



Action experience in infancy predicts visual-motor functional connectivity during action anticipation

Marc Colomer¹ | Haerin Chung¹ | Marlene Meyer^{1,2} | Ranjan Debnath^{3,4} | Santiago Morales^{3,5} | Nathan A. Fox³ | Amanda Woodward¹

¹University of Chicago, Chicago, USA

²Donders Institute, Radboud University, Nijmegen, The Netherlands

³University of Maryland, College Park, USA

⁴Leibniz Institute for Neurobiology, Magdeburg, Germany

⁵University of Southern California, Los Angeles, USA

Correspondence

Marc Colomer, 5848 S University Ave, Chicago, IL 60637, USA.

Email: marc.colomer.ca@gmail.com

Abstract

Despite substantial evidence indicating a close link between action production and perception in early child development, less is known about how action experience shapes the processes of perceiving and anticipating others' actions. Here, we developed a novel approach to capture functional connectivity specific to certain brain areas to investigate how action experience changes the networks involved in action perception and anticipation. Nine- and 12-month-old infants observed familiar (grasping) and novel (tool-use) actions while their brain activity was measured using EEG. Infants' motor competence of both actions was assessed. A link between action experience and connectivity patterns was found, particularly during the anticipation period. During action anticipation, greater motor competence in grasping predicted greater functional connectivity between visual (occipital alpha) and motor (central alpha) regions relative to global levels of whole-brain EEG connectivity. Furthermore, visual and motor regions tended to be more coordinated in response to familiar versus novel actions and for older than younger participants. Critically, these effects were not found in the control networks (frontal-central; frontal-occipital; parietal-central; parietal-occipital), suggesting a unique role of visual-motor networks on the link between motor skills and action encoding.

KEYWORDS

alpha EEG oscillations, functional connectivity, mirroring, motor development, visuomotor connectivity, whole-brain connectivity

Highlights

- Infants' motor development predicted functional connectivity patterns during action anticipation.
- Faster graspers, and older infants, showed a stronger ratio of visual-motor neural coherence.
- Overall whole-brain connectivity was modulated by age and familiarity with the actions.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Developmental Science* published by John Wiley & Sons Ltd.



- Measuring inter-site relative to whole-brain connectivity can capture specific brain-behavior links.
- Measures of phase-based connectivity over time are sensitive to anticipatory action.

1 | INTRODUCTION

The human brain undergoes significant changes during the first months of life that have long-lasting cognitive and behavioral consequences. The development of socio-cognitive capacities goes along with changes in the organization of functional neural networks, typically defined as groups of functionally interconnected brain regions that enable the integration of information (Friston, 2011). However, to date most of the research on social-cognitive development in general and early action understanding more specifically has focused on identifying isolated neural markers and brain region-specific patterns of activation (Filippi et al., 2016; Marshall et al., 2011; Meyer et al., 2019; Southgate & Vernetti, 2014). In fact, we are only at the very beginning of understanding how functional networks emerge and develop in the human brain and what factors induce changes in these networks (Gao et al., 2017). In the present study, we developed an innovative methodological approach to investigate the links between infants' action experience and the emergence of functional neural networks involved in action prediction and perception.

1.1 | Action experience and sensorimotor activity

At the core of multiple theoretical approaches on action understanding is the idea that one's own action experience impacts the encoding of others' actions (Gerson & Woodward, 2014; Hunnius & Bekkering, 2014; Meltzoff, 2007; Paulus, 2012). A substantial body of behavioral and neuroscientific work provides evidence in favor of this action-perception link from infancy (Bakker et al., 2016; Cannon et al., 2014, 2016; Gerson et al., 2015; Gerson & Woodward, 2014; Lloyd-Fox et al., 2015; Melzer et al., 2012; Sommerville et al., 2005; van Elk et al., 2008). However, in developmental cognitive neuroscience the investigation of this link has been typically limited to the measurement of neural markers of isolated brain regions associated with motor dynamics (Bakker et al., 2016; Cannon et al., 2014; Gerson et al., 2015; van Elk et al., 2008), rather capturing the relations between brain regions. A popular technique to measure brain activity related to motor behavior is mu event-related desynchronization (mu ERD), an EEG measure of power reduction relative to a resting in the alpha frequency (8–12 Hz in adults; 6–9 Hz in infants) over central brain areas that occurs both when performing actions and when encoding others' actions (Fox et al., 2016; Rayson et al., 2016). Mu ERD has been found when infants (and adults) observe others' actions as well as in anticipation of an action, and thus it is used as an index of both action perception and anticipation (Monroy et al., 2019; Southgate et al., 2010; Southgate & Vernetti,

2014). Particularly, studies tend to associate mu ERD to the recruitment of the mirror system (Fox et al., 2016; but see Hobson & Bishop, 2017), which is hypothesized to be critical for action prediction and understanding (Kilner et al., 2004; Muthukumaraswamy et al., 2004; Woodward & Gerson, 2014).

However, several neuroscientific findings and theoretical proposals point to a broader neural network underlying the encoding of others' actions. Particularly, research on adults and primates indicates that the action observation network involves several brain areas, such as parietal and premotor regions, along with occipitotemporal networks that are responsible for encoding and integrating visual and auditory information (Buccino et al., 2001; Caspers et al., 2010; Nelissen et al., 2011; Urgen & Orban, 2021). In a similar vein, theoretical models of action representation highlight the functional relations between sensorimotor regions and visual/auditory attentional processes (Hommel et al., 2001; Kilner et al., 2007; Paulus, 2012; Pineda, 2005). For example, the ideomotor theory proposes that motor mirroring allows a perceiver to associate the representation of an observed action with its typical effect and, in turn, it shapes subsequent perception by informing the visual system about relevant information to attend (Paulus, 2014).

Visual attentional processes, like motor processes, can be measured with EEG via alpha oscillations. Alpha power over occipital areas typically decreases in the presence or expectation of visual input (Thut et al., 2006; Toscani et al., 2010). However, analyzing alpha activity separately for visual and motor regions does not provide information about how visual and motor brain activity are potentially related during action encoding. In fact, the co-occurrence of motor and visual processes during action observation makes it difficult to ensure that activity at central sites arises from motor activity alone, rather than from attentional shifts (Hobson & Bishop, 2017). While mu ERD is specific to central areas during action execution, it is typically more broadly distributed over the scalp during action observation (Fox et al., 2016). These issues have raised important concerns about the validity of mu rhythm as a proxy for activity solely reflecting the mirror system (Hobson & Bishop, 2017). Thus, innovative approaches beyond the study of isolated neural markers are fundamental to uncover network dynamics in the developing brain.

1.2 | Functional connectivity and action processing

Substantial evidence indicates that when two brain regions work together, exchanging information, the synchronization of their oscillatory activity increases (Cohen, 2014; Fell & Axmacher, 2011;



Fries, 2005; Palva & Palva, 2011; Pineda, 2005). A well-established method to measure this synchronization is the analysis of phase-based connectivity between signals, which measures how consistent the phase angle difference is between the signals over time or over trials. Phase-based connectivity can be inferred using several techniques including EEG, which is an efficient and widely used technique to study developmental changes in brain-behavior relations. However, functional networks in the infant brain are relatively unexplored and more tools are needed to address challenges that are common in developmental neuroscience, such as the limited amount of data collected per session, or the fast changes that occur in the brain due to maturation.

In the field of infant action processing, three studies have explored functional connectivity networks using phase-connectivity methods (Chung et al., 2022; Debnath et al., 2019; Meyer et al., 2022). These studies used the approach developed by Debnath et al., 2019, which investigated whether mu rhythm dynamics (central electrodes) are independent from alpha dynamics measured over occipital sites, given the overlap in frequency of the two signals, and the potential confound of volume conduction. The authors argued that if mu oscillations are contaminated by alpha, stronger functional connectivity should be expected for electrodes that are more proximal in space (Cohen, 2014), such as frontal-central, parietal-central, and parietal-occipital electrode pairs (control networks), as compared to occipital-central pairs. The authors found greater connectivity between occipital and central areas relative to the control networks while 9-month-old observed an adult grasping a toy, suggesting that mu rhythm is independent from alpha, and that visual (occipital) and motor (central) processes work in concert during action processing (Debnath et al., 2019). In a similar line, Chung et al. (2022) tested 9- and 12-month-old infants observing others' actions and, as Debnath et al., 2019, found greater functional connectivity in visual-motor versus control networks. Interestingly, this pattern was only found when infants observed actions that were motorically familiar, suggesting a possible relation between action experience and visual-motor coupling. Finally, Meyer et al. (2022) found an increase in occipital-central functional connectivity as 9-month-olds observed an agent grasping a toy. Notably, this increase was only found when the observed actions and infants' own actions occurred in turns. Despite occipital-central connectivity did not differ significantly from connectivity in the control networks, as in the other two studies, the findings from Meyer et al. (2022) provide further evidence that occipital-central functional connections change as infants process others' actions.

These studies suggest that visual-motor functional connections play an important role in action perception. However, they provide a limited lens to understand how specific changes in functional connectivity relate to the development of motor skills. This is because these studies did not control for global connectivity patterns, and thus they cannot distinguish whether individual differences in functional connectivity are specific to a network or, instead, they are influenced by individual differences in the global properties of the brain, which may be influenced by factors such as maturation. Here, we developed a new methodological approach that integrates specific and global measures of connectivity to investigate whether the specialization of visual-

motor functional connections in response to others' actions can be predicted by infants' motor skills.

