ($M = -0.76, SE = 0.14$). An independent samples t -test revealed that for the observation condition, there was greater ERD across the scalp for 9-month-olds compared to 12-month-olds ($t(58) = -3.22, p < .01, r = 0.39; M_{9-months} = -1.25, SE = 0.21; M_{12-months} = -0.38, SE = 0.17$). However, for the execution condition, there was greater ERD for 12-month-olds ($t(57) = 2.41, p < .02, r = 0.30; M_{9-months} = -0.98, SE = 0.20; M_{12-months} = -1.71, SE = 0.22$). Twelve-month-olds exhibited greater ERD during execution of a grasp compared to 9-month-olds but not during observation of means-end action made with a tool. Figure 2 provides ERD means and standard errors for 9- and 12-month-olds by region and condition.

The omnibus ANOVA also revealed a main effect of Region, $F(1.59, 88.97) = 26.37, p < .001, \eta_p^2 = 0.32$, for which there was greater ERD in the occipital sites ($M = -1.76, SE = 0.19$) compared to frontal ERD ($M = -0.76, SE = 0.13$) and to centro-parietal ERD ($M = -0.94, SE = 0.11$) across conditions. Finally, the omnibus ANOVA revealed an interaction of Condition $\times$ Region, $F(1.33, 74.28) = 13.31, p < .001, \eta_p^2 = 0.19$. Pairwise comparisons revealed that for the observation condition, there was greater occipital ERD ($M = -1.90, SE = 0.22$) compared to centro-parietal ($M = -0.39, SE = 0.13; p < .01, r = -0.48$) and frontal ERD ($M = -0.34, SE = 0.16; p < 0.01, r = -0.47$). Pairwise comparisons for the execution condition did not reveal any significant effects ($ps > 0.09$). One sample t -tests compared to zero revealed significant ERD during execution (9 months: $p < .001, r = 0.70$; 12 months: $p < .001, r = 0.81$) and observation (9 months: $p < .001, r = 0.76$; 12 months: $p = .03, r = 0.36$). The omnibus repeated-measures ANOVA revealed no other main effects or interactions (Condition $\times$ Hemisphere or main effect of Hemisphere).

Relation between latency to initial grasp and ERD during observation

To examine whether age moderated the relation between infants' grasp latency and centro-parietal ERD (*a priori*) during perception of means-end action, two exploratory analyses were run using Bonferroni corrected significance criterion $\alpha < 0.025$ ($\alpha = 0.05/2$). The model with centro-parietal ERD entered as a predictor and age group (9- and 12-months) as the moderator revealed a significant effect of model ($R^2 = 0.25$, $F(3, 56) = 6.26$, $p < .01$) and a significant interaction between centro-parietal ERD and age group on grasp latency (Table 1; $b = 0.39$, $SE = 0.15$, $t = 2.55$, $p = .01$). Follow up analyses were performed to determine if the simple regression slopes for the association between centro-parietal ERD during observation and grasp latency were significant for 9-month-old and 12-month-old age groups. Results revealed a significant positive association between centro-parietal ERD during observation and grasp latency for the 12-month-old group ($b = 0.42$, 95% CI [0.22, 0.62], $t = 4.18$, $p < .01$). However, the relation was not significant for the 9-month-old group ($b = 0.03$, 95% CI [-0.19, 0.26], $t = 0.30$, $p = .77$). Figure 3 depicts the simple slopes for the interaction. When grasp latency was entered as the predictor with centro-parietal ERD as the outcome and age group as the moderator, there was a significant effect of model ($R^2 = 0.26$, $F(3, 56) = 6.47$, $p < .01$), however, there was no significant interaction between grasp latency and age group on centro-parietal ERD ($p = 0.32$). The same analyses performed with frontal and occipital ERD during observation of action made a claw-like tool were not significant (ERD as predictor: $ps > .05$; ERD as outcome; $ps > .38$).

We also performed the same regression analyses with age group as the moderator with frontal, centro-parietal, and occipital ERDs during execution of grasps. These analyses revealed no significant results (Frontal: $p = .09$; Centro-parietal: $p = .58$; Occipital: $p = .71$).

Discussion

In the current study, we examined age-related differences in EEG desynchronization in the first year of life and its relation to grasping skill. For the first aim, we expected that during perception of means-end actions made with a tool, 12-month-olds would show greater ERD, particularly over the centro-parietal areas, compared to 9-month-olds. Our results indicated that 9-month-olds showed greater ERD across the scalp compared to 12-month-olds. In contrast, during grasp execution, 12-month-olds showed greater ERD across the scalp compared to 9-month-olds. However, these age-related differences were not specific to centro-parietal region.

Consistent with a previous study (Southgate & Begus, 2013), we demonstrate that as early as 9-months of age, infants show ERD during perception of means-end actions. Not only did we find ERD in 9-month-olds during perception of an action made with a tool, we found that 9-month-olds exhibited greater ERD compared to 12-month-olds. This result was contrary to what we expected, because older infants would theoretically be more familiar with means-end actions (although not necessarily the tool use action) compared to younger infants. However, this age difference in ERD was for ERD across the scalp, not specific to centro-parietal electrodes. These results therefore may also include global attention processes to novel events, as the means-end action may also have been more novel to 9-month-olds compared to 12-month-olds. In fact, our results parallel existing evidence of greater ERD

during perception of novel events compared to familiar events or greater ERD with less motor experience (Stapel et al., 2010; Del Percio et al., 2010). In addition, there may be differences between the two age groups with regards to the different aspects of the action they are attending. For example, 9-month-olds may be attending to the tool itself whereas 12-month-olds who are more experienced with means-end actions compared to 9-month-olds are perceiving the tool to be an extension of the experimenter's arm (i.e., modified schema of the hand to incorporate the tool; Iriki, Tanaka, & Iwamura, 1996)

It is intriguing that we found greater ERD during observation of means-end actions for 9-month-olds but greater ERD during execution of grasp for 12-month-olds. The execution condition, beyond it requiring production of a grasp, differed from the observation condition in a potentially important way: it involved an action within the motor repertoire of both age groups, i.e., grasping of toys. To this end, it is reasonable that 12-month-olds would exhibit greater ERD during execution of grasps compared to 9-month-olds, because older infants would have more experience with grasping actions. As for the observation condition, the perceived means-end action may have induced greater attention in 9-month-olds compared to 12-month-olds. Unfortunately, we did not have a condition in which infants observe grasping actions, which would have allowed us to compare these two observation conditions and examine attention components of the ERDs.

For our second aim, we found that centro-parietal ERD during means-end action perception—but not frontal or occipital ERDs—predicted 12-month-olds' grasping skill but not for 9-month-olds. Our exploratory analysis also showed that this relation was present for centro-parietal ERD as a predictor but not as an outcome. Previous infant studies have investigated behavior as a predictor of ERDs (e.g., Cannon et al., 2015; Gerson, Bekkering, & Hunnius, 2014). However, ERD has been reported to predict motor performance (Babiloni et al., 2008). Future infant work should address this interesting methodological issue to elucidate the directional relation between behavior and neural activity.

Nonetheless, our results provide evidence for the relation between emerging grasping competence and sensorimotor activity during perception of means-end actions. Beginning at 5 to 6 months of age, infants display sophisticated reaching ability and become sensitive to the goal structure of reaching acts (Woodward, 1998). By 9 months of age, infants become quite proficient with grasping, but they are just beginning to acquire experience with means-end actions that include tool use. By 12 months of age, infants demonstrate the ability to perceptually detect the relational goals of means-end actions (Sommerville & Woodward, 2005a; 2005b). In fact, infants who previously engaged with a tool demonstrated the ability to detect the causal properties of the tool use action, suggesting that active motor experience is critical for the detection of goal structure during perception of actions (Sommerville, Hildebrand, & Crane, 2008). Our results suggest that the neural system for action-perception coupling may be establishing a link in 12-month-olds' own actions and actions they perceive to be similar.