1.3 | Present study

As infants collect experiences in the world, their brain grows, changes, and specializes in ways that allow them to process information more efficiently. A critical question for developmental research is how specific experiences relate to specific changes in the brain. However, connectivity estimates in a specific functional network may be influenced both by changes in the specialization of that network, as well as changes in the global properties of the developing brain. In fact, previous studies have found a positive correlation between the strength of overall functional connectivity at the whole-brain network and age, particularly in the alpha band (Boersma et al., 2011; Miskovic et al., 2015; Xie et al., 2019), which could be related to maturational increases in white matter density (Casey et al., 2005; Gogtay et al., 2004; Paus et al., 2001; Yu et al., 2020). Yet, a method that estimates functional connectivity between specific inter-site pairs, controlling for changes at the whole-brain level, has been missing. To address this gap and to better capture changes in specialized brain networks involved in action processing, we developed a novel methodological approach that integrated estimates of inter-site functional connectivity and measures of whole-brain connectivity. Specifically, we quantified the ratio of functional connectivity between two areas of interest relative to all the other possible connections across the scalp, thus controlling for global changes in whole-brain connectivity.

In addition, we used an alternative method as compared to previous studies (Chung et al., 2022; Debnath et al., 2019; Meyer et al., 2022) that allows to estimate functional connectivity in anticipatory periods, and that better accounts for the limited number of trials frequently inherent in infant studies. Instead of calculating functional connectivity over trials, we estimated how consistent the phase difference between two signals is over time, which is insensitive to phase angle differences being different trial-to-trial and thus captures both phase-locked and non-phase-locked connectivity patterns (Cohen, 2014). Substantial evidence indicates that the ability to predict others' actions emerges in the first year of life (Cannon & Woodward, 2012; Hunnius & Bekkering, 2010; Paulus et al., 2011; Rosander & von Hofsten, 2011), but little is known about how motor and visual processes are functionally related during anticipatory processing. Since action anticipation occurs before the onset of a time-locked event, activity in the anticipatory period is less likely to be phase-locked, and thus estimating connectivity over time is more optimal to detect such anticipatory neural processes.

Furthermore, calculating connectivity over time rather than over trials is more optimal when the number of trials is limited. While a common criterion in studies on the mu rhythm is to have a minimum of three trials per condition, estimates of connectivity over trials do not become stable unless the experimental design includes at least 40 trials per condition (Cohen, 2014; Nunez & Srinivasan, 2006). Instead, connectivity over time depends on the number of time points of the



window of analysis, and thus it provides a more stable measure when the number of trials is limited. For example, for a participant with three trials of useful data in a test window of 500 ms (sample rate = 500 Hz), connectivity-time will use 250 values to estimate connectivity in each trial, whereas connectivity-trial will estimate connectivity in each of the 250 points using only three values.

In the present study, we re-analyzed the data from (Chung et al., 2022) using the methodological approach described above with the aim of uncovering the relation between action experience and the activation of specialized functional networks associated with action anticipation and perception. Nine- and twelve-month-old infants watched videos of an experimenter performing either a familiar grasping action (familiar condition) or a novel tool-use action in which she pulled a cane to bring a toy closer (novel condition). In addition, infants' motor competence in performing the observed actions was measured. We investigated whether experience, measured as (1) motoric familiarity of the observed action, (2) infants' age, and (3) infants' motor competence—latency in grasping and latency in using a novel tool—was related to the global level of functional connectivity of the whole-brain network, and to the ratio of connectivity between visual (occipital alpha) and motor (central alpha) processes relative to global connectivity as infants anticipated and observed others' actions.

2 | METHODS

2.1 | Open research practices

The scripts of connectivity analysis and the output data with connectivity estimates can be obtained here: https://github.com/marccolomer/LAEEG_WB

The EEG data preprocessed and transformed using complex Morlet wavelets can be sent upon request. The derived EEG data in BIDS format and the scripts to process the data can be obtained here: <https://osf.io/f9da5/>

2.2 | Participants

Participants were 17 9-month-old ($M = 9$ months 21 days, $SD = 10$; range: 9;0–10;15; 13 males) and 19 12-month-old ($M = 12$ months 21 days, $SD = 17.8$; range: 11;15–13;15; 11 males) typically developing full-term infants. Participants were recruited in Chicago and represented a relatively diverse racial background (73% Caucasian, 3% Hispanic, 18% African-American, and 6% mixed-racial) and were from highly educated backgrounds (maternal education: 91% with a bachelor degree or higher education). A power analysis with $f^2 = 0.33$ (Yoo et al., 2016) indicated that 36 infants should yield > 90% power at an alpha rate of 0.05 to detect an effect of motor skills (grasp latency) on neural activity. An additional 13 infants were tested but excluded from the analysis due to being distressed shortly after application of

the EEG electrode net (2), unusable EEG data prior to data analysis (6), and for not having at least three artifact-free EEG trials per condition after all EEG processing steps (5). This study was approved by the by the campus Institutional Review Board at the University of Chicago.

2.3 | Procedure

After the caregiver provided written consent, infants were fitted with a 128-sensor HydroCel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR). Impedances were kept below 100 k Ω where possible. The EEG was digitized at 1000 Hz (Net Station software, EGI, v4.5.7) and electrode Cz was used as an online reference. Infants seated on a high-chair or caregiver's lap at ~70 cm from the computer monitor. Areas surrounding the computer monitor were covered with black panels to create a homogeneous environment and to hide the experimenter monitoring the infant during the study. Each testing session was video recorded with two cameras, one focusing on the infant and the other on the stimuli presented at the monitor. Caregivers were asked to be passive observers during the task and to not exhibit any behavior unless when the infants were in distress. The experiment was structured in two blocks presented in the following order: an action observation block and an action execution block (See Figure 1a). At the end of the testing session, parents were debriefed about the goal of the study and families received a small gift (toy or t-shirt) and 20 US dollars as compensation of participating in the study.

2.3.1 | Action observation

During the action observation block, infants faced a computer screen on a table at approximately 70 cm distance on which stimuli videos were presented via Eprime 2.0 (Schneider et al., 2012). Participants saw two types of test trials: a grasping action (*familiar condition*) and a tool-use action (*novel condition*). When videos were presented via Eprime, triggers indicating the onset and end of videos were sent to the EEG recording software. In the test trials, the experimenter appeared with a toy in the familiar condition and with a toy and a cane in the novel condition. In both conditions, the experimenter faced the center of the screen for 500 ms and then she said “Hey Baby!” or “Hi there!” to get infants' attention. In the familiar condition, the experimenter looked down at the toy, grasped it and brought the toy closer to herself. In the novel condition, the experimenter looked down at the toy and then pulled the cane to bring the toy closer to herself. The test trials had a length of 4000–4500 ms and were presented in a pseudorandomized order, with a maximum of 20 trials per condition and a maximum of three trials of the same condition in a row. Ten unique toys were used for the two types of action conditions such that all toys appeared twice for each trial type. After 40 trials or once the infants lost interest, the observation block ended and infants then performed an action execution block.

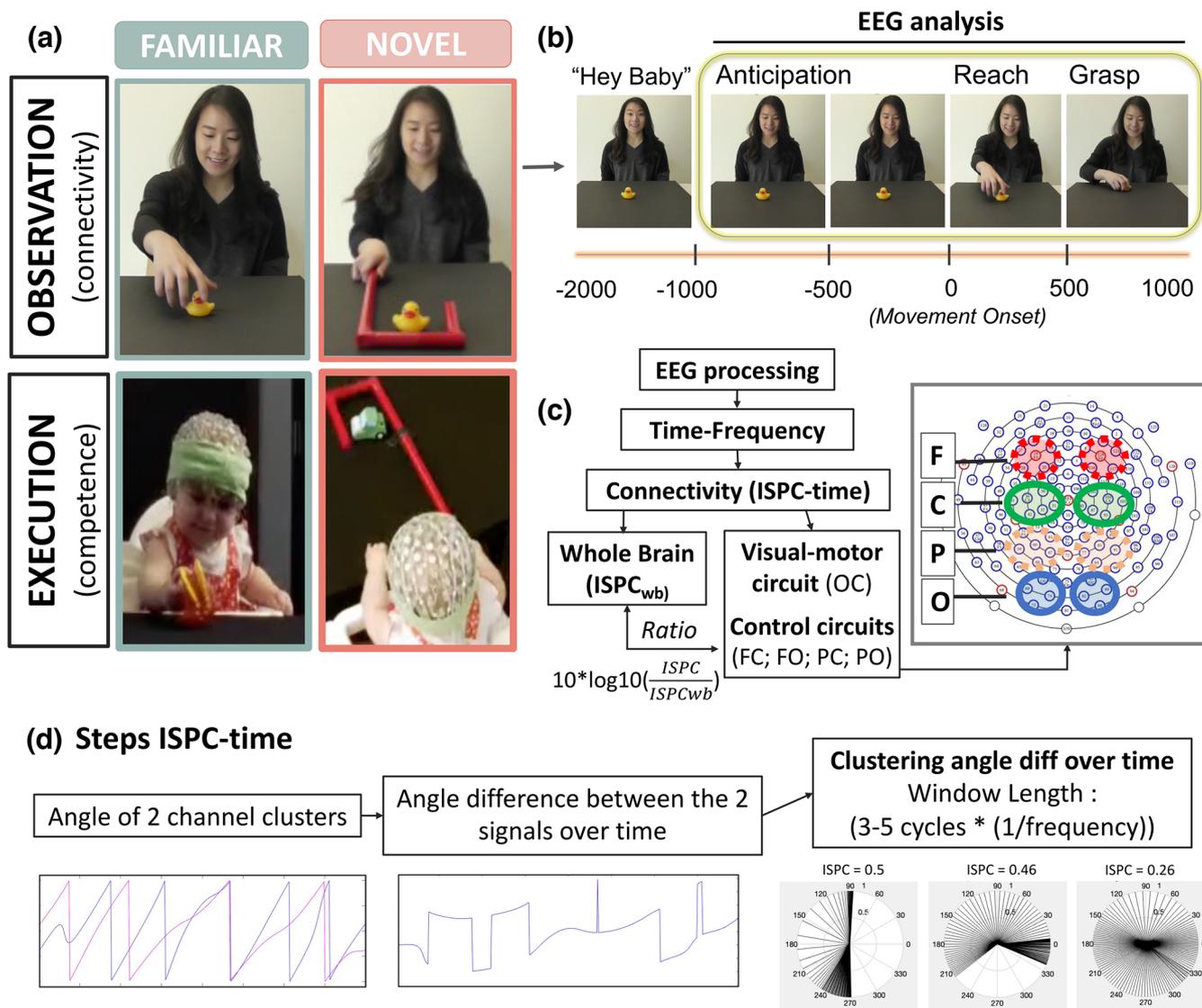


FIGURE 1 Experimental paradigm. (a) Representation of the two types of actions (novel vs. familiar) and the two blocks (observation and execution) used in the study. (b) Example of trial timing (familiar action condition) in which 0 represents the movement onset. Connectivity estimates were calculated from -1000 ms to 1000 ms and averaged in windows of 500 ms. (c) Steps to calculate connectivity values in each network of interest. Scalp plot on the right depicts the ROIs of interest, including frontal, central, parietal, and occipital areas. (d) Steps required to calculate connectivity estimates over time together with the representation of two example signals. Graphics were plotted using MATLAB and clustering was calculated as $\text{abs}(\text{mean}(\exp(1i * (\text{phase_difference}))))$