One limitation of the study is that we did not include an assessment of infants' means-end abilities. However, we were interested in examining a motor behavior already in the motor repertoire of both age groups (grasping), and how this skill *extends* to the perception of

means-end actions. Future research can examine how infants' developmental trajectory of means-end actions (e.g., tool use abilities) is related to EEG activity during perception of these actions.

Lastly, Cannon et al. (2015) found a relation between grasp competence and mu ERD during perception of a grasp at 9-months of age. They used a broader definition of grasp latency, a composite comprised of latencies to begin reach, from start of reach to toy touch, and touch to grasp completion, as well as other components of infants' grasping competence (hand pre-shaping, unimanual/bimanual reaches). However, their findings appeared to be driven primarily by the grasp latency composite, which is why we focused on this measure of grasp competence. In contrast to Cannon and colleagues' (2015) findings, we did not find a relation at 9-months, but we did at 12-months. However, our findings were based on ERD during tool use perception and not during grasp perception, thus, it is difficult to directly compare our findings to those of Cannon et al. (2015).

The current study provides evidence for age-related differences in the emergence of action-perception coupling and its relation to infants' motor skills. Results support the notion that action—as measured by reach-grasp skill—and perception are linked to a broader class of actions by the end of the first year. Future studies should investigate the plasticity of the action-perception system and how infants' training in actions such as tool use can lead to changes in mu rhythm activity in concert with their emerging motor abilities.

Acknowledgments

This research was supported by NIH grant (NICHD P01 HD064653) to NAF. We thank Tanya Tavassolie and Kayla Finch for assistance in collecting and coding the data, and the many undergraduate research assistants at the UMD Child Development Lab. We are especially thankful for the families who participated in this work.

References

- Arnstein D, Cui F, Keysers C, Maurits NM, Gazzola V. μ -suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*. 2011; 31(40):14243–14249. [PubMed: 21976509]
- Avanzini P, Fabbri-Destro M, Dalla Volta R, Daprati E, Rizzolatti G, Cantalupo G. The dynamics of sensorimotor cortical oscillations during the observation of hand movements: an EEG study. *PLoS One*. 2012; 7(5):e37534. [PubMed: 22624046]
- Avikainen S, Forss N, Hari R. Modulated activation of the human SI and SII cortices during observation of hand actions. *NeuroImage*. 2002; 15(3):640–646. [PubMed: 11848707]
- Babiloni C, Del Percio C, Iacoboni M, Infarinato F, Lizio R, Marzano N, Eusebi F. Golf putt outcomes are predicted by sensorimotor cerebral EEG rhythms. *The Journal of Physiology*. 2008; 586(1):131–139. [PubMed: 17947315]
- Barrett TM, Davis EF, Needham A. Learning about tools in infancy. *Developmental Psychology*. 2007; 43(2):352–368. [PubMed: 17352544]
- Biro S, Verschoor S, Coenen L. Evidence for a unitary goal concept in 12-month-old infants. *Developmental Science*. 2011; 14(6):1255–1260. [PubMed: 22010886]
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P. Action observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral Cortex*. 2005; 15(8):1243–1249. [PubMed: 15616133]

- Cannon EN, Simpson EA, Fox NA, Vanderwert RE, Woodward AL, Ferrari PF. Relations between infants' emerging reach-grasp competence and event-related desynchronization in EEG. *Developmental Science*. 2015;1–13. [PubMed: 25546559]
- Cannon EN, Yoo KH, Vanderwert RE, Ferrari PF, Woodward AL, Fox NA. Action experience, more than observation, influences mu rhythm desynchronization. *PloS One*. 2014; 9(3):e92002. [PubMed: 24663967]
- Cuevas K, Cannon EN, Yoo K, Fox NA. The infant EEG mu rhythm: Methodological considerations and best practices. *Developmental Review*. 2014
- Del Percio C, Infarinato F, Iacoboni M, Marzano N, Soricelli A, Aschieri P, Babiloni C. Movement-related desynchronization of alpha rhythms is lower in athletes than non-athletes: a high-resolution EEG study. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*. 2010; 121(4):482–491. [PubMed: 20097129]
- Gerson SA, Bekkering H, Hunnius S. Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *Journal of Cognitive Neuroscience*. 2014
- Hadjidimitriou SK, Zacharakis AI, Doulgeris PC, Panoulas KJ, Hadjileontiadis LJ, Panas SM. Revealing Action Representation Processes in Audio Perception Using Fractal EEG Analysis. *IEEE Transactions on Biomedical Engineering*. 2011; 58(4):1120–1129. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/20388591>. [PubMed: 20388591]
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*. 1998; 95(25):15061–15065. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=24575&tool=pmcentrez&rendertype=abstract>. [PubMed: 9844015]
- Hayes AF. PROCESS: A versatile computational tool for observed variable mediation, moderation, and conditional process modeling [White paper]. 2012 Retrieved from <http://www.afhayes.com/public/process2012.pdf>.
- Hyvärinen A. Fast and Robust Fixed-Point Algorithms for Independent Component Analysis. *IEEE Transactions on Neural Networks*. 1999; 10(3):626–634. [PubMed: 18252563]
- Hyvärinen A, Hurri J. Blind separation of sources that have spatiotemporal variance dependencies. *Signal Processing*. 2004; 84(2):247–254.
- Iriki A, Tanaka M, Iwamura Y. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*. 1996; 7:2325–2330. 14, PMID: 8951846. [PubMed: 8951846]
- Lee T-W, Girolami M, Sejnowski T. Independent component analysis using an extended infomax algorithm for mixed subgaussian and supergaussian sources. *Neural Computation*. 1999; (11):417–441. [PubMed: 9950738]
- Marshall PJ, Bar-Haim Y, Fox NA. Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology*. 2002; 113(8):1199–1208. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/21840603>. [PubMed: 12139998]
- Marshall PJ, Bouquet CA, Shipley TF, Young T. Effects of brief imitative experience on EEG desynchronization during action observation. *Neuropsychologia*. 2009; 47(12):2100–2106. [PubMed: 19467360]
- Marshall PJ, Meltzoff AN. Neural Mirroring Systems: Exploring the EEG Mu Rhythm in Human Infancy. *Developmental Cognitive Neuroscience*. 2011; 1(2):110–123. [PubMed: 21528008]
- Marshall PJ, Saby JN, Meltzoff AN. Infant Brain Responses to Object Weight: Exploring Goal-Directed Actions and Self-Experience. *Infancy*. 2013;1–19. [PubMed: 25632273]
- Marshall PJ, Young T, Meltzoff AN. Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Developmental Science*. 2010; 14(3):474–480. [PubMed: 21477187]
- Muthukumaraswamy SD, Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*. 2004; 41(1):152–156. [PubMed: 14693010]
- Neuper C, Pfurtscheller G. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *International Journal of Psychophysiology*. 2001; 43(1):41–58. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11742684>. [PubMed: 11742684]