2.3.2 | Action execution

During the action execution block, infants sat in front of a table, the experimenter who appeared in the videos of the action observation block (E1) was positioned behind the curtains and a second experimenter (E2) was positioned behind infants, out of their visual scene. The execution phase began with two warm-up trials to ensure that the infants were attending. In each warm-up trial, E1 opened the curtains, said "Hi, baby. Are we ready?" and closed the curtains again. After the warm-up, infants completed up to five trials in each condition. The order was fixed, such that grasp execution trials always preceded the cane execution trials to ensure maximum data of grasp latency, which

is a more common measure of motor competence in the literature (Cannon et al., 2016).

In the grasp execution trials, E1 opened the curtains, saying "Hey baby, look!" while she showed a toy to the infant and then she placed the toy within infant's reach. The grasp execution trial ended when the infant grasped the toy. If infants did not attempt to grasp the toy within 10 s, E1 pointed or tapped the toy to get infants' attention. After three repetitions of the prompt, or when infants reached for and grasped the toy, E1 retracted the toy, provided positive encouragement (i.e., "Good job" or "Alright") and closed the curtains. Infants completed up to five trials ($M_{9mo} = 4.8$; range = 3–5; $M_{12mo} = 4.68$; range = 1–5). Cane execution trials were the same, but the toy was placed beyond infants'



reach, and a cane (length of cane: 48 cm, width of crook: 13.5 cm) was placed around the toy. The cane-use trial ended after infants either successfully retrieved the toy by pulling the cane or 60 s elapsed. Infants completed up to five trials ($M_{9mo} = 4.14$; range = 1–5; $M_{12mo} = 4$; range = 1–5).

2.4 | Data processing and analysis

2.4.1 | Video coding

During the observation block, video data were coded to mark periods of time in which data should be excluded from analysis due to participants' behavior. Data were coded via an open-source software named Datavyu (Datavyu Team, 2014). Trials that included parental interference (e.g., parents talking to infants or bouncing them), crying, infant not-looking at the screen or infants' own grasping actions (e.g., grasping the caregiver's hand, or producing grasping movements in the air) were excluded from further analysis.

2.4.2 | Measures of motor competence

Grasp latency

Grasp latency was measured as an index of motor competence (Cannon et al., 2016). In each trial, coders marked when infants first touched the object and when they completed the grasp. First touch was considered the first video-frame in which infants touched the toy. Grasp completion was considered the onset of picking up the toy or the first frame in which infants wrapped their fingers around the toy completely, in the case that toys were not picked up. Only trials with a grasp completion were included in the analysis to calculate an averaged grasp latency measure. Two or more valid trials were required for participants to be included in the analysis. An independent coder coded 73% of the data. The inter-rater agreement within three frames (30 frames/s) was achieved (ICC = 0.78) with 95% confidence interval from 0.57 to 0.9 for grasp latency measures.

Cane latency

Cane latency was calculated from the onset of the cane pulling until the first video-frame in which the toy appeared to be within infants' reach. Only trials in which infants provided a clear pull without breaks were included in the analysis. Two or more valid trials were required for participants to be included in the analysis. An independent coder coded 70% of the data. The inter-rater agreement within three frames was achieved (ICC = 0.95) with 95% confidence interval from 0.86 to 0.98 for cane-pulling latency measure.

2.4.3 | EEG data processing

The procedure to process EEG data followed the Maryland Analysis of Developmental EEG (MADE) pipeline developed by researchers at University of Maryland (Debnath et al., 2020). Recordings were exported

from Net Station software to a Matlab-compatible format (Mathworks, Natick, MA, USA) and processed using EEGLAB (v14.0.0) toolbox (Delorme & Makeig, 2004). Video-coded markers were imported onto the EEG dataset and data were downsampled to 500 Hz. The following processing steps were identical to Debnath et al. (2019), Chung et al. (2022), and Meyer et al. (2022). See Supplementary Information (SI) for the details. To be included in further analysis, participants had to provide a minimum of three artifact-free epochs per condition. Nine-month-old infants provided a mean of 8.3 epochs in the familiar action condition (range 3–17) and 7.5 in the novel action condition (range 3–19). Twelve-month-old infants provided a mean of 10.4 epochs in the familiar action condition (range 4–19) and nine in the novel action condition (range 4–19). Artifact-free epochs were then converted into current source density (CSD) waveform using the CSD toolbox (Kayser & Tenke, 2006) to minimize spread of brain activity due to volume conduction and improve the spatial resolution of the EEG signal.

2.4.4 | Time-frequency analysis

Complex Morlet wavelets were used to extract estimates of the time-varying frequency band-specific phase from the EEG signal in the frequency range from 4 Hz to 20 Hz (in 30 linearly spaced steps). The wavelet cycles ranged from three cycles in the lowest frequency to five cycles in the highest frequency. Data convolution resulted in a frequency \times time \times trial \times channel matrix with values on the complex plane. Prior to performing connectivity analysis, the phase of the complex number was calculated using the function *angle* from MATLAB. To eliminate distortion created by the transform, the first and last 500 ms of each epoch were removed, resulting in trials containing segments from 1500 ms before to 1500 ms after E1's movement onset.

2.4.5 | Connectivity analysis

Following methodological recommendations (Cohen, 2015), phase-based connectivity was assessed using Inter Site Phase Clustering (ISPC). This approach is maximally sensitive to detecting connectivity as compared to other common methods such as weighted Phase-Lag Index (wPLI) and it is recommended for hypothesis-driven analysis as targeted here (Cohen, 2014; Yordanova et al., 2017). As compared to wPLI, ISPC is robust to time dynamics, time lag and frequency non-stationarities, as expected for event-related EEG responses. In addition, it is sensitive to detecting phase-connectivity across conditions regardless of condition differences in the preferred phase-lag-based index. However, ISPC is susceptible to volume conduction, which is a potential confound that can lead to spurious connectivity results (Bastos & Schoffelen, 2016). To address this, we followed several steps to test against the potential confound of volume conduction (see below in the "Control analysis of volume conduction" section). Note that this approach was optimal given that we performed a small number of hypothesis-driven analyses. In studies that require a large amount of data exploration, a method that is insensitive to volume



conduction (e.g., wPLI) may be more useful, even at the risk of missing some potentially true connectivity patterns (Cohen, 2014).

ISPC over-time (ISPC-time) calculates how consistent phase angle differences are between two electrodes (or cluster of electrodes) by calculating the average of phase angle differences over time (See Figure 1d). ISPC-time is calculated as follows:

$$\text{ISPC} = \left| n^{-1} \sum_{t=1}^n e^{i(\phi_{xt} - \phi_{yt})} \right| \quad (1)$$

where n is the number of time samples for each trial and frequency bin, ϕ_{xt} and ϕ_{yt} are the phase angles of electrodes x and y at frequency f and time t , and e^i is from Euler's formula and provides complex polar representation of phase angle difference. ISPC values are scaled between 0 and 1, where 1 means identical phase angle differences at each time point and 0 indicates no clustering at all.

This formula provides a value of connectivity for each trial and frequency on a given time period of analysis. To calculate time-varying connectivity, we defined sliding-time windows from 1000 ms before to 1000 ms after the action onset that increased in steps of 10 ms. The length of the window of analysis was N cycles of the corresponding frequency. Time windows are recommended to have a length that includes at least three cycles of the frequency of analysis (Cohen, 2014). As in the time-frequency analysis, N ranged from three cycles (4 Hz) to five cycles (20 Hz).

Following previous studies, ISPC-time data were filtered in the alpha-band range, which in infants at this age typically includes frequencies from 6 Hz to 9 Hz¹ (Debnath et al., 2019; Marshall & Meltzoff, 2011; Meyer et al., 2022). Connectivity estimates were then averaged across frequency and trials. Thus, connectivity analysis between two given electrodes or clusters resulted in a time-varying connectivity vector from -1000 to 1000 ms increasing in steps of 10 ms for each participant and condition. Then, following (Chung et al., 2022), connectivity estimates were averaged in windows of 500 ms to compare connectivity patterns across different periods of action processing (See Figure 1b). Connectivity analyses were performed to obtain two types of results: whole brain connectivity, which measured global levels of connectivity between all electrodes, and specific connectivity between pairs of electrode clusters that were selected based on previous studies (Chung et al., 2022; Debnath et al., 2019).