- Orgs G, Dombrowski J-H, Heil M, Jansen-Osmann P. Expertise in dance modulates alpha/beta event-related desynchronization during action observation. *The European Journal of Neuroscience*. 2008; 27(12):3380–3384. [PubMed: 18598273]
- Paulus M, Hunnius S, van Elk M, Bekkering H. How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: electrophysiological evidence for action-effect binding in infancy. *Developmental Cognitive Neuroscience*. 2012; 2(1):90–96. [PubMed: 22682730]
- Pineda J. The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. *Brain Research. Brain Research Reviews*. 2005; 50(1):57–68. [PubMed: 15925412]
- Provasi J, Dubon CD, Bloch H. Do 9- and 12-month-olds learn means-ends relation by observing? *Infant Behavior and Development*. 2001; 24:195–213.
- Ritter P, Moosmann M, Villringer A. Rolandic alpha and beta EEG rhythms' strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Human Brain Mapping*. 2009; 30(4):1168–1187. [PubMed: 18465747]
- Ruysschaert L, Warreyn P, Wiersema JR, Metin B, Roeyers H. Neural mirroring during the observation of live and video actions in infants. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*. 2013; 124(9):1765–1770. [PubMed: 23673063]
- Saby J, Marshall P, Meltzoff A. Neural correlates of being imitated: an EEG study in preverbal infants. *Social Neuroscience*. 2012; 7(6):650–661. [PubMed: 22646701]
- Sommerville JA, Woodward AL. Pulling out the intentional structure of action: the relation between action processing and action production in infancy. *Cognition*. 2005a; 95(1):1–30. [PubMed: 15629472]
- Sommerville JA, Woodward AL. Infants' Sensitivity to the Causal Features of Means-End Support Sequences in Action and Perception. *Infancy*. 2005b; 8(2):119–145.
- Sommerville J, Hildebrand E, Crane C. Experience matters: The impact of doing versus watching on infants' subsequent perception of tool use events. *Developmental Psychology*. 2008; 44(5):1249–1256. [PubMed: 18793059]
- Southgate V, Begus K. Motor activation during the prediction of nonexecutable actions in infants. *Psychological Science*. 2013; 24(6):828–835. [PubMed: 23678509]
- Southgate V, Johnson MH, El Karoui I, Csibra G. Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*. 2010; 21(3):355–359. [PubMed: 20424068]
- Southgate V, Johnson MH, Osborne T, Csibra G. Predictive motor activation during action observation in human infants. *Biology Letters*. 2009; 5(6):769–772. [PubMed: 19675001]
- Stapel JC, Hunnius S, van Elk M, Bekkering H. Motor activation during observation of unusual versus ordinary actions in infancy. *Social Neuroscience*. 2010; 5(5–6):451–460. [PubMed: 20602285]
- Thelen E. Motor Development: A New Synthesis. *American Psychologist*. 1995; 50(2):79–95. [PubMed: 7879990]
- Thorpe SG, Cannon EN, Fox NA. Spectral and source structural development of mu and alpha rhythms from infancy through adulthood. *Clinical Neurophysiology*. 2015
- Van Elk M, van Schie HT, Hunnius S, Vesper C, Bekkering H. You'll never crawl alone: neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage*. 2008; 43(4):808–814. [PubMed: 18760368]
- Virji-Babul N, Rose A, Moiseeva N, Makan N. Neural correlates of action understanding in infants: influence of motor experience. *Brain and Behavior*. 2012; 2(3):237–242. [PubMed: 22741097]
- Warreyn P, Ruysschaert L, Wiersema JR, Handl A, Pattyn G, Roeyers H. Infants' mu suppression during the observation of real and mimicked goal-directed actions. *Developmental Science*. 2013; 16(2):173–185. [PubMed: 23432828]
- Woodward AL. Infants selectively encode the goal object of an actor's reach. *Cognition*. 1998; 69:1–34. [PubMed: 9871370]

Figure 1.
Example of an observation trial in which an experimenter is grasping a toy using a claw-like tool (panel A) and an execution trial in which an infant grasps a toy (panel B).

Figure 2. Means and standard errors of ERDs for each region (frontal, centro-parietal, and occipital), condition (observation and execution), and age group. Panel A shows ERDs during observation of tool use and panel B shows ERDs during execution of toy grasp.

Figure 3.

Regression analysis results indicate that centro-parietal ERD during observation predicts latency to initial grasp for 12-month-olds. Shorter latencies (i.e., greater competence) are related to greater centro-parietal ERD during observation of grasp using a claw-like tool.

Table 1

Summary of moderation analysis for centro-parietal ERD during observation predicting infants' latencies to grasp toys moderated by age group.

		Coeff.	SE	t	p
Intercept	i_1	0.86	0.32	2.72	0.00
Centro-parietal ERD (X)	b_2	-0.35	0.25	-1.42	0.16
Age group (M)	b_2	0.18	0.18	1.01	0.32
Centro-parietal ERD $\times$ Age group (XM)	b_3	0.39	0.15	2.55	0.01*
$R^2 = 0.25, MSE = 0.36$					
$F(3,56) = 6.26, p < 0.01$					

* $p < 0.05$

Approximate location of Table 1 is in the section *Latency to initial grasp and ERD during observation*.