Whole brain connectivity (ISPC_{WB})

We calculated ISPC-time between each pair of electrodes, which resulted in a 104×104 adjacency matrix per participant, condition, trial, frequency step and time step. Adjacency matrices were then averaged across frequencies and trials and organized in 15 clusters of electrodes to obtain a more robust estimate of connectivity between regions (Xie et al., 2019). The clusters included electrodes over the frontal pole, central, left and right frontal electrodes, left and right temporal electrodes, Central Z, left and right central electrodes, central, left and right parietal electrodes, and central, left and right occipital electrodes (See SI for detail information about the selected electrodes). Finally, a value of overall whole brain ISPC (ISPC_{WB}) was calculated per time step, participant, and condition as one standard deviation over the

median connectivity of all cluster pairs. Using one standard deviation above the median is common to threshold connectivity matrices for graph theory-based analyses (Cohen, 2014; Cohen & van Gaal, 2013; Philips et al., 2017).

Pairs of clusters

Connectivity between five clusters of electrodes was calculated (see SI for a description of the selected channels): occipital-central (ISPC_{OC}), parietal-central (ISPC_{PC}), parietal-occipital (ISPC_{PO}), frontal-central (ISPC_{FC}), and frontal-occipital (ISPC_{FO}). Before calculating ISPC, values on the complex plane were averaged across clusters of electrodes. ISPC-time was calculated between each pair of clusters and averaged across trials, hemisphere (left and right) and across the alpha frequency range. This resulted in a time-varying ISPC vector per participant and condition. In order to calculate how strong the level of connectivity was between specific pairs relative to the global connectivity of the whole-brain network, we normalized each vector relative to ISPC_{WB} of the corresponding participant, time and condition. The outcome of this normalization was the ratio of connectivity of the corresponding cluster pair relative to ISPC_{WB}, calculated as $10 * \log_{10} \left(\frac{\text{pair-ISPC}}{\text{wb-ISPC}} \right)$. A value of 0 indicated identical level of connectivity between the cluster pair and ISPC_{WB}. Values > 0 indicated more connectivity in the cluster pair, whereas values < 0 indicated less connectivity as compared to ISPC_{WB}.

Control analysis of volume conduction

To address the potential confound of volume conduction, we performed three strategies. First, we used a Laplacian spatial filter that significantly attenuates volume conduction artifacts before performing data analysis (Cohen, 2015). Second, we included four control networks (frontal-central, frontal-occipital, parietal-central, and parietal-occipital) with areas that were closer to each other than the areas of the network of interest (occipital-central). Since electrodes with less inter-electrode distance will in general have greater spurious connectivity due to volume conduction, we would expect that any effect that is an artifact of volume conduction would be similar or stronger at the control networks as compared to the motor-visual network (Debnath et al., 2019). However, any effect that is stronger at the visual-motor network relative to the control networks is likely to indicate true connectivity patterns. Third, statistical analyses were computed for connectivity patterns as well as for power patterns to help dissociate connectivity from volume conduction. If significant effects between conditions are found for connectivity patterns, but there is no analogous effect for power, then the connectivity results are unlikely to be due to volume-conducted activity (Cohen, 2014). The analysis with power did not show the same pattern of results as the connectivity analyses (see SI), further suggesting that results with functional connectivity are not due to volume-conducted activity.

2.5 | Analysis plan

Analyses were conducted to investigate the relation between action experience and connectivity patterns. First, we investigated how age

and motoric familiarity influenced the level of global connectivity across time. Then, we investigated the effect of the same variables on the level of specific visual-motor ISPC, and the level of ISPC in the four control networks. Before the main analysis, a Shapiro Test was performed to test for normality in each cell of interest. In case of a skewed distribution, data were log transformed to make the data conform more closely to a normal distribution. Data were log-transformed only for whole-brain analysis. For each analysis, we constructed an ANOVA using the ezANOVA package (Lawrence, 2016) with condition (novel vs. familiar) and time window (−1000: −500 vs. −500:0 vs. 0:500 vs. 500:1000) as within-subject factors, age (9 m vs. 12 m) as between-subject factor, and either global whole-brain ISPC or ISPC in each network of interest (visual-motor and control) as dependent variables. Finally, for any time window in which action experience significantly modulated connectivity patterns, we investigated the relation between motor competence and connectivity levels on the visual-motor network. To address this, a mixed-effect model (LMM) was constructed using the lme4 package (Bates et al., 2015). The LMM included condition, age, grasp latency and all the possible interactions as fixed effects, with subject-specific intercepts as random effects. A similar LMM was also constructed with cane latency rather than grasp latency to investigate whether competence performing novel rather than familiar actions related to connectivity patterns. Resulting p-values for fixed effects and their interactions were obtained using Likelihood Ratio tests with the ANOVA function from R (R Core Team, 2014), and significant interactions were followed up on by planned pairwise comparisons. For any significant effects or interactions in the visual-motor network, a LMM model was constructed including ISPC in each control network as a dependent variable, and the effects of interest as predictors.

3 | RESULTS

3.1 | Global patterns of connectivity (Whole-Brain: ISPC_{WB})

The model detected a main effect of age ($F(1,34) = 4.84, p = 0.035, \eta^2 = 0.124$). Greater ISPC_{WB} was found for 12-month-old infants than 9-month-old infants (See Figure 2), suggesting that overall connectivity at the whole brain level may be related to maturation. This result is consistent with previous findings on the increase of functional connectivity strength across age (Boersma et al., 2011; Miskovic et al., 2015; Smit et al., 2012; Xie et al., 2019). In addition, there was a main effect of time window that was qualified by an interaction between time window and condition ($F(3,102) = 3.43, p = 0.020, \eta^2 = 0.092$). Post-hoc analysis investigated how condition influenced ISPC_{WB} at each time window, finding greater ISPC_{WB} for the novel than the familiar condition only in the anticipatory window from −1000 to −500 ms ($F(1,34) = 5.26, p = 0.028, \eta^2 = 0.134$; See Figure 2). Thus, motoric familiarity modulated ISPC_{WB} during the anticipation of others' actions.

3.2 | Patterns of connectivity in the networks of interest

3.2.1 | Visual-motor network (ISPC_{OC})

The model showed a marginally significant main effect of condition ($F(1, 34) = 3.55, p = 0.068, \eta^2 = 0.095$). ISPC_{OC} tended to be greater in the familiar than the novel action condition. The model also detected an interaction between age and time window ($F(3,102) = 3.99, p = 0.01, \eta^2 = 0.105$). Post-hoc tests indicated greater ISPC_{OC} for older relative to younger infants in the window from −1000 to −500 ms ($F(1, 34) = 7.28, p = 0.011, \eta^2 = 0.176$; See Figure 3 right panel). No other effects were found in the other time windows.

3.2.2 | Control networks (ISPC_{PC}; ISPC_{FC}; ISPC_{PO}; ISPC_{FO})

The model found no significant effects or interactions in the ISPC_{PC} and ISPC_{FO} pairs. In the ISPC_{PO} pair, the model found a significant main effect of condition that was qualified by an interaction between condition and time window ($F(1,102) = 4.32, p = 0.007, \eta^2 = 0.113$). In line with the whole-brain analysis, connectivity was greater in the novel than the familiar condition in the window from −1000 to −500 ms ($F(1,35) = 12.32, p = 0.001, \eta^2 = 0.260$). Finally, in the F-C pair, the model revealed a marginally significant main effect of condition that was qualified by a marginally significant interaction between age, time window and condition ($F(3, 102) = 2.31, p = 0.08, \eta^2 = 0.064$). Post-hoc analyses revealed that 12-month-olds, but not 9-month-olds, showed greater ISPC_{FC} in the novel than familiar action condition ($F(1,18) = 8.99, p = 0.008, \eta^2 = 0.333$) in the last window of processing (500 to 1000 ms; See Figure 3 left panel). Because there was no prior hypothesis about this effect, and the interaction was only marginally significant, it remains an open question whether greater coupling between central and frontal areas is related to the processing of unfamiliar actions.

To summarize, infants tended to show greater ISPC_{OC} during the processing of familiar actions (grasping) as compared to novel actions (pulling a cane). Although this effect was only marginally significant, it is consistent with previous analysis on the same data set using a different method (Chung et al., 2022), suggesting that motoric familiarity may shape how specialized the coupling of sensorimotor and visual (attention) processes is during action processing. In addition, 12-month-old infants showed greater ISPC_{OC} than 9-month-olds during action anticipation (−1000 to −500 ms) both in the familiar and novel action conditions, suggesting that with more experience sensorimotor and visual processes become more synchronized during action anticipation. This greater coupling was not specific to grasping, but it was also found for less familiar actions such as pulling a cane to obtain a toy. In the control networks, in contrast, age did not have a significant influence on connectivity, and condition was either not significant, or the effects were in the opposite direction as for the ISPC_{OC} pair.

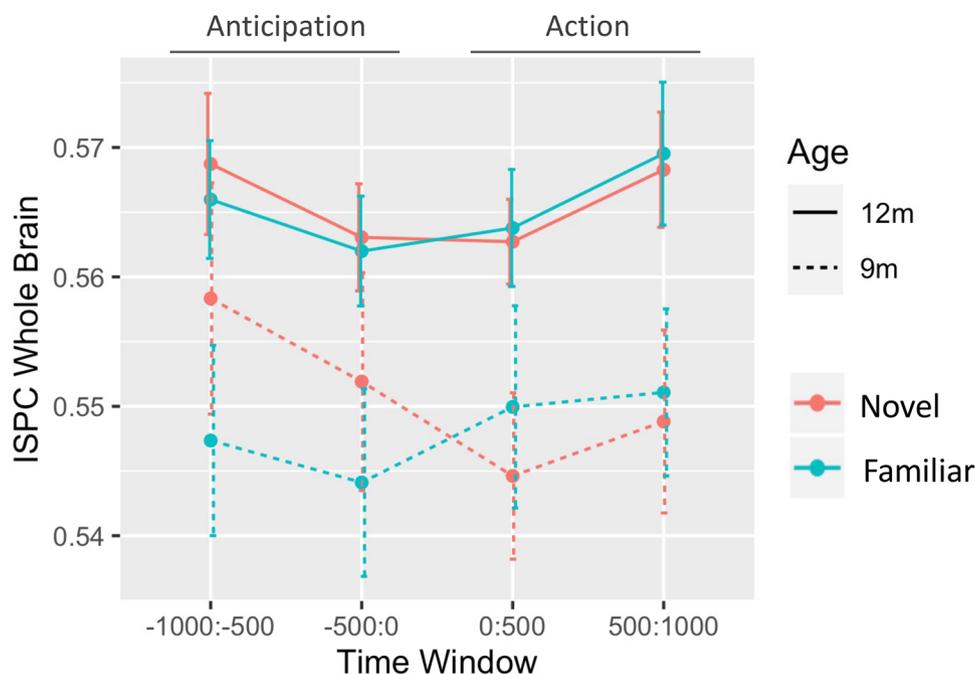


FIGURE 2 ISPC_{WB} estimates from -1000 to 1000 ms in windows of 500 ms for each condition and age group. The model found a main effect of age ($p = 0.043$) and an interaction between time window and condition ($p = 0.018$). Post-hoc tests found a significant effect of condition only in the window from -1000 to -500 ms ($p = 0.029$)

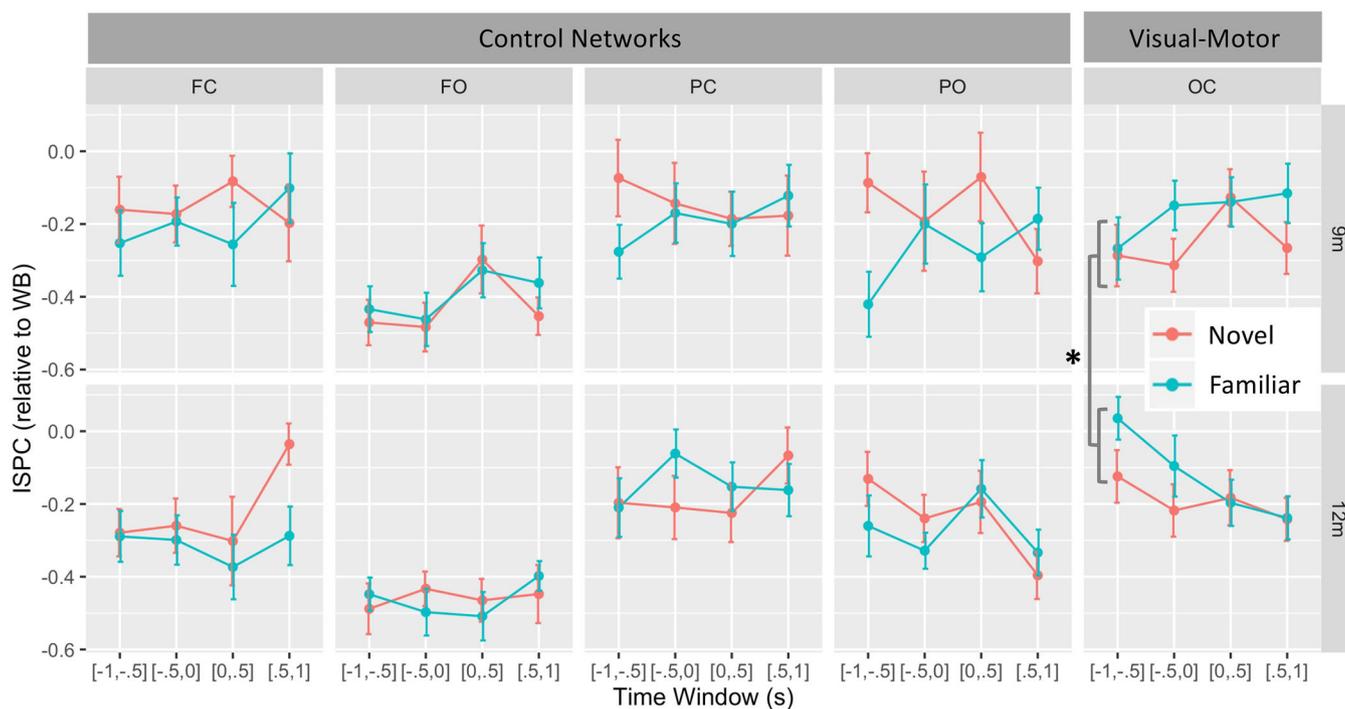


FIGURE 3 ISPC estimates from -1 to 1 s in windows of 0.5 s for each inter-site pair (ISPC_{FC}; ISPC_{FO}; ISPC_{PC}; ISPC_{PO}; ISPC_{OC}), condition and age group. For the ISPC_{OC} pair the analysis found a marginally significant effect of condition ($p = 0.068$) and an interaction of age and time window ($p = 0.01$). Post-hoc tests found a main effect of age only in the window from -1 to -0.5 s ($p = 0.011$). No significant main effects or interactions were found in the control networks



3.3 | Motor competence and functional connectivity

Analyses were performed in the anticipatory window from -1000 to -500 ms, since in this period other forms of experience (age and motoric familiarity) modulated patterns of whole-brain and visual-motor connectivity (see sections 3.1 and 3.2). In addition, we chose to analyze the observation period from 0 to 500 ms, since previous findings found increased visual-motor coupling in the moment that the observed action begun to unfold (Chung et al., 2022; Debnath et al., 2019). Results from the action observation window were reported in SI².

3.3.1 | Visual-motor network (ISPC_{OC})

Consistent with the results of section 3.2.1, the analysis revealed a marginally significant effect of condition ($\chi^2 = 3.32$, $p = .069$) – connectivity tended to be greater in the familiar versus novel action condition—and a main effect of age ($\chi^2 = 6.78$, $p = .009$) – greater ISPC_{OC} was found for older as compared to younger infants. Critically, the analysis also found a main effect of grasp latency ($\chi^2 = 8.12$, $p = .004$)³. The faster infants were at grasping toys, the greater was the functional connectivity in the visual-motor network (ISPC_{OC}) during the anticipation of others' actions (See Figure 4 left panel). Next, the same LMM with ISPC_{OC} as dependent variable was constructed, but this time with cane latency rather than grasp latency as a predictor. The model revealed no significant main or interaction effects for the latency to pull the cane.

3.3.2 | Control Networks (ISPC_{PC}; ISPC_{PO}; ISPC_{FC}; ISPC_{FO})

No significant effects of age, condition and grasp latency were found (all $p > 0.1$; See Figure 4 right panel), except for a significant effect of condition in ISPC_{PC} ($\chi^2 = 8.83$, $p = .003$) as reported in section 3.2.2.

To summarize, these analyses extended the results of previous sections by showing a significant link between grasp latency and ISPC_{OC}. Faster grasping, but not faster pulling of the cane, predicted greater ISPC_{OC} during the anticipation of familiar and novel actions. Critically, no significant relations between connectivity and grasp latency were found for the control networks, indicating that the results were specific to the visual-motor network, and suggesting that it is unlikely that the effects were an artifact of volume conduction.

4 | DISCUSSION

The current study focused on investigating the links between infants' action experience and the neural networks recruited during the prediction and observation of others' actions. A novel experimental approach was applied to calculate the extent of connectivity in the visual-

motor network relative to the strength of global connectivity at the whole-brain network level when infants anticipated and observed others' actions. The same analyses were applied to control networks (frontal-central; frontal-occipital; parietal-central; parietal-occipital). The results revealed a striking link between action experience and the patterns of visual-motor and whole-brain connectivity, particularly during the action anticipation period. Infants showed lower whole-brain ISPC (non-specific network) and tended to show greater visual-motor ISPC (specific network) when anticipating familiar (grasping) relative to less familiar (tool-use) actions (but note that this effect was marginally significant). In addition, older infants showed greater specific visual-motor ISPC than younger infants during action anticipation, and infants' grasping competence predicted the strength of visual-motor ISPC, with more competent infants showing higher levels of connectivity between visual and motor areas. Critically, either no effects or the opposite effects were found for the control networks, suggesting that the effects in the visual-motor network were not due to volume conduction.

The relation between action experience and visual-motor ISPC was specific to the anticipatory window, and no relation was found during the action observation window. This finding suggests that infants' experience with actions influences the neural substrates associated to the prediction rather reaction to others' actions. The results are thus inconsistent with traditional views of the mirror neuron system, which propose that visual information from an observed action maps onto the observer's own motor system, which in turn allows the observer to encode and understand the observed action (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004). In fact, this account would expect motor experience to influence the functional connectivity between visual and motor areas during action observation, rather than during the anticipatory period.

The current findings are more consistent with the predictive model framework of the action observation network (Kilner et al., 2007). In this account, mirror neurons discharge not because they are driven by the visual input, but because they are part of a generative hierarchical model that predicts the sensory input (e.g., kinematics of the action). By comparing the sensory input to the predicted information, the system can then assess the likelihood of the predicted goal. In this view, one might speculate that the context in which the action occurred—the presence or not of the cane—allowed infants in our study to infer the most likely action goal and activate a generative model that predicted the sensory consequences of the upcoming action. This generative model could be supported by the coordination of visual and motor processes via alpha oscillations, enabling the two processes to work together when generating predictions (Palva & Palva, 2011). Critically, our findings suggest that the strength and specificity of this visual-motor ISPC was modulated by infants' motor development. This modulation could have consequences at different levels of the hierarchical model, ranging from the ability to generate goal predictions to the ability to predict sensory input based on a predicted goal.

A further question is why action experience only modulated connectivity patterns during the beginning of the anticipatory period. According to the predictive coding framework, the generative model

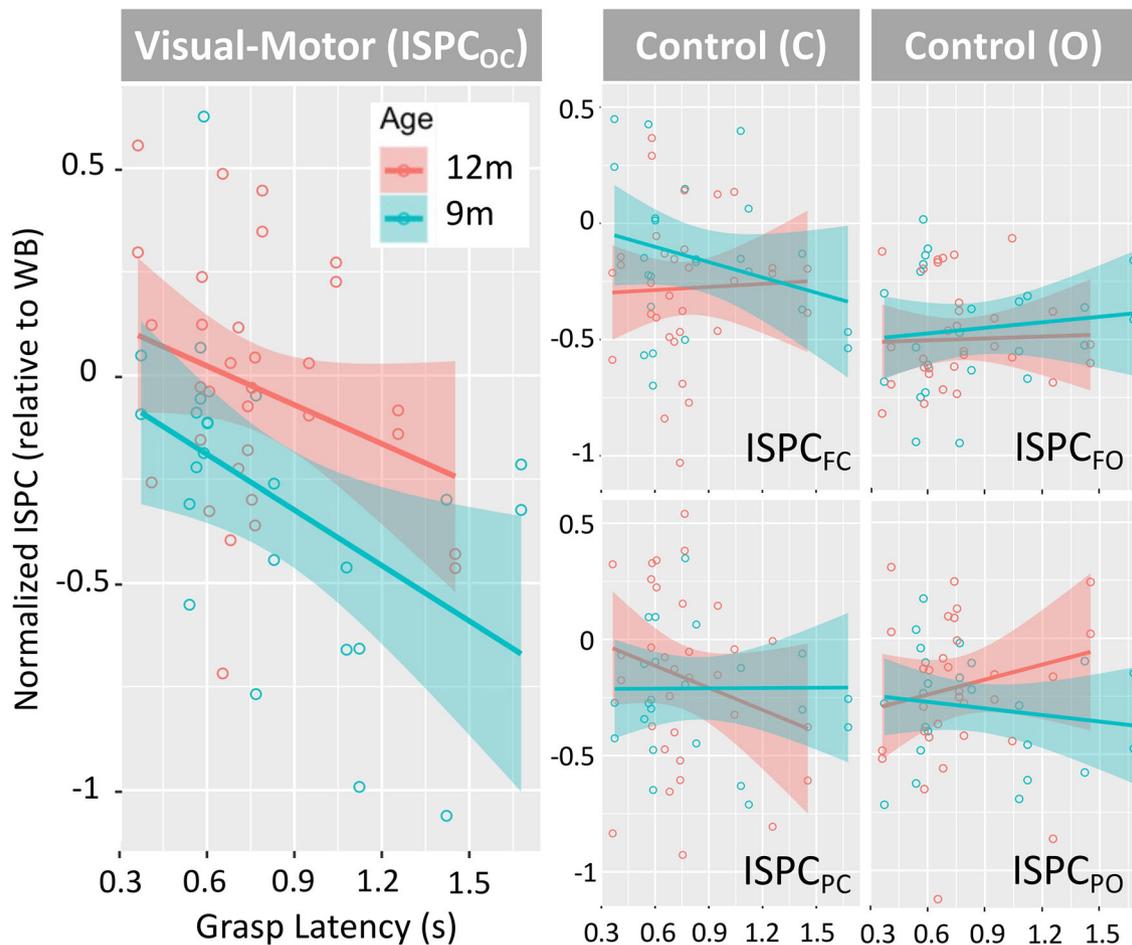


FIGURE 4 Relation between grasp latency (in seconds) and ISPC during anticipation (-1 to -0.5 s). Each dot represents data of a participant one in the familiar action condition and one in the novel condition. The line represents a linear model of the relation between grasp latency and ISPC for each inter-site pair. The shaded area around the lines represents the 95% confidence level interval for predictions from a linear model (“lm”)

does not only produce sensory predictions but also compares the prediction with the sensory input. In case of a mismatch, the model produces a prediction error, which is sent back via forward connections to the higher levels of the hierarchy to adjust the neural representations of the action. In this iterative process, one could expect motor and visual processes to become coordinated as the representation of the action is re-adjusted via prediction errors. However, it is important to note that in the current experimental design the goal and kinematics of the action were consistent across trials, and only differed based on differences in the context (cane was present vs. cane was absent). In this scenario, infants could generate accurate predictions about the sensory consequences of the upcoming action, which would in turn minimize the production of prediction error signals. Thus, based on our findings one can speculate that motor and visual process in the infant brain become functionally related as the system produces new predictions, which can occur at different stages of action processing depending on the task.

In the current study, the motoric familiarity of the upcoming action, infants' age, and grasping latency modulated connectivity patterns during action anticipation. Whereas grasping latency is a direct indicator

of motor competence, age and familiarity could be related both with infants' own motor skills as well as with their experience observing others' actions. Thus, it is possible that experience with both action production and action observation plays a role in shaping the neural networks involved in action prediction (Hunnius & Bekkering, 2014). However, infants' latency in pulling the cane did not significantly predict the level of visual-motor connectivity. Still, this null effect could be due to limitations of the measure, since 15 of the 36 infants provided less than two successful trials and were excluded from the analysis. In addition, acting fast may not be the most optimal strategy when infants are presented with a novel action, and thus cane latency may not capture competence with the novel action sufficiently. Instead, grasp latency is a common measure of motor competence in infancy that has been found previously to modulate the recruitment of infants' motor processes when observing others' actions (Cannon et al., 2016; Yoo et al., 2016).

Intriguingly, here grasp latency did not only relate to connectivity patterns during the anticipation of grasping actions, but also during the anticipation of a less familiar action. Similarly, older infants showed greater levels of visual-motor ISPC than younger infants during the



anticipation of both familiar and novel actions. One possibility is that infants focused on the hand that grasped the cane rather than the pulling event. Indeed, infants at this age spend a considerable amount of time attending to others' hands (Fausey et al., 2016; Yu & Smith, 2013). However, if this was the case, we would not expect to see significant differences in mu desynchronization between the two conditions, as the analysis of power on the same dataset found (Chung et al., 2022). Thus, a more plausible explanation is that infants' experience with familiar actions does not only refine how they predict and process these same actions, but it also has an impact on their capacity to encode actions that are unfamiliar.

Although previous work has shown incongruent findings in terms of how active training generalizes to novel actions (Gerson & Woodward, 2014; Yang et al., 2010), a previous study using grasp latency to measure motor competence found a relation between this measure and infants' sensorimotor activity during the observation of unfamiliar actions (Yoo et al., 2016). Particularly, 12-month-olds but not 9-month-olds showed greater mu ERD as a function of grasp competence when viewing an experimenter who reached for and picked up a toy with a hand-operated claw-like tool. Consistently with this finding, our results raise the intriguing possibility that greater grasping competence relates to a better capacity to predict and learn from the observation of actions that are perceived to be similar. This generalization of motor skills could be associated to greater functional connectivity between visual and motor processes during the prediction of the unfamiliar action.

Beyond investigating the action-perception link, the current study highlights the value of phase-connectivity measures to investigate the development of socio-cognitive abilities. Analysis of mu ERD in the same data set had proven useful to distinguish activation of motor processes as a function of action familiarity (Chung et al., 2022). While both conditions elicited engagement of the motor system, the authors found greater activation when infants anticipated familiar rather than unfamiliar actions. In addition, the authors found a correlation between 9-month-old infants' grasp latency and mu ERD during the observation of grasping actions, but no relations for 12-month-olds, and no differences on mu power based on age. The current findings extended these results by showing that age, motoric familiarity, and grasp competence shape the neural networks involved in action prediction, but not action observation, and that this link is not limited to the anticipation of familiar actions. Thus, although action experience may modulate both region-specific activity and functional neural networks, the current work indicates that the two types of analysis provide unique information about the neural correlates of infants' action processing. Despite functional connectivity techniques having only recently been introduced in infant research, future studies might consider these techniques to investigate the neural underpinnings of infants' socio-cognitive development. Here, we provide example scripts on how such measures could be calculated (see section 2.1).

Furthermore, a novel method to investigate functional connectivity in infancy was developed in the present study, which accounts and controls for changes in the global properties of the developing brain. This method allowed us to investigate individual variation in the recruit-

ment and specificity of the visual-motor network, as well as global changes in whole-brain ISPC. In fact, the results of whole-brain ISPC provided support for the need of controlling for global patterns of functional connectivity. Whole-brain ISPC increased with age, and was modulated by condition, with higher levels in anticipation to novel as compared to familiar actions. These findings open the possibility that an hyperconnectivity across the scalp is related to the processing of novel actions. Consistent with this idea, it has been proposed that in the initial stages of learning a motor skill in infancy (e.g., locomotion) there is an overproduction of cortical connections in the brain (Bell & Fox, 1996; Corbetta et al., 2014), as compared to pre-learning or when infants become experts. Although these studies investigated functional networks in resting state, it is possible that task-related patterns of hyperconnectivity are also associated with the initial stages of learning. Then, as infants become experts in a task, functional connections may become more specialized and efficient in response to the task-related information. The current project shows preliminary evidence in support for this hypothesis and provides tools for future researchers interested in investigating the specialization of task-related functional networks in the developing brain.

In summary, the current work provides a new methodological approach to investigate specific neural networks in socio-cognitive development and highlights the value of studying neural networks rather than limiting analyses to isolated markers of brain activity such as oscillatory power in the EEG. Overall, the results indicated that motor development relates to how functionally connected visual and motor areas are during the anticipation of others' actions. Infants with better motor skills showed greater visual-motor coherence, which could have downstream consequences on how infants encode and learn about others' actions.

ACKNOWLEDGMENTS

We thank the families who participated in our study. We also wish to acknowledge the contributions of and thank our lab manager Riley Abeles and research assistants Rebecca Wixted and Christina Hartman for their help with testing and video coding. This research was supported by Eunice Kennedy Shriver National Institute of Child Health and Human Development Grant (P01-HD064653).

CONFLICT OF INTEREST

The authors declare to have no conflict of interest.

DATA AVAILABILITY STATEMENT

The scripts of connectivity analysis and the output data with connectivity estimates can be obtained here: https://github.com/marccolomer/LAEEG_WB. The EEG data preprocessed and transformed using complex Morlet wavelets can be sent upon request. The derived EEG data in BIDS format and the scripts to process the data can be obtained here: <https://osf.io/f9da5/>

CREDIT AUTHOR STATEMENT

Marc Colomer: Conceptualization, Formal analysis, Visualization, Writing- Original draft. Haerin Chung: Investigation, Methodology,

Writing- Review & Editing. Marlene Meyer: Investigation, Methodology, Writing- Review & Editing. Ranjan Debnath: Resources, Writing- Review & Editing. Santiago Morales: Writing- Review & Editing. Nathan A. Fox: Funding acquisition, Supervision, Writing- Review & Editing. Amanda Woodward: Funding acquisition, Supervision, Writing- Review & Editing.

ORCID

Marc Colomer  <https://orcid.org/0000-0002-4337-0373>

Haerin Chung  <https://orcid.org/0000-0002-1428-5866>

Marlene Meyer  <https://orcid.org/0000-0003-2229-6933>

ENDNOTES

¹ Per reviewer suggestion, exploratory connectivity analyses were also conducted for the theta (4–6Hz) and beta (16–19Hz) bands. The results are described in Supplementary Information (SI). As expected, the strongest link between action experience and connectivity was found in the visual-motor network and the alpha band (See Section 4 of SI for more detailed information about the analysis and results).

² See section 4 of Supplementary Information (SI) to find an analysis of the relation between motor skills and ISPC in each sample across time (10 ms steps).

³ More information about effect sizes (R-squared) can be found in section 4 of SI.

REFERENCES

- Bakker, M., Somerville, J. A., & Gredebäck, G. (2016). Enhanced neural processing of goal-directed actions after active training in 4-month-old infants. *Journal of Cognitive Neuroscience*, 28(3), 472–482. https://doi.org/10.1162/jocn_a_00909
- Bastos, A. M., & Schoffelen, J. M. (2016). A tutorial review of functional connectivity analysis methods and their interpretational pitfalls. *Frontiers in Systems Neuroscience*, 9(JAN2016), 175. <https://doi.org/10.3389/FNSYS.2015.00175/BIBTEX>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/JSS.V067.I01>
- Bell, M. A., & Fox, N. A. (1996). Crawling experience is related to changes in cortical organization during infancy: Evidence from EEG coherence. *Developmental Psychobiology*, 29(7), 551–561. [https://doi.org/10.1002/\(SICI\)1098-2302\(199611\)29:7](https://doi.org/10.1002/(SICI)1098-2302(199611)29:7)
- Boersma, M., Smit, D. J. A., de Bie, H. M. A., van Baal, G. C. M., Boomsma, D. I., de Geus, E. J. C., Delemarre-Van De Waal, H. A., & Stam, C. J. (2011). Network analysis of resting state EEG in the developing young brain: Structure comes with maturation. *Human Brain Mapping*, 32(3), 413–425. <https://doi.org/10.1002/hbm.21030>
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, 13(2), 400–404. <https://doi.org/10.1111/J.1460-9568.2001.01385.X>
- Cannon, E. N., Simpson, E. A., Fox, N. A., Vanderwert, R. E., Woodward, A. L., & Ferrari, P. F. (2016). Relations between infants' emerging reach-grasp competence and event-related desynchronization in EEG. *Developmental Science*, 19(1), 50–62. <https://doi.org/10.1111/desc.12295>
- Cannon, E. N., & Woodward, A. L. (2012). Infants generate goal-based action predictions. *Developmental Science*, 15(2), 292–298. <https://doi.org/10.1111/j.1467-7687.2011.01127.x>
- Cannon, E. N., Yoo, K. H., Vanderwert, R. E., Ferrari, P. F., Woodward, A. L., & Fox, N. A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS ONE*, 9(3). <https://doi.org/10.1371/journal.pone.0092002>
- Casey, B. J., Galvan, A., & Hare, T. A. (2005). Changes in cerebral functional organization during cognitive development. *Current Opinion in Neurobiology*, 15(2), 239–244. <https://doi.org/10.1016/J.CONB.2005.03.012>
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, 50(3), 1148–1167. <https://doi.org/10.1016/J.NEUROIMAGE.2009.12.112>
- Chung, H., Meyer, M., Debnath, R., Fox, N. A., & Woodward, A. (2022). Neural correlates of familiar and unfamiliar action in infancy. *Journal of Experimental Child Psychology*, 220. <https://doi.org/10.1016/J.JECP.2022.105415>
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*.
- Cohen, M. X. (2015). Effects of time lag and frequency matching on phase-based connectivity. *Journal of Neuroscience Methods*, 250, 137–146. <https://doi.org/10.1016/J.JNEUMETH.2014.09.005>
- Cohen, M. X., & van Gaal, S. (2013). Dynamic interactions between large-scale brain networks predict behavioral adaptation after perceptual errors. *Cerebral Cortex*, 23(5), 1061–1072. <https://doi.org/10.1093/CERCOR/BHS069>
- Corbetta, D., Friedman, D. R., & Bell, M. A. (2014). Brain reorganization as a function of walking experience in 12-month-old infants: Implications for the development of manual laterality. *Frontiers in Psychology*, 5(MAR). <https://doi.org/10.3389/FPSYG.2014.00245>
- Datavyu Team. (2014). *Datavyu: Video coding and data visualization tool*. Databrary Project, New York University. <https://datavyu.org/>
- Debnath, R., Buzzell, G. A., Morales, S., Bowers, M. E., Leach, S. C., & Fox, N. A. (2020). The Maryland analysis of developmental EEG (MADE) pipeline. *Psychophysiology*, 57(6), e13580. <https://doi.org/10.1111/PSYP.13580>
- Debnath, R., Salo, V. C., Buzzell, G. A., Yoo, K. H., & Fox, N. A. (2019). Mu rhythm desynchronization is specific to action execution and observation: Evidence from time-frequency and connectivity analysis. *NeuroImage*, 184, 496–507. <https://doi.org/10.1016/J.NEUROIMAGE.2018.09.053>
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. <https://doi.org/10.1016/J.JNEUMETH.2003.10.009>
- Fausey, C. M., Jayaraman, S., & Smith, L. B. (2016). From faces to hands: Changing visual input in the first two years. *Cognition*, 152, 101–107. <https://doi.org/10.1016/J.COGNITION.2016.03.005>
- Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. In *Nature Reviews Neuroscience* (Vol. 12, Issue 2, pp. 105–118). Nature Publishing Group. <https://doi.org/10.1038/nrn2979>
- Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L. (2016). Motor system activation predicts goal imitation in 7-month-old infants. *Psychological Science*, 0956797616632231-. <https://doi.org/10.1177/0956797616632231>
- Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., Ferrari, P. F., & van Ijzendoorn, M. H. (2016). Assessing human mirror activity with EEG Mu rhythm: a meta-analysis. *Psychological Bulletin*, 142(3), 291–313. <http://doi.org/10.1037/bul0000031.supp>
- Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9(10), 474–480. <https://doi.org/10.1016/j.tics.2005.08.011>
- Friston, K. J. (2011). Functional and effective connectivity: A review. *Brain Connectivity*, 1(1), 13–36. <https://doi.org/10.1089/BRAIN.2011.0008>
- Gao, W., Lin, W., Grewen, K., & Gilmore, J. H. (2017). Functional connectivity of the infant human brain: Plastic and modifiable. *Neuroscientist*, 23(2), 169–184. <https://doi.org/10.1177/1073858416635986>
- Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms



- of action processing in infancy. *Journal of Cognitive Neuroscience*, 27(6), 1207–1214. https://doi.org/10.1162/jocn_a_00774
- Gerson, S. A., & Woodward, A. L. (2014). Learning from their own actions: The unique effect of producing actions on infants' action understanding. *Child Development*, 85(1), 264–277. <https://doi.org/10.1111/CDEV.12115>
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., Nugent, T. F., Herman, D. H., Clasen, L. S., Toga, A. W., Rapoport, J. L., & Thompson, P. M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences*, 101(21), 8174–8179. <https://doi.org/10.1073/PNAS.0402680101>
- Hobson, H. M., & Bishop, D. V. M. (2017). The interpretation of mu suppression as an index of mirror neuron activity: Past, present and future. *Royal Society Open Science*, 4(3). <https://doi.org/10.1098/rsos.160662>
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24(5), 849–878. <https://doi.org/10.1017/S0140525%D7;01000103>
- Hunnis, S., & Bekkering, H. (2010). The early development of object knowledge: A study of infants' visual anticipations during action observation. *Developmental Psychology*, 46(2), 446–454. <https://doi.org/10.1037/a0016543>
- Hunnis, S., & Bekkering, H. (2014). What are you doing? How active and observational experience shape infants' action understanding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1644), 20130490. <https://doi.org/10.1098/rstb.2013.0490>
- Kayser, J., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: II. Adequacy of low-density estimates. *Clinical Neurophysiology*, 117(2), 369–380. <https://doi.org/10.1016/J.CLINPH.2005.08.033>
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. In *Cognitive Processing* (Vol., 8, Issue 3, pp. 159–166). Cogn Process. <https://doi.org/10.1007/s10339-007-0170-2>
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S.-J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, 7(12), 1299–1301. <https://doi.org/10.1038/nn1355>
- Lawrence, M. A. (2016). *Package "ez": Easy Analysis and Visualization of Factorial Experiments*. <http://github.com/mike-lawrence/ez>
- Lloyd-Fox, S., Wu, R., Richards, J. E., Elwell, C. E., & Johnson, M. H. (2015). Cortical activation to action perception is associated with action production abilities in young infants. *Cerebral Cortex (New York, NY)*, 25(2), 289. <https://doi.org/10.1093/CERCOR/BHT207>
- Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG μ rhythm in human infancy. *Developmental Cognitive Neuroscience*, 1(2), 110–123. <https://doi.org/10.1016/j.dcn.2010.09.001>
- Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Developmental Science*, 14(3), 474–480. <https://doi.org/10.1111/j.1467-7687.2010.00991.x>
- Meltzoff, A. N. (2007). "Like me": A foundation for social cognition. In *Developmental Science* (Vol., 10, Issue 1, pp. 126–134). <https://doi.org/10.1111/j.1467-7687.2007.00574.x>
- Melzer, A., Prinz, W., & Daum, M. M. (2012). Production and perception of contralateral reaching: A close link by 12 months of age. *Infant Behavior and Development*, 35(3), 570–579. <https://doi.org/10.1016/j.infbeh.2012.05.003>
- Meyer, M., Chung, H., Debnath, R., Fox, N., & Woodward, A. L. (2022). Social context shapes neural processing of others' actions in 9-month-old infants. *Journal of Experimental Child Psychology*, 213, 105260. <https://doi.org/10.1016/J.JECP.2021.105260>
- Meyer, M., Endedijk, H. M., van Ede, F., & Hunnis, S. (2019). Theta oscillations in 4-year-olds are sensitive to task engagement and task demands. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-42615-x>
- Miskovic, V., Ma, X., Chou, C. A., Fan, M., Owens, M., Sayama, H., & Gibb, B. E. (2015). Developmental changes in spontaneous electrocortical activity and network organization from early to late childhood. *NeuroImage*, 118, 237–247. <https://doi.org/10.1016/j.neuroimage.2015.06.013>
- Monroy, C. D., Meyer, M., Schröder, L., Gerson, S. A., & Hunnis, S. (2019). The infant motor system predicts actions based on visual statistical learning. *NeuroImage*, 185, 947–954. <https://doi.org/10.1016/j.neuroimage.2017.12.016>
- Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Brain Research. Cognitive Brain Research*, 19(2), 195–201. <https://doi.org/10.1016/j.cogbrainres.2003.12.001>
- Nelissen, K., Borra, E., Gerbella, M., Rozzi, S., Luppino, G., Vanduffel, W., Rizzolatti, G., & Orban, G. A. (2011). Action observation circuits in the Macaque Monkey Cortex. *Journal of Neuroscience*, 31(10), 3743–3756. <https://doi.org/10.1523/JNEUROSCI.4803-10.2011>
- Nunez, P. L., & Srinivasan, R. (2006). *Electric Fields of the Brain The Neurophysics of EEG Second Edition*.
- Palva, S., & Palva, J. M. (2011). Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in Psychology*, 0(SEP), 204. <https://doi.org/10.3389/FPSYG.2011.00204>
- Paulus, M. (2012). Action mirroring and action understanding: an ideomotor and attentional account. *Psychological Research*, 76(6), 760–767. <https://doi.org/10.1007/s00426-011-0385-9>
- Paulus, M. (2014). How and why do infants imitate? An ideomotor approach to social and imitative learning in infancy (and beyond). *Psychonomic Bulletin & Review*, 8(2), 77–81. <http://www.ncbi.nlm.nih.gov/pubmed/24578090>
- Paulus, M., Hunnis, S., van Wijngaarden, C., Vrans, S., van Rooij, I., & Bekkering, H. (2011). The role of frequency information and teleological reasoning in infants' and adults' action prediction. *Developmental Psychology*, 47(4), 976–983. <https://doi.org/10.1037/a0023785>
- Paus, T., Collins, D. L., Evans, A. C., Leonard, G., Pike, B., & Zijdenbos, A. (2001). Maturation of white matter in the human brain: a review of magnetic resonance studies. *Brain Research Bulletin*, 54(3), 255–266. [https://doi.org/10.1016/S0361-9230\(00\)00434-2](https://doi.org/10.1016/S0361-9230(00)00434-2)
- Philips, G. R., Daly, J. J., & Principe, J. C. (2017). Topographical measures of functional connectivity as biomarkers for post-stroke motor recovery. *Journal of NeuroEngineering and Rehabilitation*, 14(1), 67. <https://doi.org/10.1186/S12984-017-0277-3>
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into doing." In *Brain Research Reviews* (Vol., 50, Issue 1, pp. 57–68). Elsevier. <https://doi.org/10.1016/j.brainresrev.2005.04.005>
- R Core Team. (2014). *R: The R Project for Statistical Computing*. Vienna, Austria. <https://www.r-project.org/>
- Rayson, H., Bonaiuto, J. J., Ferrari, P. F., & Murray, L. (2016). Mu desynchronization during observation and execution of facial expressions in 30-month-old children. *Developmental Cognitive Neuroscience*, 19, 279–287. <https://doi.org/10.1016/j.dcn.2016.05.003>
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews. Neuroscience*, 2(9), 661–670. <https://doi.org/10.1038/35090060>
- Rosander, K., & von Hofsten, C. (2011). Predictive gaze shifts elicited during observed and performed actions in 10-month-old infants and adults. *Neuropsychologia*, 49(10), 2911–2917. <https://doi.org/10.1016/j.neuropsychologia.2011.06.018>
- Schneider, W., Eschman, A., & Zuccolotto, A. (2012). E-Prime User's Guide. In Eschman, A. https://www.researchgate.net/publication/260296789_E-prime_User%27;s_Guide



- Smit, D. J. A., Boersma, M., Schnack, H. G., Micheloyannis, S., Boomsma, D. I., Hulshoff Pol, H. E., Stam, C. J., & de Geus, E. J. C. (2012). The brain matures with stronger functional connectivity and decreased randomness of its network. *PLoS ONE*, 7(5), e36896. <https://doi.org/10.1371/journal.pone.0036896>
- Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, 96(1), B1–11. <https://doi.org/10.1016/j.cognition.2004.07.004>
- Southgate, V., Johnson, M. H., el Karoui, I., & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*, 21(3), 355–359. <https://doi.org/10.1177/0956797610362058>
- Southgate, V., & Vernetti, A. (2014). Belief-based action prediction in preverbal infants. *Cognition*, 130(1), 1–10. <https://doi.org/10.1016/j.cognition.2013.08.008>
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). A-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26(37), 9494–9502. <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>
- Toscani, M., Marzi, T., Righi, S., Viggiano, M. P., & Baldassi, S. (2010). Alpha waves: A neural signature of visual suppression. *Experimental Brain Research*, 207(3–4), 213–219. <https://doi.org/10.1007/s00221-010-2444-7>
- Urgen, B. A., & Orban, G. A. (2021). The unique role of parietal cortex in action observation: Functional organization for communicative and manipulative actions. *NeuroImage*, 237, 118220. <https://doi.org/10.1016/j.neuroimage.2021.118220>
- van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage*, 43(4), 808–814. <https://doi.org/10.1016/j.neuroimage.2008.07.057>
- Woodward, A. L., & Gerson, S. A. (2014). Mirroring and the development of action understanding. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol., 369, Issue 1644). Royal Society. <https://doi.org/10.1098/rstb.2013.0181>
- Xie, W., Mallin, B. M., & Richards, J. E. (2019). Development of brain functional connectivity and its relation to infant sustained attention in the first year of life. *Developmental Science*, 22(1), e12703. <https://doi.org/10.1111/desc.12703>
- Yang, D., Sidman, J., & Bushnell, E. W. (2010). Beyond the information given: Infants' transfer of actions learned through imitation. *Journal of Experimental Child Psychology*, 106(1), 62–81. <https://doi.org/10.1016/j.jecp.2009.12.005>
- Yoo, K. H., Cannon, E. N., Thorpe, S. G., & Fox, N. A. (2016). Desynchronization in EEG during perception of means-end actions and relations with infants' grasping skill. *The British Journal of Developmental Psychology*, 34(1), 24. <https://doi.org/10.1111/BJDP.12115>
- Yordanova, J., Kolev, V., Verleger, R., Heide, W., Grumbt, M., & Schürmann, M. (2017). Synchronization of fronto-parietal beta and theta networks as a signature of visual awareness in neglect. *NeuroImage*, 146, 341–354. <https://doi.org/10.1016/j.neuroimage.2016.11.013>
- Yu, C., & Smith, L. B. (2013). Joint attention without gaze following: human infants and their parents coordinate visual attention to objects through eye-hand coordination. *PLOS ONE*, 8(11), e79659. <https://doi.org/10.1371/JOURNAL.PONE.0079659>
- Yu, Q., Peng, Y., Kang, H., Peng, Q., Ouyang, M., Slinger, M., Hu, D., Shou, H., Fang, F., & Huang, H. (2020). Differential white matter maturation from birth to 8 years of age. *Cerebral Cortex*, 30(4), 2674–2690. <https://doi.org/10.1093/CERCOR/BHZ268>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Colomer, M., Chung, H., Meyer, M., Debnath, R., Morales, S., Fox, N. A., & Woodward, A. (2023). Action experience in infancy predicts visual-motor functional connectivity during action anticipation. *Developmental Science*, 26, e13339. <https://doi.org/10.1111/desc.13339>